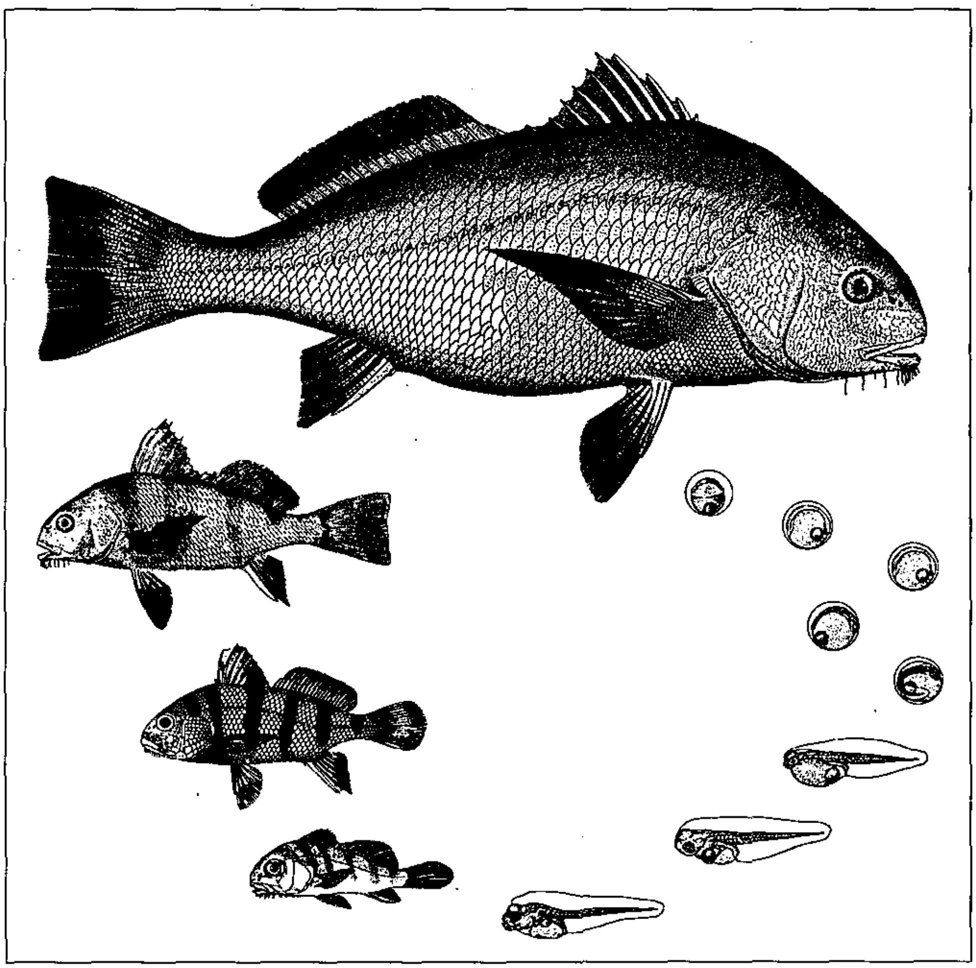
NOAA's Estuarine Living Marine Resources Program

# Distribution and Abundance of Fishes and Invertebrates in Gulf of Mexico Estuaries
# Volume II: Species Life History Summaries



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*U.S. Department of Commerce*
*National Oceanic and Atmospheric Administration*
*National Ocean Service*

# NOAA's Estuarine Living Marine Resources Program

The Strategic Environmental Assessments (SEA) Division of NOAA's Office of Ocean Resources Conservation and Assessment (ORCA) was created in response to the need for comprehensive information on the effects of human activities on the nation's coastal ocean. The SEA Division performs assessments of the estuarine and coastal environments and of the resources of the U.S. Exclusive Economic Zone (EEZ). SEA Divison's Biogeographic Characterization Branch develops and disseminates information on the distribution and ecology of living marine resources throughout the Nation's estuarine and coastal environments (Monaco and Christensen 1997).

In June 1985, NOAA began a program to develop a comprehensive information base on the life history, relative abundance, and distribution of fishes and invertebrates in estuaries throughout the nation. The Estuarine Living Marine Resources (ELMR) program has been conducted jointly by the SEA Division, the National Marine Fisheries Service (NMFS), and other agencies and institutions. The nationwide ELMR data base was completed in 1994, and includes data for 153 species found in 122 estuaries and coastal embayments. Ten reports and reprints are now available free upon request. This report, *Distribution and Abundance of Fishes and Invertebrates in Gulf of Mexico Estuaries, Volume II: Species Life History Summaries,* summarizes information on the estuarine life history characteristics of 44 fish and invertebrate species of the Gulf of Mexico. It complements distribution and abundance information presented in *Volume I: Data Summaries* (Nelson et al. 1992). A national report summarizing the data and results from the ELMR program is planned for publication in late 1997.

Three to five salinity zones, as defined in NOAA's *National Estuarine Inventory* Program (NOAA 1985) provided the spatial framework for organizing information on species distribution and abundance within each estuary. The primary data developed for each species include spatial distribution by salinity zone, temporal distribution by month, and relative abundance by life stage, e.g., adult, spawning, juvenile, larva, and egg. In addition, life history summaries and tables are developed for each species.

Additional information on this or other programs of NOAA's SEA Division is available from:

NOAA/NOS SEA Division, N/ORCA1
1305 East-West Hwy., 9th Floor
Silver Spring, Maryland 20910
Phone (301) 713-3000, Fax (301) 713-4384

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Selected reports and reprints available from NOAA's Estuarine Living Marine Resources program include:

Monaco, M.E., et al. 1990. Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol. I: Data summaries. ELMR Rep. No. 4. NOAA/NOS Strategic Assessment Branch, Rockville, MD. 232 p.

Emmett, R.L., et al. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol. II: Species life history summaries. ELMR Rep. No. 8. NOAA/NOS SEA Division, Rockville, MD. 329 p.

Nelson, D.M., et al. 1991. Distribution and abundance of fishes and invertebrates in southeast estuaries. ELMR Rep. No. 9. NOAA/NOS SEA Division, Rockville, MD. 167 p.

Monaco, M.E., et al. 1992. Assemblages of U.S. west coast estuaries based on the distribution of fishes. Journal of Biogeography 19: 251-267.

Nelson, D.M. (editor), et al. 1992. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. I: Data summaries. ELMR Rep. No. 10. NOAA/NOS SEA Division, Rockville, MD. 273 p.

Bulger, A.J., et al. 1993. Biologically-based salinity zones derived from a multivariate analysis. Estuaries 16: 311-322.

Stone, S.L., et al. 1994. Distribution and abundance of fishes and invertebrates in Mid-Atlantic estuaries. ELMR Rep. No. 12. NOAA/NOS SEA Division, Silver Spring, MD. 280 p.

Jury, S.H., et al. 1994. Distribution and abundance of fishes and invertebrates in North Atlantic estuaries. ELMR Rep. No. 13. NOAA/NOS SEA Division, Silver Spring, MD. 221 p.

Christensen, J.D., et al. 1997. An index to assess the sensitivity of Gulf of Mexico species to changes in estuarine salinity regimes. Gulf Res. Rep. 9(4):219-229.

Pattillo, M.E., et al. 1997. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. II: Species life history summaries. ELMR Rep. No. 11. NOAA/NOS SEA Division, Silver Spring, MD. 377 p.

# *Distribution and Abundance of Fishes and Invertebrates in Gulf of Mexico Estuaries Volume II: Species Life History Summaries*

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# Contents

## Introduction

This is the second of two volumes that present information on the spatial and temporal distributions, relative abundance, and life history characteristics of 44 fish and invertebrate species in 31 Gulf of Mexico estuaries. This volume contains life history summaries for each species. Each summary identifies the life history characteristics that describe a species' occurrence in these estuaries. These summaries were developed to complement data presented in *Distribution and Abundance of Fishes and Invertebrates in Gulf of Mexico Estuaries, Volume I: Data Summaries* (Nelson et al.1992), hereafter referred to as *Volume I.*

The summaries presented here are not a complete treatise on all aspects of each species' biology, but they provide a concise account of the most important physical and biological factors known to affect a species' occurrence within estuaries. As a supplement to the life history summaries, their content was augmented with additional physical and biological criteria and condensed into three life history tables. These tables present life history characteristics for each species along with behavioral traits and preferred habitats.

This report is a product of the National Oceanic and Atmospheric Administration's (NOAA) Estuarine Living Marine Resources (ELMR) Program (see inside front cover), a cooperative study of the National Ocean Service (NOS), the National Marine Fisheries Service (NMFS), and other research institutions. The objective of the ELMR program is to develop a consistent data base on the distribution, abundance, and life history characteristics of important fishes and invertebrates in the Nation's estuaries. This data base contains the relative abundance and monthly occurrence of each species' life stage by estuary for three to five salinity zones identified in NOAA's *National Estuarine Inventory (NEI)* Program (NOAA 1985b). The nationwide data base is divided into five study regions (Figure 1), and contains information for 153 fish and invertebrate species found in 122 U.S. estuaries.

## Rationale

Estuaries are among the Earth's most productive natural systems and are important nursery areas that provide food, refuge from predation, and valuable habitat for many species (Gunter 1967, Joseph 1973, Weinstein 1979, Mann 1982). Estuarine-dependent organisms that support important commercial and recreational fisheries include sciaenids, clupeids, shrimps, and crabs. In spite of the well-documented importance of estuaries to fishes and invertebrates, few consistent and comprehensive data bases exist which allow examinations of the relationships between estuarine species found in or among groups of estuaries. Furthermore, much of the distribution and abundance information for estuarine-dependent species (i.e., species that

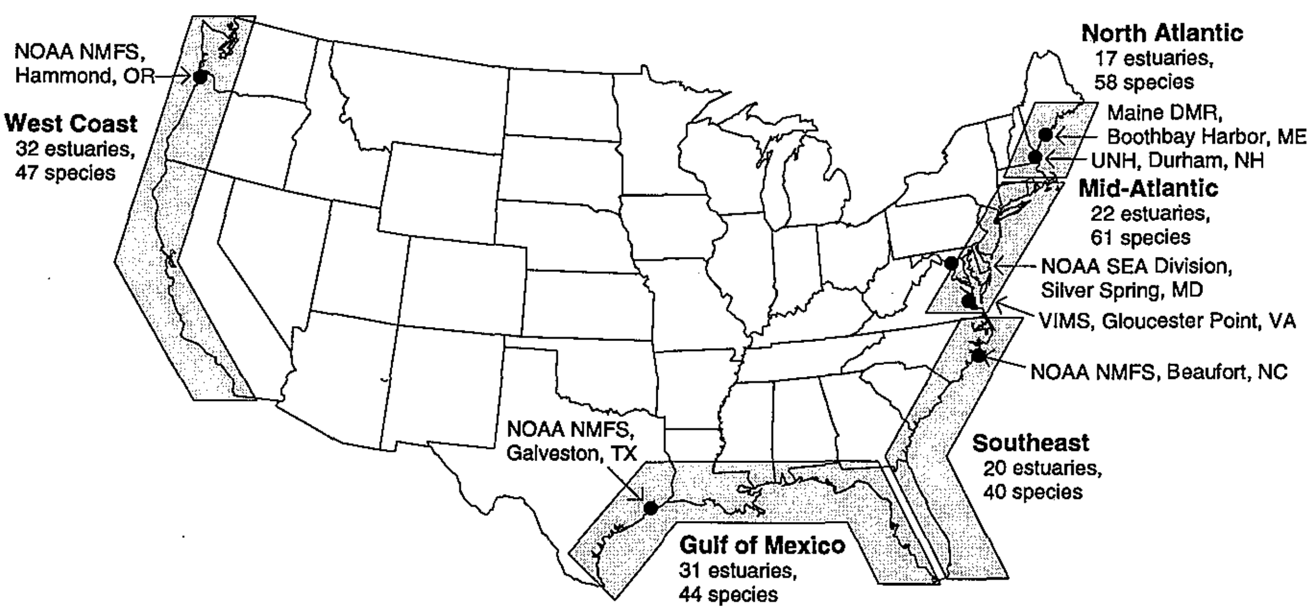



Figure 1. ELMR study regions and regional research institutions.

require estuaries during their life cycle) is for offshore life stages and does not adequately describe estuarine distributions (Darnell et al. 1983, NOAA 1985a).

Only a few comprehensive sampling programs collect fishes and invertebrates with identical methods across groups of estuaries within a region (Hammerschmidt and McEachron 1986). Therefore, most existing estuarine fisheries data cannot be compared among estuaries because of the variable sampling strategies. In addition, existing research programs do not focus on how groups of estuaries may be important for regional fishery management, and few compile information for species having little or no economic value.

Because life stages of many species use both estuarine and marine habitats, information on distribution, abundance, temporal utilization, and life history characteristics is needed to understand the coupling of estuarine, nearshore, and offshore areas. To date, a national, comprehensive, and consistent data base of this type does not exist. Consequently, there is a need to develop a program which integrates fragments of information on marine and estuarine species and their associated habitats into a useful, comprehensive, and consistent format. The ELMR program was designed to help fulfill this need by developing a uniform nationwide data base on selected estuarine species. Results complement NOAA efforts to develop a national estuarine assessment capability (NOAA 1985b), identify information gaps, and assess the content and quality of existing estuarine fisheries data.

## Data Collection and Organization

*Volume I* contains detailed distribution and abundance data for 44 fish and invertebrate species in 31 Gulf of Mexico estuaries, and a complete discussion of the methods used to compile these data. However, a brief description of methods from *Volume I* is presented here to aid interpretation of distribution and relative abundance tables included in the species life history summaries presented in this report. Figure 2 summarizes the major steps taken to collect and organize information on the distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries. The following sections provide an overview of the estuary/species selection process, and development of the ELMR data base.

***Selection of Estuaries.*** Thirty estuaries of the Gulf of Mexico (Table 1, Figure 3) were initially selected from the *National Estuarine Inventory (NEI) Data Atlas: Volume I* (NOAA 1985b). However, Florida Bay was added to the NEI, and to the ELMR program, because of its importance as habitat for Gulf of Mexico fishes and invertebrates. Data on the spatial and temporal distributions of species were initially compiled and organized based on three salinity zones delineated for each estuary in the NEI; tidal fresh (0.0 to 0.5 parts per thousand (‰)), mixing (0.5 to 25.0‰), and seawater (>25.0‰). The ELMR Gulf of Mexico data base is now being revised and updated for five biologically relevant salinity zones (Bulger et al. 1993, Christensen et al. 1997, NOAA 1997). While some Gulf of Mexico estuaries do not contain all salinity zones (e.g., Laguna Madre has no mixing or tidal fresh zone), they were

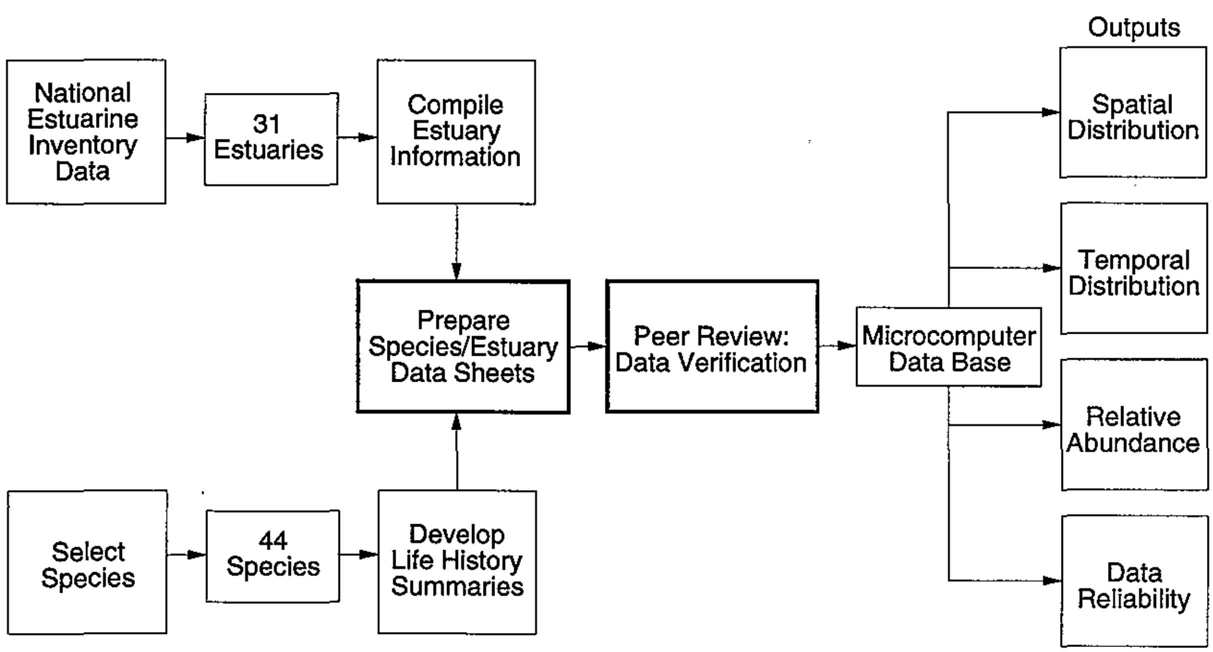



Figure 2. Major steps to complete the Gulf of Mexico ELMR study.

Table 1. ELMR Gulf of Mexico estuaries (n=31) and associated salinity zones.

| Estuary, State | Zones present | | |
|---|---|---|---|
| Florida Bay, FL | T | M | S |
| Ten Thousand Islands, FL | T | M | S |
| Caloosahatchee River, FL | T | M | * |
| Charlotte Harbor, FL | T | M | S |
| Tampa Bay, FL | T | M | S |
| Suwannee River, FL | T | M | S |
| Apalachee Bay, FL | T | M | S |
| Apalachicola Bay, FL | T | M | S |
| St. Andrew Bay, FL | T | M | S |
| Choctawhatchee Bay, FL | T | M | S |
| Pensacola Bay, FL | T | M | S |
| Perdido Bay, FL/AL | T | M | S |
| Mobile Bay, AL | T | M | S |
| Mississippi Sound, MS/AL/LA | T | M | S |
| Lake Borgne, LA | T | M | * |
| Lake Pontchartrain, LA | * | M | * |
| Breton/Chandeleur Sounds, LA | * | M | S |
| Mississippi River, LA | T | M | * |
| Barataria Bay, LA | T | M | S |
| Terrebonne/Timbalier Bays, LA | T | M | S |
| Atchafalaya/Vermilion Bays, LA | T | M | * |
| Calcasieu Lake, LA | T | M | * |
| Sabine Lake, LA/TX | T | M | * |
| Galveston Bay, TX | T | M | S |
| Brazos River, TX | T | M | * |
| Matagorda Bay, TX | T | M | S |
| San Antonio Bay, TX | * | M | S |
| Aransas Bay, TX | * | M | S |
| Corpus Christi Bay, TX | * | M | S |
| Laguna Madre, TX | * | * | S |
| Baffin Bay, TX | * | * | S |

T - Tidal fresh zone
M - Mixing zone
S - Seawater zone
* - salinity zone not present

Estuary names are primarily from NOAA 1985b.

Table 2. ELMR Gulf of Mexico species (n=44).

| Common Name | Scientific Name |
|---|---|
| Bay scallop | *Argopecten irradians* |
| American oyster | *Crassostrea virginica* |
| Common rangia | *Rangia cuneata* |
| Hard clam | *Mercenaria* species |
| Bay squid | *Lolliguncula brevis* |
| Brown shrimp | *Penaeus aztecus* |
| Pink shrimp | *Penaeus duorarum* |
| White shrimp | *Penaeus setiferus* |
| Grass shrimp | *Palaemonetes pugio* |
| Spiny lobster | *Panulirus argus* |
| Blue crab | *Callinectes sapidus* |
| Gulf stone crab | *Menippe adina* |
| Florida stone crab | *Menippe mercenaria* |
| Bull shark | *Carcharhinus leucas* |
| Tarpon | *Megalops atlanticus* |
| Alabama shad | *Alosa alabamae* |
| Gulf menhaden | *Brevoortia patronus* |
| Yellowfin menhaden | *Brevoortia smithi* |
| Gizzard shad | *Dorosoma cepedianum* |
| Bay anchovy | *Anchoa mitchilli* |
| Hardhead catfish | *Arius felis* |
| Sheepshead minnow | *Cyprinodon variegatus* |
| Gulf killifish | *Fundulus grandis* |
| Silversides | *Menidia* species |
| Snook | *Centropomus undecimalis* |
| Bluefish | *Pomatomus saltatrix* |
| Blue runner | *Caranx crysos* |
| Crevalle jack | *Caranx hippos* |
| Florida pompano | *Trachinotus carolinus* |
| Gray snapper | *Lutjanus griseus* |
| Sheepshead | *Archosargus probatocephalus* |
| Pinfish | *Lagodon rhomboides* |
| Silver perch | *Bairdiella chrysoura* |
| Sand seatrout | *Cynoscion arenarius* |
| Spotted seatrout | *Cynoscion nebulosus* |
| Spot | *Leiostomus xanthurus* |
| Atlantic croaker | *Micropogonias undulatus* |
| Black drum | *Pogonias cromis* |
| Red drum | *Sciaenops ocellatus* |
| Striped mullet | *Mugil cephalus* |
| Code goby | *Gobiosoma robustum* |
| Spanish mackerel | *Scomberomorus maculatus* |
| Gulf flounder | *Paralichthys albigutta* |
| Southern flounder | *Paralichthys lethostigma* |

Common and scientific names are primarily from Robins et al. 1980, Turgeon et al. 1988, Williams et al. 1989, and Robins et al. 1991.

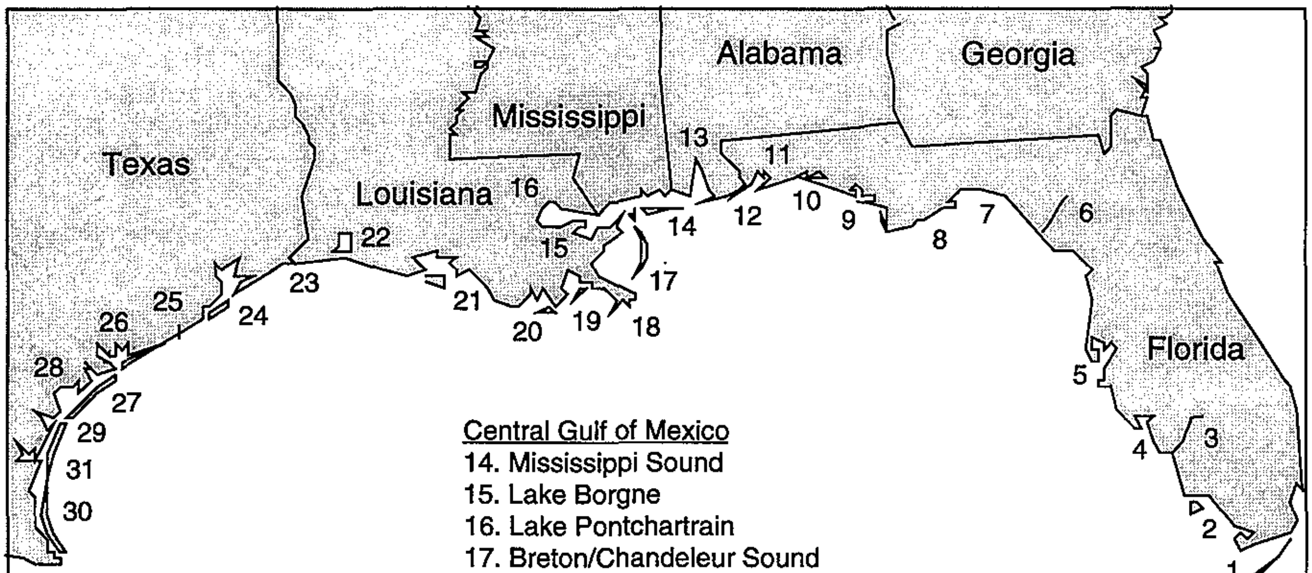
included because they provide important habitat for many euryhaline species.

***Selection of Species.*** To ensure that important Gulf of Mexico estuarine species were included in the ELMR study, a species list was developed (Table 2) and reviewed by regional experts. Four criteria were used to identify the 44 species entered into the data base:

1) Commercial value - a species that commercial fishermen specifically try to catch (e.g., gulf menhaden, *Brevoortia patronus*, and blue crab, *Callinectes sapidus*), as determined from catch and value statistics of the NMFS and state agencies.

2) Recreational value - a species that recreational fishermen specifically try to catch that may or may not be of commercial importance. Recreational species (e.g., red drum, *Sciaenops ocellatus*, and common snook, *Centropomus undecimalis*) were determined by consulting regional experts and NMFS reports.

3) Indicator species of environmental stress - identified from the literature, discussions with fisheries experts, and from monitoring programs such as NOAA's National Status and Trends Program (O'Connor 1990). These species (e.g., American oyster, *Crassostrea virginica*, and Atlantic croaker, *Micropogonias undulatus*) are molluscs or bottom fishes that consume benthic invertebrates or have a strong association with bottom sediments. Their physiological disorders, mor-




Central Gulf of Mexico
14. Mississippi Sound
15. Lake Borgne
16. Lake Pontchartrain
17. Breton/Chandeleur Sound
18. Mississippi River
19. Barataria Bay
20. Terrebonne/Timbalier Bay
21. Atchafalaya/Vermilion Bay
22. Calcasieu Lake

Eastern Gulf of Mexico
1. Florida Bay
2. Ten Thousand Islands
3. Caloosahatchee River
4. Charlotte Harbor
5. Tampa Bay
6. Suwannee River
7. Apalachee Bay
8. Apalachicola Bay
9. St. Andrew Bay
10. Choctawhatchee Bay
11. Pensacola Bay
12. Perdido Bay
13. Mobile Bay

Western Gulf of Mexico
23. Sabine Lake
24. Galveston Bay
25. Brazos River
26. Matagorda Bay
27. San Antonio Bay
28. Aransas Bay
29. Corpus Christi Bay
30. Laguna Madre
31. Baffin Bay

Figure 3. ELMR Gulf of Mexico estuaries.

phological abnormalities, and ability to bioaccumulate contaminants indicate environmental pollution or stress.

4) Ecological value - based on several species attributes, including trophic level, relative abundance, and importance of species as a key predator or prey organism (e.g., grass shrimp, *Palaemonetes pugio*, and bay anchovy, *Anchoa mitchilli*).

***Data Sheets.*** A data sheet was developed for each species in each estuary to enable quick compilation and data presentation. For example, Figure 4 depicts the data sheet for red drum in Galveston Bay. Data sheets were developed by project staff and reviewed by local experts. Data compiled for each species' life stage included: 1) the salinity zones it occupies, 2) its monthly occurrence in the zones, and 3) its relative abundance in the zones.

The relative abundance of a species was defined using one of the following categories:

- Highly abundant - species is numerically dominant relative to other species

- Abundant - species is often encountered in substantial numbers relative to other species.

- Common - species is generally encountered but not in large numbers; does not imply an even distribution over a specific salinity zone.

- Rare - species is present but not frequently encountered.

- Not present - species or life stage not found, questionable data as to identification of the species, or recent loss of habitat or environmental degradation suggests absence.

- No information available - no data available, and after expert review it was determined that even an educated guess would not be appropriate.

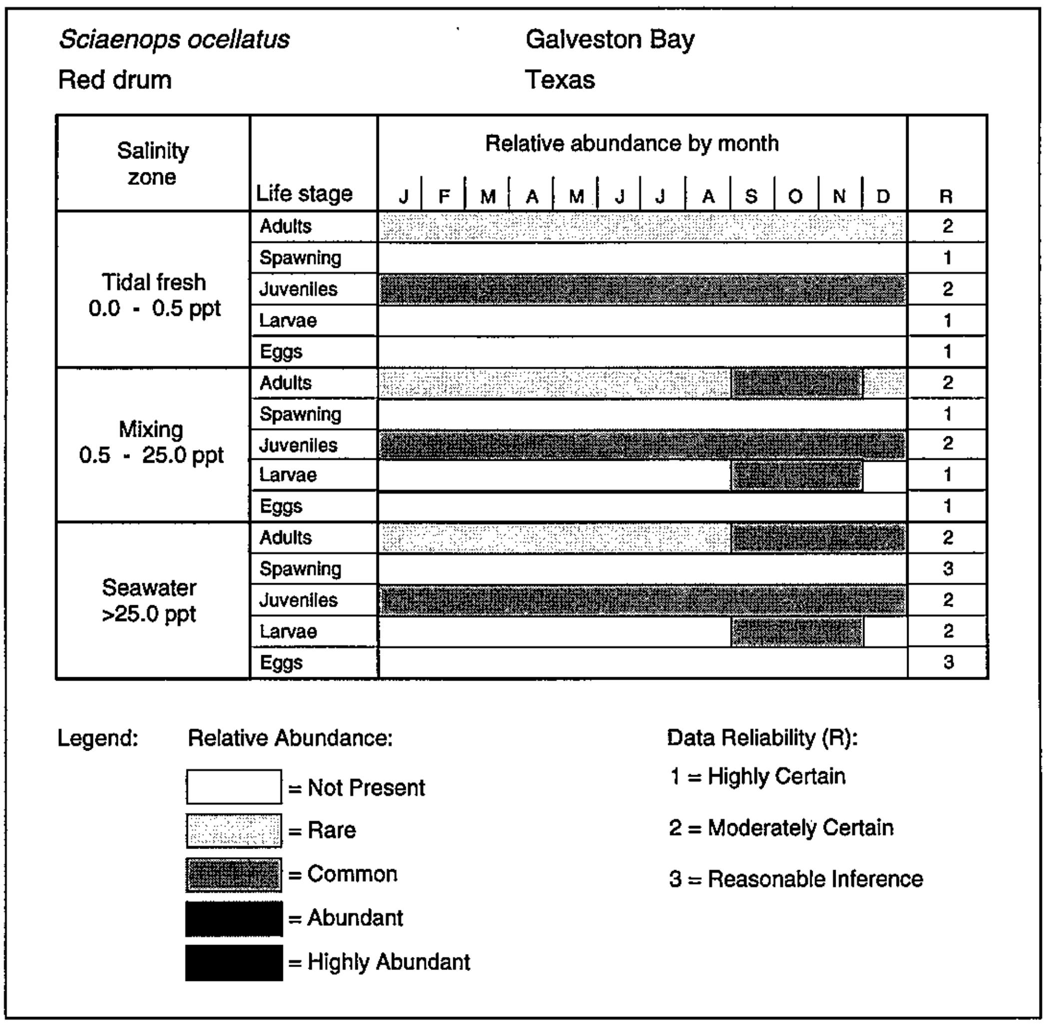



Figure 4. Example of a species/estuary data sheet: red drum in Galveston Bay.

Information was compiled for each of five life stages. Adults were defined as sexually mature individuals, juveniles as immature but otherwise similar to adults, and spawning adults as those releasing eggs or sperm. A few exceptions existed to these defined life stages, such as mating of crabs and spiny lobster, and parturition (live birth) of the viviparous bull shark.

For well-studied species such as shrimp, quantitative data were used to estimate abundance levels. For many species, however, reliable quantitative data were limited. Therefore, regional and local experts were consulted to estimate relative abundances based on the above criteria. Several reference or "guide" species with abundance levels corresponding to the above criteria were identified for each estuary. These guide species typified fishes and invertebrates belonging to a particular life mode (e.g., pelagic, demersal) or occupying similar habitats. Once guide species were selected, other species were then placed into the appropriate abundance categories relative to them. These data represent relative abundance levels within a specific estuary only; relative abundance levels across Gulf of Mexico estuaries could not be determined.

Information was compiled for each species and estuary combination, and organized into four data summaries in *Volume I*:

- Presence/absence
- Spatial distribution and relative abundance
- Temporal distribution
- Data reliability

The presence/absence information is also presented here in *Volume II*, with some minor revisions based on peer review. Table 4 (p. 8-9) was developed to readily convey the occurrence of each of the 44 ELMR species in each of the 31 Gulf of Mexico estuaries. This table depicts the highest relative abundance of the adult or juvenile life stage of each species, in any month, in any salinity zone within each estuary. The spawning, egg, and larval life stages are not considered. This table also suggests the zoogeographic distribution of species among Gulf of Mexico estuaries.

***Data Verification.*** Several years were required to develop the 1,364 data sheets and consult with regional and local experts. Each data sheet was carefully reviewed during consultations or by mail. These consultations complemented the published and unpublished literature and data sets compiled by NOAA. Over 100 scientists at approximately 50 institutions or agencies were consulted. Local experts were particularly helpful in providing estuary/species-specific information. They also provided additional references and contacts and identified additional species to be included in the ELMR data base.

## Life History Summaries and Tables

***Life History Summaries.*** A concise life history summary was written for each species to provide an overview of how and when a species uses estuaries and what specific habitats it uses. The summaries emphasize species-specific life history characteristics that relate directly to estuarine spatial and temporal distribution and abundance (e.g., many molluscs have particular salinity and substrate preferences). Information for the species life history summaries was gathered primarily from published and unpublished literature, and experts with species-specific knowledge were also consulted. Summaries were written using the format shown in Table 3, p. 7. A glossary of scientific terms used is provided on pages 341-353.

Included with each summary is a relative abundance table based on ELMR data from *Volume I*, with minor revisions based on review. These tables (Tables 5.01-5.44) provide a synopsis of the species' occurrence in the 31 ELMR Gulf of Mexico estuaries. Information for each table was obtained by summarizing the ELMR data for each month of the year and across all salinity zones to obtain the highest level of abundance for each life stage. Hence, these tables depict a species' highest abundance within an estuary, but lack the temporal and spatial resolution provided in *Volume I*.

***Life History Tables.*** While the species life history summaries provide brief accounts of important life history attributes, they do not permit a direct and simple assessment of characteristics that a species shares with others. Furthermore, many life history attributes are categorical (e.g., feeding types can be classified as carnivore, herbivore, detritivore, etc.) and more easily viewed in a tabular format. Therefore, information found in the species life history summaries was augmented with additional physical and biological criteria and condensed into three life history tables: Table 6, Habitat Associations, p. 355-363; Table 7, Biological Attributes, p. 365-373; and Table 8, Reproduction, p. 375-377. Column headers for these three tables are depicted in Figure 5. These tables present life history characteristics for each species along with behavior traits and preferred habitats. They reflect the most current information about a species as gathered from published and unpublished literature and can be used to quickly identify species with similar traits. For example, a reader interested in only benthic species can use Table 6, Habitat Associations, to identify relevant species. Terms used in the life history tables are defined at the beginning of each table, and in the Glossary, p. 341-353.

Table 3. Format of species life history summaries.

**Common Name:** the most often used common name.
**Scientific Name:** the most recent taxonomic genus and species name.
**Other Common Names:** other names that are sometimes used for a species.
**Classification:** the most recent taxonomic classification (Phylum, Class, Order, and Family).

**Value**
Commercial: information on commercial harvest.
Recreational: information on recreational fisheries.
Indicator of Environmental Stress: identifies if a species is an indicator of environmental degradation.
Ecological: the role (e.g., key predator or prey) a species plays in marine/estuarine ecosystems.

**Range**
Overall: the complete range of a species.
Within Study Area: the range of a species within Gulf of Mexico estuaries. In addition, each summary contains a relative abundance table (derived from information in *Volume I*) for the 31 ELMR Gulf of Mexico estuaries.

**Life Mode**: the life history strategy of a species and its life stages (e.g., anadromous, estuarine resident).

**Habitat**
Type: the habitats used by specific life stages (e.g., riverine, neritic, epipelagic).
Substrate: the substrate preferences of specific life stages.
Physical/Chemical Characteristics: the physical and water chemistry preferences of specific life stages (e.g., temperature and salinity).
Migrations and Movements: the movements and migratory behavior of a species/life stage between or within habitats.

**Reproduction**
Mode: type of reproductive strategy (e.g., oviparous, viviparous) and fertilization (e.g., external, internal).
Mating/Spawning: timing of spawning and description of mating or spawning behavior.
Fecundity: the number of eggs or young produced by an individual.

**Growth and Development**
Egg Size and Embryonic Development: the size of an egg and length of time for embryonic development.
Age and Size of Larvae: the age and size range of larvae.
Juveniles Size Range: the size range of juveniles.
Age and Size of Adults: the age and size range of adults.

**Food and Feeding**
Trophic mode: type of feeder (e.g., carnivorous, herbivorous).
Food Items: the types of prey eaten (e.g., copepods, amphipods, larval fish).

**Biological Interactions**
Predation: predators known to consume a species.
Factors Influencing Populations: biological and physical parameters that are known to influence a species' population abundance (e.g., overfishing, ocean productivity, spawning habitat, parasites).

**Personal communications:** individuals that provided relevant information.

**References:** alphabetical listing of literature cited.

## Table 4. Occurrence* of ELMR species in Gulf of Mexico estuaries

*highest relative abundance of adults or juveniles in any salinity zone, in any month (Nelson et al. 1992).

| | Estuary | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Florida Bay | Ten Thousand Islands | Caloosahatchee River | Charlotte Harbor | Tampa Bay | Suwannee River | Apalachee Bay | Apalachicola Bay | St. Andrew Bay | Choctawhatchee Bay | Pensacola Bay | Perdido Bay | Mobile Bay | Mississippi Sound | Lake Borgne | Lake Pontchartrain | Breton/Chandeleur Sound | Mississippi River | Barataria Bay | Terrebonne/Timbalier Bay | Atchafalaya/Vermilion Bay | Calcasieu Lake | Sabine Lake | Galveston Bay | Brazos River | Matagorda Bay | San Antonio Bay | Aransas Bay | Corpus Christi Bay | Laguna Madre | Baffin Bay |
| Bay scallop | √ | √ | √ | √ | √ | | ○ | √ | ○ | | √ | | | ○ | | | √ | | | | | | | √ | | √ | √ | √ | √ | √ | |
| American oyster | | ○ | ◉ | ○ | ○ | ◉ | ◉ | ◉ | ○ | ○ | ○ | √ | ◉ | ○ | ○ | ○ | ◉ | √ | ◉ | ◉ | ◉ | ○ | ○ | ● | na | ○ | ◉ | ○ | ○ | √ | |
| Atlantic rangia | | | ● | ● | ● | ◉ | ○ | ◉ | ○ | ○ | ○ | ◉ | ◉ | ○ | ◉ | ◉ | ○ | ○ | ◉ | ◉ | ○ | ○ | ● | ◉ | na | ○ | √ | √ | √ | | |
| Hard clam | | ○ | | ○ | ◉ | ○ | ○ | | ○ | ○ | | ○ | √ | ○ | | | ○ | | ○ | √ | | | | ○ | na | ○ | ○ | ○ | ○ | | |
| Bay squid | √ | √ | ○ | ○ | ◉ | ○ | ○ | ◉ | ◉ | ○ | ○ | ○ | ○ | ● | ◉ | ○ | ○ | | ○ | ○ | ○ | ○ | √ | ○ | ○ | ◉ | ◉ | ○ | ○ | ○ | ○ |
| Brown shrimp | √ | √ | √ | √ | | | | ◉ | ◉ | ◉ | ● | ● | ● | ● | ● | ◉ | ◉ | ○ | ● | ● | ● | ● | ◉ | ● | ◉ | ● | ● | ● | ● | ◉ | ● |
| Pink shrimp | ● | ● | ◉ | ◉ | ● | ● | ◉ | ◉ | ◉ | ◉ | ○ | ○ | ○ | ○ | √ | √ | ◉ | | ○ | √ | √ | | | √ | ○ | ○ | ○ | ○ | ○ | ◉ | ○ |
| White shrimp | | | | | | √ | ● | ● | ○ | ◉ | ◉ | ○ | ● | ● | ● | ● | ○ | ○ | ● | ◉ | ● | ● | ● | ● | ● | ● | ● | ◉ | ◉ | ◉ | √ |
| Grass shrimp | ○ | ○ | ● | ● | ● | ● | ● | ● | ◉ | ◉ | ● | | ● | ● | ● | ○ | ◉ | ○ | ◉ | ◉ | ● | ● | ● | ● | ◉ | ● | ◉ | ◉ | ● | ● | ● |
| Spiny lobster | ◉ | √ | | √ | √ | | √ | | √ | | | | | √ | | | | | | | | | | | | | | | | √ | |
| Blue crab | ◉ | ◉ | ● | ◉ | ◉ | ● | ● | ● | ● | ◉ | ◉ | ◉ | ● | ● | ● | ◉ | ◉ | ○ | ◉ | ◉ | ◉ | ● | ● | ◉ | ○ | ◉ | ● | ● | ● | ◉ | ◉ |
| Gulf stone crab | | | | | | √ | ○ | ○ | √ | √ | √ | √ | ○ | ○ | √ | √ | ○ | ○ | ○ | ○ | √ | ○ | √ | ○ | na | ○ | ○ | ○ | ○ | √ | ○ |
| Florida stone crab | ○ | ○ | √ | ○ | ○ | ○ | ○ | √ | | | | | | | | | | | | | | | | | | | | | | | |
| Bull shark | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | √ | ○ | ○ | ○ | ○ | ◉ | √ | ○ | ○ | ○ | √ | √ | ○ | na | ○ | ○ | ○ | ○ | √ | √ |
| Tarpon | ○ | ○ | ◉ | ◉ | ◉ | ○ | ○ | ○ | ○ | ○ | ○ | √ | ○ | ○ | ○ | ○ | | ○ | √ | √ | √ | | √ | √ | na | ○ | ○ | √ | √ | √ | √ |
| Alabama shad | | | | | | | √ | ○ | √ | √ | | | √ | √ | √ | √ | √ | | | | | | | | | | | | | | |
| Gulf menhaden | √ | √ | √ | √ | ● | ○ | ◉ | ◉ | ● | ● | ● | ◉ | ● | ● | ● | ● | ● | ◉ | ● | ◉ | ● | ● | ● | ● | ◉ | ● | ◉ | ◉ | ◉ | ◉ | ● |
| Yellowfin menhaden | ◉ | ● | ○ | ○ | ◉ | | √ | | | | | | | √ | √ | √ | | | | | | | | | | | | | | | |
| Gizzard shad | | | | | | ○ | ○ | ○ | | ○ | ○ | √ | ◉ | ◉ | ● | ○ | ○ | ◉ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ◉ | ○ | √ | ○ | √ | ◉ |
| Bay anchovy | ● | ● | ● | ● | ● | ● | ● | ● | ◉ | ● | ● | ◉ | ● | ● | ● | ● | ◉ | ● | ● | ● | ● | ● | ◉ | ● | ● | ● | ● | ● | ● | ● | ● |
| Hardhead catfish | ◉ | ○ | ◉ | ● | ○ | ● | ◉ | ● | ● | ◉ | ◉ | ◉ | ◉ | ● | ● | ◉ | ◉ | ● | ● | ◉ | ◉ | ◉ | ○ | ◉ | ○ | ◉ | ● | ◉ | ◉ | ● | ● |
| Sheepshead minnow | ◉ | ○ | ○ | ○ | ● | ● | ● | ◉ | ◉ | ◉ | ◉ | ○ | ◉ | ◉ | ○ | ○ | ○ | ◉ | ● | ○ | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ● | ● |

<u>Relative abundance</u>:

● - Highly Abundant ◉ - Abundant ○ - Common √ - Rare Blank - Not present na - No data available

**Table 4, continued.**

| Species | Florida Bay | Ten Thousand Islands | Caloosahatchee River | Charlotte Harbor | Tampa Bay | Suwannee River | Apalachee Bay | Apalachicola Bay | St. Andrew Bay | Choctawhatchee Bay | Pensacola Bay | Perdido Bay | Mobile Bay | Mississippi Sound | Lake Borgne | Lake Pontchartrain | Breton/Chandeleur Sound | Mississippi River | Barataria Bay | Terrebonne/Timbalier Bay | Atchafalaya/Vermilion Bay | Calcasieu Lake | Sabine Lake | Galveston Bay | Brazos River | Matagorda Bay | San Antonio Bay | Aransas Bay | Corpus Christi Bay | Laguna Madre | Baffin Bay |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Estuary** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Gulf killifish | O | ◉ | O | ◉ | O | ◉ | ◉ | O | O | O | O | O | ◉ | ◉ | ◉ | O | O | ◉ | ● | ● | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | O | ◉ | ◉ |
| Silversides | ● | ◉ | ● | ● | ● | ◉ | ● | ● | ◉ | ◉ | ◉ | ◉ | ◉ | ● | ◉ | ◉ | O | ◉ | ● | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ● | ● |
| Snook | O | ◉ | ◉ | ◉ | O | O | O | O | | | | | | | | | | | √ | | | | | √ | | √ | | √ | √ | O | |
| Bluefish | O | O | | O | O | O | O | O | ◉ | ◉ | O | O | O | O | | | √ | √ | O | √ | √ | √ | √ | O | O | √ | √ | √ | √ | | |
| Blue runner | √ | O | | O | O | O | O | O | ◉ | O | O | O | O | ◉ | | | | | O | √ | | | | √ | | | | | | | |
| Crevalle jack | ◉ | O | O | ◉ | ◉ | O | O | O | O | O | O | O | O | O | O | O | O | O | O | O | O | O | √ | O | O | O | O | O | O | ◉ | O |
| Florida pompano | ● | O | √ | ◉ | O | √ | O | √ | O | O | O | O | O | ◉ | | | O | O | O | O | √ | O | | O | | O | O | O | O | ◉ | √ |
| Gray snapper | ◉ | O | √ | O | O | O | O | √ | O | O | ◉ | O | O | O | | | O | | O | √ | | √ | | √ | | √ | √ | √ | √ | O | √ |
| Sheepshead | O | O | √ | √ | O | O | √ | O | O | O | O | ◉ | ◉ | O | ◉ | O | O | O | ◉ | ◉ | O | O | O | O | O | ◉ | ◉ | O | O | ◉ | O |
| Pinfish | ● | ● | ● | ● | ● | ● | ◉ | ◉ | ● | ◉ | ● | ◉ | ◉ | ● | ◉ | ◉ | O | O | ◉ | ◉ | O | O | O | ◉ | ◉ | ● | ◉ | ◉ | ◉ | ● | ◉ |
| Silver perch | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | O | ◉ | ◉ | O | O | O | O | ● | ● | O | O | O | ◉ | ◉ | O | O | O | O | O | O | O | O | O | ◉ | ◉ |
| Sand seatrout | √ | ◉ | ● | ● | ◉ | ● | ● | ● | ◉ | ◉ | O | O | ● | ● | ● | ◉ | O | ● | ◉ | ◉ | ◉ | ◉ | √ | ◉ | O | O | O | O | ◉ | √ | O |
| Spotted seatrout | ◉ | O | O | ◉ | O | ◉ | O | O | ◉ | ◉ | O | O | ◉ | ◉ | ◉ | O | ◉ | ◉ | O | ◉ | ◉ | O | O | O | O | O | O | O | O | O | O |
| Spot | O | O | O | O | ● | ◉ | ● | ◉ | ◉ | ● | ● | ◉ | ● | ● | ● | O | ◉ | ◉ | ● | ◉ | ◉ | O | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ● | ● |
| Atlantic croaker | √ | √ | √ | O | √ | O | O | ● | ◉ | ◉ | ● | O | ● | ● | ● | ● | ◉ | ● | ● | ● | ● | ● | ◉ | ● | ● | ● | ● | ◉ | ◉ | ◉ | ◉ |
| Black drum | O | O | O | O | O | O | O | O | O | O | O | O | O | O | O | O | ◉ | O | ◉ | ◉ | O | O | O | O | O | O | O | O | O | O | ◉ |
| Red drum | O | √ | ◉ | ◉ | ● | O | O | O | ◉ | O | O | O | O | O | ◉ | O | ◉ | O | O | O | O | ◉ | O | O | O | O | O | O | O | O | O |
| Striped mullet | ● | ● | ● | ● | ● | ◉ | ● | ◉ | ● | ◉ | ◉ | ◉ | ◉ | ● | ● | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ | O | ◉ | O | ◉ | ◉ | ◉ | ◉ | ◉ | ◉ |
| Code goby | ● | ● | ◉ | ● | ◉ | O | O | O | ◉ | O | O | √ | | ◉ | ◉ | O | | | √ | | | | | √ | na | O | √ | O | O | ◉ | ◉ |
| Spanish mackerel | O | O | √ | O | O | O | √ | √ | ◉ | O | O | ◉ | O | ◉ | √ | √ | O | √ | O | O | O | O | O | O | √ | √ | √ | √ | √ | √ | |
| Gulf flounder | O | O | √ | O | O | O | O | O | ◉ | O | O | O | O | O | | | | | | | | | | √ | | √ | √ | √ | √ | √ | √ |
| Southern flounder | √ | √ | | √ | √ | O | O | O | O | O | O | O | O | ◉ | O | O | ◉ | ◉ | ◉ | ◉ | O | ◉ | ● | ● | O | ◉ | ◉ | O | O | ◉ | O |

<u>Relative abundance</u>:

● - Highly Abundant ◉ - Abundant O - Common √ - Rare Blank - Not present na - No data available

## Figure 5. Life History Table Headers: Habitat Associations, Biological Attributes, and Reproduction.

### Table 6. Habitat Associations

**Habitat Associations** — Domain

| Species / life stage | | Freshwtr. | | | Estuarine | | | Salinity range – NEI | | | Salinity range – Venice system | | | | | Temperature range | | | | | | | Marine | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Lacustrine | Riverine - coastal plain | Riverine - inland | Inlet mouth | Channel | Inter- and subtidal flats | Tidal fresh (0-0.5‰) | Mixing (0.5-25‰) | Seawater (>25‰) | Limnetic (0-0.5‰) | Oligohaline (0.5-5‰) | Mesohaline (5-18‰) | Polyhaline (18-30‰) | Euhaline (>30‰) | 0-5°C | 5-10°C | 11-15°C | 16-20°C | 21-25°C | 26-30°C | >30°C | Beach/surf | Neritic | Oceanic |
| Bay scallop *Argopecten irradians* | A | | | | | | ● | | ● | ● | | | | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | |
| | S | | | | | | ● | | ● | ● | | | | ● | ● | | | | | | ● | | | ● | |
| | J | | | | | | ● | | ● | ● | | | | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | |
| | L | | | | | | ● | | ● | ● | | | | ● | ● | | | | ● | ● | ● | | | ● | |
| | E | | | | | | ● | | ● | ● | | | | ● | ● | | | | ● | ● | | | | ● | |

**Habitat Associations** — Substrate preference; Depth preference

| Species / life stage | | Substrate preference | | | | | | | | | Depth preference – Littoral | | Depth preference – Sublittoral | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Mud/silt/clay | Sand | Pebble/cobble/gravel | Boulder/rocky outcrop | Shell | Submergent vegetation | Emergent vegetation | Floating vegetation | None | Intertidal | Subtidal | Inner shelf (10-50 m) | Middle shelf (50-100 m) | Outer shelf (100-200 m) |
| Bay scallop *Argopecten irradians* | A | ● | ● | | | | ● | | | | ● | ● | ● | | |
| | S | ● | ● | | | | ● | | | | ● | ● | ● | | |
| | J | ● | ● | | | ● | ● | | ● | | ● | ● | ● | | |
| | L | | | | | ● | ● | ● | ● | | ● | ● | ● | | |
| | E | | | | | | | | | ● | ● | ● | ● | | |

### Table 7. Biological Attributes

**Biological Attributes**

| Species / life stage | | Life Mode | | | | | Spatial Strategy | | | | | Mobility | | | Feed* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Epibenthic | Benthic | Demersal | Nektonic | Planktonic | Freshwater resident | Estuarine resident | Marine resident | Coastal migrant | Ocean migrant | Nonmobile | Low mobility | High mobility | Filter feeder | Non-filter feeder |
| Bay scallop *Argopecten irradians* | A | ● | | | | | | ● | ● | | | | ● | | ● | |
| | S | ● | | | | | | ● | ● | | | | | | | |
| | J | ● | | | | | | ● | ● | | | | ● | | ● | |
| | L | ● | | | | ● | | ● | ● | | | | ● | | ● | |
| | E | | | ● | | ● | | ● | ● | | | | ● | | | |

**Biological Attributes** (continued); **Value**

| Species / life stage | | Prey Items | | | | | | | | | | Longevity | | | | | | Value | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Detritus | Phytoplankton | Zooplankton | Infauna | Epibenthos | Insects | Fish (eggs, larvae) | Fish (juveniles, adults) | Macroalgae | Vascular plants | 1 day | 1-30 days | 1-12 months | 1-5 years | 5-20 years | >20 years | Recreational | Commercial | Ecological | Indicator of stress |
| Bay scallop *Argopecten irradians* | A | ● | ● | ● | | | | | | | | | | | ● | | | ● | ● | ● | ● |
| | S | | | | | | | | | | | | | | | | | | | | |
| | J | ● | ● | ● | | | | | | | | | | ● | | | | | ● | ● | ● |
| | L | | ● | ● | | | | | | | | | ● | | | | | | | ● | |
| | E | | | | | | | | | | | ● | | | | | | | | | |

### Table 8. Reproduction

**Reproduction**

| Species | Fertilization/ development | | | | | Mating type | | | Spawning strategy | | | | | Pamtl. care | | Domain | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | External | Internal | Oviparous | Ovoviviparous | Viviparous | Monogamous | Polygamous | Broadcast spawner | Andromous | Catadromous | Iteroparous | Semelparous | Batch | Protected | Non-protected | Riverine | Estuarine | Marine |
| Bay scallop *Argopecten irradians* | ● | | ● | | | | | ● | | | | ● | ● | | ● | | ● | ● |

| Species | Temporal Schedule | | | | | | | | | | | | Periodicity | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | January | February | March | April | May | June | July | August | September | October | November | December | Annual spawning | 2 or more per year | 2 or more years | Undescribed |
| Bay scallop *Argopecten irradians* | | | | | | | | ● | ● | ● | | | | ● | | |

| Species | Fecundity | | | | | | | | Maturation age | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | <100 | 100-1,000 | 1,000-10,000 | 10,000-100,000 | 100,000-1 million | 1-10 million | >10 million | Undescribed | <6 months | 0.5 to 1 Year | 1 to 3 Years | 3 to 5 Years | > 5 Years | Undescribed |
| Bay scallop *Argopecten irradians* | | | | | ● | | | | | ● | | | | |

## Concluding Comments

As it becomes apparent that the cumulative effects of small alterations in many estuaries have a total systemic impact on coastal ocean resources, it is more important than ever to compile consistent information on the Nation's estuarine fishes and invertebrates. Although the knowledge available to effectively preserve and manage estuarine resources is limited, the ELMR data base provides an important tool for assessing the status of estuarine fauna and examining their relationships with other species and their environment. These life history summaries and life history tables highlight many of the biological and environmental factors that play a role in determining each species' distribution and abundance. Together, the ELMR data base and life history information will provide valuable baseline information on the biogeography and ecology of estuarine fishes and invertebrates, and identify gaps in our knowledge of these valuable natural resources.

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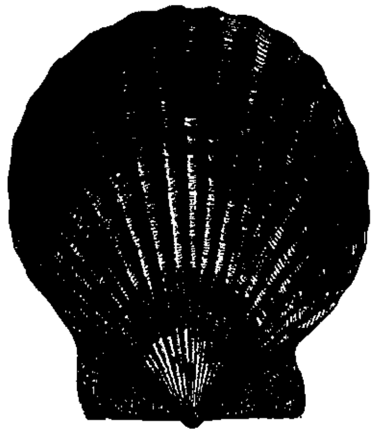
# Bay scallop

***Argopecten irradians***
**Adult**



2 cm

(from Goode 1884)

**Common Name:** bay scallop
**Scientific Name:** *Argopecten irradians*
**Other Common Names:** Atlantic bay scallop, *peigne baie de l'Atlantique* (French), *peine caletero atlántico* (Spanish) (Fischer 1978).
**Classification** (Turgeon et al. 1988)

| | |
|---|---|
| Phylum: | Mollusca |
| Class: | Bivalvia |
| Order: | Ostreoida |
| Family: | Pectinidae |

## Value

Commercial: Bay scallops are harvested commercially by dredging, dip netting, raking, and hand picking (Peters 1978). Reported U.S. 1992 bay scallop landings were161.5 metric tons (mt), with a dollar value of $2.1 million (NMFS 1993). This an important commercial species along the U.S. Atlantic coast, with fisheries in Massachusetts, Rhode Island, New York, North Carolina, and the Gulf coast of Florida (Heffernan et al. 1988, MacKenzie 1989, Rhodes 1991). Landings for 1992 totaled 58.5 mt in the Gulf of Mexico (Newlin 1993). However, the commercial scallop fishery in Florida has been closed since 1995 (Arnold pers. comm.). There is no apparent commercial fishery for this species in the remaining Gulf coastal states because of their relatively low abundance, but their high value and the available market has sparked considerable interest in maricultural production (Hall 1984, Rhodes 1991). There are few commercial scallop mariculture ventures currently in operation, but hatchery technology is well developed and research is in progress (Hall 1984, Crenshaw et al. 1991, Rhodes 1991, Walker et al. 1991).

Recreational: Bay scallops are sometimes collected by hand picking while wading in seagrass beds. In Florida waters of the Gulf of Mexico, recreational harvest is common from Steinhatchee north and west to Panama City (Arnold pers. comm.). However, recreational harvest elsewhere in the Gulf of Mexico is not especially common because of the bay scallop's relatively low abundance. In Florida, the recreational seasons extends from July 1 to September 10, from Suwannee River southward (Arnold pers. comm.). The bag limit is two gallons of whole bay scallops in the shell, or one pint of meat, per day per person, or ten gallons of whole scallops per day per boat (Arnold pers. comm.). In Texas, they may be taken year-round in waters approved by the Texas Department of Health.

Indicator of Environmental Stress: Filter feeders such as bay scallops often ingest and accumulate resuspended detritus and organic matter from polluted areas. This species has been used to test the effects of pollutants from the petroleum industry (Hamilton et al. 1981). Mortality of juvenile bay scallops has been demonstrated in the laboratory in the presence of heavy metals (Nelson et al. 1976).

Ecological: The bay scallop is an important part of the estuarine food web through its conversion of phytoplankton and detritus into available biomass for second order consumers.

## Range

Overall: The range of this species extends along the western Atlantic from Cape Cod into the Gulf of Mexico, and down to Colombia (Turner and Hanks 1960, Sastry 1962, Fischer 1978, Peters 1978, Robert 1978, Fay et al. 1983). Areas of abundance as determined from

Table 5.01. Relative abundance of bay scallop in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | √ | √ | √ | √ | √ |
| Ten Thousand Islands | √ | √ | √ | √ | √ |
| Caloosahatchee River | √ | √ | √ | √ | √ |
| Charlotte Harbor | √ | √ | √ | √ | √ |
| Tampa Bay | √ | √ | √ | √ | √ |
| Suwannee River | | | | | |
| Apalachee Bay | O | O | O | O | O |
| Apalachicola Bay | √ | √ | √ | √ | √ |
| St. Andrew Bay | O | O | O | O | O |
| Choctawhatchee Bay | | | | | |
| Pensacola Bay | √ | √ | √ | √ | √ |
| Perdido Bay | | | | | |
| Mobile Bay | | | | | |
| Mississippi Sound | O | O | O | O | O |
| Lake Borgne | | | | | |
| Lake Pontchartrain | | | | | |
| Breton/Chandeleur Sounds | √ | √ | √ | √ | √ |
| Mississippi River | | | | | |
| Barataria Bay | | | | | |
| Terrebonne/Timbalier Bays | | | | | |
| Atchafalaya/Vermilion Bays | | | | | |
| Calcasieu Lake | | | | | |
| Sabine Lake | | | | | |
| Galveston Bay | √ | √ | √ | √ | √ |
| Brazos River | | | | | |
| Matagorda Bay | √ | √ | √ | √ | √ |
| San Antonio Bay | √ | √ | √ | √ | √ |
| Aransas Bay | √ | √ | √ | √ | √ |
| Corpus Christi Bay | √ | √ | √ | √ | √ |
| Laguna Madre | √ | √ | √ | √ | √ |
| Baffin Bay | | | | | |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- O Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning adults
- J - Juveniles
- L - Larvae
- E - Eggs

commercial landings are coastal areas of Massachusetts, Rhode Island, New York, North Carolina, and the gulf coast of Florida (Heffernan et al. 1988, Rhodes 1991).

In the United States, *Argopecten irradians* is considered to include three subspecies: *A. i. irradians*, ranging from Cape Cod to New Jersey; *A. i. concentricus*, New Jersey to the Chandeleur Islands, east of the Mississippi River; and *A. i. amplicostatus*, Galveston Bay to Tuxapan, Veracruz, Mexico (Andrews 1981, Fay et al. 1983).

Within Study Area: Along the Florida Gulf coast, bay scallops are most abundant from Pepperfish Keys, south of Steinhatchee, north and westward to St. Andrew Bay (Arnold pers. comm.). Populations are scattered in the northwestern Gulf, but become more common in the western Gulf. In Texas, the bay scallop is most abundant in bays of the southern coast where the salinities are generally higher and seagrass meadows are extensive. The subspecies *Argopecten irradians concentricus* ranges from Key West, Florida to the Chandeleur Islands of Louisiana (Broom 1976). *Argopecten irradians amplicostatus* ranges from Galveston, Texas to the Laguna Madre (Broom 1976, Andrews 1981) (Table 5.01).

**Life Mode**

Fertilized eggs are demersal (Belding 1910). Early larval stages are pelagic and planktonic. Late larval stages are epibenthic. Juveniles up to 20-30 mm in length attach to a surface suspended off the bottom by byssal threads (Sastry 1965). Adults and juveniles >30 mm in length are epibenthic, sometimes motile, and gregarious (Belding 1910, Gutsell 1930, Marshall 1947, Sastry 1962, Robert 1978, Peters 1978, Fonseca et al. 1984).

**Habitat**

Type: All life stages are estuarine, and marine in nearshore waters, occurring in high salinity (euhaline to polyhaline) waters. Bay scallops are typically subtidal, but may be exposed during especially low tides (Rhodes 1991). Collections have been recorded at depths from 0 to 10 m and a maximum of 18 m. They are most abundant in waters from 0.3 to 0.6 m at low tide (Marshall 1960, Sastry 1962, Thayer and Stuart 1974, Peters 1978, Robert 1978, Fay et al. 1983, Fonseca et al. 1984). Larvae inhabit the water column while searching for a settlement site (Sastry 1965). At settlement the young scallop attaches epifaunally to a surface suspended off the bottom (rock, seagrass, algae, rope) by means of byssal threads (Belding 1910). At 20 to 30 mm in length the juvenile scallop settles to the bottom, beginning a demersal existence that continues through the adult stage (Castagna 1975).

Substrate: Late larval/early juvenile stages use various substrates for attachment, including oyster shells, rope, algae, seagrass, and submerged macrophytes (Gutsell 1930, Marshall 1947, Marshall 1960, Thayer and Stuart 1974, Fay et al. 1983). Seagrasses, such as eel grass (*Zostera marina*) and shoal grass (*Halodule wrightii*), appear to be the preferred settling site given the abundance that is often associated with seagrass habitats (Belding 1910, Gutsell 1930, Sastry 1962, Thayer and Stuart 1974, Castiglione pers. comm.). However, if seagrass density is too great, current velocity is reduced and bay scallop abundance may decline (MacKenzie 1989). Scallops can settle and survive in areas lacking seagrass (Marshall 1947, Marshall 1960), but individuals <10 mm generally cannot tolerate silty substrates (Castagna 1975), and burial can occur in muddy substrates (Tettelbach et al. 1990). Smith et al. (1988) have demonstrated that transplanted seagrass does not serve as a highest quality habitat, due to greater losses from predation and/or transport as compared to a natural seagrass site.

Physical/Chemical Characteristics:
Temperature: Eggs and larvae are stenothermal, with 15 to 20°C required for early development. Optimal embryonic development occurs from 20 to 25° and best larval growth from 25 to 30°C (Tettlebach and Rhodes 1981). Wright et al. (1983, 1984) found larvae subjected to temperatures below the spawning temperature experienced a cold-shock which resulted in higher mortalities. Juveniles and adults are eurythermal, and Connecticut bay scallops are reportedly able to tolerate temperatures as low as -6.6°C for short periods (Marshall 1960). Throughout their range they occur in areas where summer maximum water temperatures do not exceed 32°C (Sastry 1965, Barber and Blake 1983).

Salinity: Eggs and larval stages are generally found in polyhaline salinities (18 to 30‰), and egg and larval development are most successful within that range. In laboratory studies, normal embryo development occurs over a narrow range of salinities. Egg development was successful at 25‰, but no embryo development occurred at 10 or 15‰ (Castagna 1975, Tettlebach and Rhodes 1981). Larvae develop at salinities from 20 to 35‰ with optimal development at 25‰ (Tettlebach and Rhodes 1981), and are not found below 22‰. Although they tend to occur in higher estuarine salinities (15-30‰), juveniles and adults are considered euryhaline and can tolerate moderate salinities. However, symptoms of stress appear when salinities drop below 16‰ (Sastry 1966, Duggan 1973). The minimum salinity determining overall distributions is approximately 14‰ (Belding 1910, Gutsell 1930). Laboratory experiments examining the influence of reduced salinities on scallop behavior indicated that at salinities of 16‰ and temperatures of 10° to 15°C the animals became inactive, and at 20° to 25°C reduced activity occurred at 22‰ and 18‰ (Duggan 1973). Mortality of scallops has been demonstrated in the laboratory at salinities of 10‰ and less over a range of temperatures (Mercaldo and Rhodes 1982).

Dissolved Oxygen: Oxygen resting requirements of 70 ml/kg/hour at 20° have been reported (Van Dam 1954). Critical dissolved oxygen (DO) concentrations for this species may be related to individual size and ambient water temperature (Voyer 1992).

Other: Turbidities greater than 500 ppm may interfere with normal growth and reproduction (Fay et al. 1983). Water currents can displace scallops from their "home" habitat, and current velocity can have effects on growth related to food availability (Moore and Marshall 1967, Kirby-Smith 1972, Rhodes 1991). An optimal amount of current is necessary to maintain high concentrations of suspended food and remove waste materials rapidly (Kirby-Smith 1972).

Movements and Migrations: Egg and early larval stages may be transported by tidal currents. Late larval stages are capable of swimming by use of the ciliated velum and crawling with the foot (Gutsell 1930, Sastry 1965, Hall 1984). Juvenile and adult scallops are capable of swimming via propulsion created by the clapping of the two valves (Belding 1910, Gutsell 1930, Moore and Marshall 1967). This ability apparently serves to maintain position in grassbeds and avoid competitors and predators (Peterson et al. 1982, Winter and Hamilton 1985). The extent of late juvenile and adult movements is unclear. There are, however, some reports of scallops migrating in mass (Roessler and Tabb 1974).

**Reproduction**
Mode: Bay scallops are hermaphroditic, usually protandrous (Peters 1978), and semelparous (Bricelj et al. 1987). Fertilization is external, in the water column or on the bottom. Male gametes are generally (but not always) released before female gametes, reducing the chance of self-fertilization (Belding 1910, Gutsell 1930, Loosanoff and Davis 1963, Hall 1984).

Spawning: Spawning is influenced by temperature, photoperiod, salinity and food abundance (Sastry 1975). It occurs in estuaries and in nearshore areas at various times throughout the range. In the New England area, spawning is triggered by increasing temperatures (Belding 1910, Cooper and Marshall 1963, Taylor and Capuzzo 1983), while spawning south from North Carolina is triggered by decreasing temperatures (Barber and Blake 1983). In Florida, spawning begins with the decline in summer temperatures, August to October (Sastry 1962, Barber and Blake 1983). Scallops can be conditioned in the laboratory to spawn out of season by raising the temperature to 30°C followed by gradual cooling to 28-26°C (Castagna and Duggan 1971, Castagna 1975). Gametogenesis is triggered by food and temperature (Sastry 1975, Hall 1984). With adequate food supplies, a minimum temperature of 15-20°C is necessary for its initiation (Sastry 1968, Sastry and Blake 1971), with slightly higher temperatures required for complete maturation of gametes and spawning (Sastry 1966, Sastry 1968). As the gonads mature, nutrients stored during the nonreproductive period are diverted to their development (Sastry 1975). Few studies have investigated salinity as a factor in spawning.

Fecundity: Kraeuter et al. (1982) reported a fecundity estimate of 100,000 to 1,000,000 eggs per female. Bricelj et al. (1987) reported fecundities ten to twenty times greater. Some scallops may survive to spawn a second time, but most do not (Robert 1978).

**Growth and Development**

Egg Size and Embryonic Development: The unfertilized mature oocyte is 62-63 µm in diameter (Sastry 1965, Sastry 1966). After fertilization, the first polar body occurs in 35 minutes with the second cleavage stage occurring in 105 minutes. By 5 hours and 15 minutes the blastula has formed and rapidly develops to the ciliated gastrula stage by 9 to 10 hours and reaches the trochophore stage by about 24 hours (Gutsell 1930, Sastry 1965).

Age and Size of Larvae: Larval development in bay scallops proceeds rapidly. The transition from trochophore to straight-hinged larval stage occurs in about 24 hours (Gutsell 1930, Sastry 1965, Rhodes 1991). In laboratory studies at 24° C the veliger (shelled) larval stage develops within 48 hours at a size of approximately 101 µm (Sastry 1965). By the tenth day of the veliger phase, the pediveliger begins to develop and is complete by day 12, beginning the settlement process at a size of approximately 184 µm (Sastry 1965, Castagna and Duggan 1971, Hall 1984). Attachment with byssal threads occurs between the 10th and 19th day of the veliger stage with the development of the prodissoconch (≈190 µm) and metamorphosis into the juvenile stage commences. The juvenile stage is reached about 29 days from fertilization when larval development is complete (Sastry 1965). Loosanoff and Davis (1963) reported larval growth rate to be greater than 10 µm/day.

Juvenile Size Range: By day 35 the young scallop resembles the adult and is approximately 1.175 mm in length (Sastry 1965). Juveniles remain attached by byssal threads until 20-30 mm in size, but retain the ability to attach throughout their lives (Hall 1984, Garcia-Esquivel and Bricelj 1993). Growth is dependent on temperature and food availability (Sastry 1965). Growth rates are rapid during the warm months, and a marketable size of 50 mm is reportedly reached within 12 to 13 months on the U.S. east coast (Castagna and Duggan 1971, Spitsbergen 1979, Rhodes 1991), or within 6 to 8 months in Florida (Arnold pers. comm.). Little growth occurs during winter, especially in the northern part of the bay scallop's range. When growth resumes in the spring, a raised shell check or color change occurs in the shells of these individuals. Growth rates of 3.8 to 8.0 mm/month (umbo to ventral margin) have been determined. Optimal growth occurs in currents <1cm/s and no growth occurs in currents >12 cm/second (Kirby-Smith 1972).

Age and Size of Adults: Maturity is reached by the end of the first year, and is a function of age and not size (Gutsell 1930, Sastry 1963). Adult sizes range from 60 to 70 mm with a reported maximum of 90 mm. Life expectancy is 12-30 months, and is usually less than two years (Belding 1910, Gutsell 1930, Robert 1978).

**Food and Feeding**

Trophic Mode: The bay scallop filter feeds at all development stages (Castagna 1975). Veliger feed by means of cilia on their velum (Hall 1984). Chipman (1954) determined that young scallops filter at a rate of 3 l/hour, which increases as they grow reaching an average of 15 l/hour, and a maximum of 25.4 l/hour. Intensity of feeding increases with temperature.

Food Items: The bay scallop feeds primarily on phytoplankton, but it also consumes zooplankton, suspended benthic particles, bacteria, detritus, organic matter, gametes from other species and algae spores. In the laboratory larvae grow and develop well on a diet of unicellular algae and naked dinoflagellates (Castagna 1975), although some algal species have low nutritive value and can result in poor growth and survival (Nelson and Siddall 1988). Juveniles and adults ingest phytoplankton and detritus as well as benthic diatoms (Gutsell 1930, Davis and Marshall 1961, Broom 1976, Fay et al. 1983), but what is actually assimilated has not been determined.

**Biological Interactions**

Predation: Known and suspected predators of the bay scallop include various gulls and wading birds, starfish, cow-nosed rays, pinfish, boxfish, toadfish, whelks, and various crabs (Thayer and Stuart 1974, Broom 1976, Peterson et al. 1989, Prescott 1990). Scallops in intertidal and/or bare bottom areas appear to be more vulnerable to predation than individuals in seagrass beds or covered by 1-3 cm of water or more (Peterson et al. 1989, Prescott 1990).

Factors Influencing Populations: A probable limiting factor for distribution in the southern range of the bay scallop is its increased metabolic rate in this area associated with the higher temperatures of this region and a decreased food supply that causes a net loss of available energy for reproduction (Barber and Blake 1983). Excessive turbidities and current velocities can inhibit growth and reproduction (Kirby-Smith 1972, Fay et al 1983). Bay scallops living on soft mud substrate are subject to burial during events that increase current velocity (Tettelbach et al. 1990). Seagrass provides a substrate for attachment by bay scallop larvae, and the abundance of this species is influenced by its presence (Thayer and Stuary 1974, MacKenzie 1989). Destruction of seagrass areas results in decreased abundance of this species. Smith et al. (1988) have demonstrated that transplanted seagrass does not serve as a quality habitat with apparently greater loss due to predation and/or transport in the transplanted seagrass as compared to the natural seagrass. Blooms of red tide algae in sufficient concentrations can result in conditions toxic to adult and larval bay scallops (Summerson and Peterson 1990). Nuisance blooms of algae can affect bay scallops by altering feeding rates. These species are often low in nutritive value causing poor recruitment and settlement of the bay scallop due to the algae's inability to suport adequate larval growth (Nelson and Siddal 1988, Summerson and Peterson 1990). Population sizes are subject to a large degree of variation within the year because of the bay scallop's short life span and semelparous reproductive cycle (Fay et al. 1983, Nelson and Siddall 1988, MacKenzie 1989). Bay scallops generally spawn only once during their lives when they reach the end of their first year. Although two year old animals occur rarely, populations are almost entirely composed of only one year class, upon which the following year class is completely dependent. Unfavorable conditions that result in poor larval recruitment in any given year may therefore lower abundance the following year. Low DO episodes may have long-term population effects due to the bay scallops semelparous reproductive cycle as well as effecting short-term mortality (Voyer 1992). Predation by visually oriented carnivores may be exerting selection pressures on populations of bay scallops resulting in shell color polymorphism (Elek and Adamkewicz 1990). Known parasites include the pea crab, *Pinnotheres maculatus* (Kruczynski 1972). Bay scallops parasitized by this organism display stunted growth rates and reduced weights. Another parasite is the polychaete *Polydora* which can penetrate bay scallop shells and sometimes produce blisters on the interior shell surfaces (Rhodes 1991).

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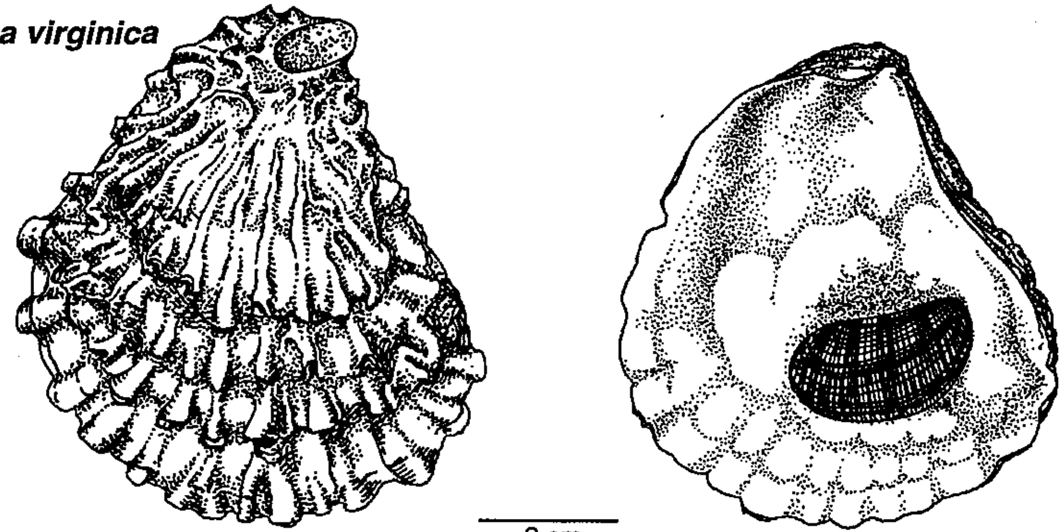
## American oyster

**_Crassostrea virginica_**
**Adult**



2 cm

(from Galtsoff 1964)

**Common Name**: American oyster
**Scientific Name**: *Crassostrea virginica*
**Other Common Names**: Eastern oyster (Turgeon et al. 1988), *huître creuse americaine* (French), *ostión americano* (Spanish) (Fischer 1978).
**Classification** (Turgeon et al. 1988)
Phylum: Mollusca
Class: Bivalvia
Order: Ostreoida
Family: Ostreidae

**Value**
Commercial: The American oyster has historically supported a valuable fishery throughout the Gulf of Mexico (Stanley and Sellers 1986). In 1993, 15,241 metric tons (mt) of oyster meat valued at $86.7 million were landed in the United States, and the Gulf region led in production with 9,072 mt of meats (O'Bannon 1994). Led by Louisiana, the Gulf region produced about 8,390 mt and nearly 41% of the national total during that year. Individual state harvests for the Gulf during 1992 have been compiled by Newlin (1993). The west coast of Florida ranked second in Gulf production with 1,571 mt harvested during that season. Alabama and Mississippi landings are typically small, but landings during 1992 were much higher than usual totaling 543 and 321 mt respectively. Louisiana led the Gulf states in production during that year with 5,015 mt of meats. In Texas, the harvest was about 936.7 mt. Harvest methods include hand picking, tonging from boats, and dragging or dredging from boats (Stanley and Sellers 1986). Most of the Gulf landings are from publically-owned oyster beds, but an estimated 30% of the harvest is from privately-leased beds (MacKenzie 1989). Oysters from restricted waters are sometimes moved to approved waters for depuration or further growth. Broken oyster shell, rangia shell, or limestone are sometimes used as substrate to enhance oyster settlement and growth in Florida and Louisiana (MacKenzie 1996). Commercial fishery regulations vary among the Gulf coast states, but all oysters harvested must measure at least three inches from hinge to mouth (GSMFC 1993, TPWD 1993a). A regional fishery management plan has been developed for this species (Berrigan et al. 1991).

Recreational: Oysters are often collected from approved areas for personal use by hand (cooning), tongs, or sport dredges. Recreational fishery regulations vary among the Gulf coast states, but a three inch minimum size limit generally applies, along with bag limits and closed seasons (GSMFC 1993, TPWD 1993b).

Indicator of Environmental Stress: Oysters are ideal for use as indicators of pollution due to their sessile, filter feeding life mode (NOAA 1989). Broutman and Leonard (1988) review the methodology and problems of water classification, predominantly based on fecal coliform bacteria, for shellfish throughout the Gulf of Mexico. The American oyster is often used for pesticide and petroleum by-product LD-50 analyses. It is used by NOAA's Status and Trends program and other state and federal agencies to monitor concentrations and accumulation of organic and metallic contaminants in the marine environment (Lytle and Lytle 1982, Morales-Alamo and Haven 1982, NOAA 1989, Wade 1989, Sericano et al. 1990, Alvarez et al. 1991, Palmer et al. 1993). In addition, shell thickness and condition is used to detect heavy metal pollution (Marcus et al. 1989). This species has also been used by the U.S. Environmental Protection Agency (EPA) to study the

Table 5.02. Relative abundance of American oyster in 31 Gulf of Mexico estuaries (Nelson et al. 1992, Van Hoose pers. comm.).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| | *Life stage* | | | | |
| Florida Bay | | | | | |
| Ten Thousand Islands | ○ | ○ | ○ | ○ | ○ |
| Caloosahatchee River | ◉ | ○ | ○ | ○ | ○ |
| Charlotte Harbor | ○ | ○ | ○ | ○ | ○ |
| Tampa Bay | ○ | ○ | ○ | ○ | ○ |
| Suwannee River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Apalachee Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Apalachicola Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| St. Andrew Bay | ○ | ○ | ○ | ○ | ○ |
| Choctawhatchee Bay | ○ | ○ | ○ | ○ | ○ |
| Pensacola Bay | ○ | ○ | ○ | ○ | ○ |
| Perdido Bay | √ | √ | √ | √ | √ |
| Mobile Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Mississippi Sound | ○ | ● | ○ | ● | ● |
| Lake Borgne | ○ | ○ | ○ | ○ | ○ |
| Lake Pontchartrain | ○ | ○ | ○ | ○ | ○ |
| Breton/Chandeleur Sounds | ◉ | ◉ | ◉ | ◉ | ◉ |
| Mississippi River | √ | √ | √ | √ | √ |
| Barataria Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Terrebonne/Timbalier Bays | ◉ | ◉ | ◉ | ◉ | ◉ |
| Atchafalaya/Vermilion Bays | ◉ | ◉ | ◉ | ● | ◉ |
| Calcasieu Lake | ○ | ○ | ○ | ○ | ○ |
| Sabine Lake | ○ | ○ | ○ | ○ | ○ |
| Galveston Bay | ◉ | ◉ | ● | ◉ | ◉ |
| Brazos River | na | na | na | na | na |
| Matagorda Bay | ○ | ○ | ○ | ○ | ○ |
| San Antonio Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Aransas Bay | ○ | ○ | ○ | ○ | ○ |
| Corpus Christi Bay | ○ | ○ | ○ | ○ | ○ |
| Laguna Madre | √ | √ | √ | √ | √ |
| Baffin Bay | | | | | |
| | A | S | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present
- na No data available

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

effects of bioaccumulation of toxic substances from dredge materials (Parrish et al. 1989). Rates of accumulation and depuration of mercury from the environment by this species have also been studied (Palmer et al. 1993).

Ecological: This species is important in providing reef habitats that serve as areas of concentration for many other organisms (Wells 1961, Bahr and Lanier 1981), as well as a food source for a variety of estuarine fish and invertebrates (Burrell 1986). Oysters form an important link between pelagic and benthic food webs by making available a portion of the organic material they filter as dense, mucus-bound biodeposits that can provide a food resource for benthic organisms (Newell 1988). Oysters and other molluscan suspension feeders may also act as a natural control against the adverse effects of eutrophication in estuaries by filtering out both inorganic and organic particles and limiting turbidity and phytoplankton blooms. This could enable greater light penetration through the water column, and benefit submerged aquatic vegetation. Thus, oysters can affect many aspects of an estuarine ecosystem (Kennedy 1991).

**Range**

Overall: The American oyster occurs from the Gulf of St. Lawrence to the Yucatan Peninsula of Mexico and to Venezuela. It is abundant in the estuaries along the coast of the Gulf of Mexico. Along the Atlantic coast, it is historically abundant in Chesapeake Bay and Long Island Sound (Burrell 1986, Stanley and Sellers 1986). Results of biochemical analyses suggest that four distinct races occur: Canadian, U.S. Atlantic, U.S. Gulf of Mexico, and Bay of Campeche (King and Gray 1989).

Within Study Area: Along the U.S. Gulf coast, this species occurs from Texas to Florida (Table 5.02). The estuaries of Louisiana and Texas east of Corpus Christi generally have the highest abundances. Recent evidence indicates two races occupying the Texas coast, with the upper Laguna Madre being the location of the transition zone (King and Gray 1989). It is not yet known if this is a race unique to the Texas coast, or the northernmost population of the Bay of Campeche race.

**Life Mode**

Eggs are planktonic. Larvae are meroplanktonic to benthic. Larvae are gregarious, enabling oysters to form extensive reefs over long periods of time. Juveniles (spat) and adults are sessile and benthic (Burrell 1986, Stanley and Sellers 1986).

**Habitat**

Type: All oyster life stages are estuarine, and can occur in coastal sounds, bays, and estuaries of the coastal

U.S. Egg, larval, juvenile, and adult stages all occur in mesohaline to euhaline environments in depths up to 10 m (Galtsoff 1964, Bahr and Lanier 1981, Burrell 1986). Price (1954) discusses the various development, shapes and location of oyster reefs with respect to shoreline, channels and distance from the Gulf. Reefs grow from the shoreline out; as a current is encountered the reef turns to a right angle and parallels the current, eventually turning back on itself. Other reefs grow parallel to channels. Oysters can grow and survive over a wide range of environmental conditions, but they are most successful when attached to firm substrate in areas where water circulation provides sufficient food (Berrigan et al. 1991). The preferred habitats are estuarine intertidal areas, shallow bays, other oyster shell and hard surfaces, mud flats and offshore sand bars (Butler 1954, Marshall 1954, Copeland and Hoese 1966, Menzel et al. 1966). The intertidal zone affords oysters some protection from predation by carnivorous gastropods and other common oyster predators (Marshall 1954). Wild populations of oysters need to be in the vicinity of freshwater discharges such as rivers, creeks, and bayous (Berrigan et al. 1991). These discharges provide food and dilute the higher salinity waters of the Gulf of Mexico. The resulting moderate salinity habitats that are created are necessary for successful oyster settling and growth, and provide protection from high salinity predators and disease.

Substrate: Hard, elevated substrates provide increased surface area on the bottom to help support oysters as they grow and prevent them from sinking into the sediment and smothering (Marshall 1954, Berrigan et al. 1991). Any type of hard substrate such as glass, rock, concrete, metal, wood, rubber, or shell is suitable for settlement of oyster spat (Burrell 1986, Berrigan et al. 1991). Oyster reefs are typically on hard bottoms, but individuals are also abundant on surrounding mud bottoms. Maximum setting occurs on horizontal surfaces (Clime 1976). Larvae do, however, show preference for established oyster beds, responding perhaps to pheromones, ammonia, or other metabolites released by adult oysters or to proteins on the surface of oyster shells (Hidu and Haskin 1971, Bahr and Lanier 1981, Fitt and Coon 1992). Harry (1976) demonstrated that the American oyster can thrive on bottoms consisting of 17 to 100% sand.

Physical/Chemical Characteristics: The American oyster is typically exposed to wide variation in environmental parameters (salinity, temperature, dissolved oxygen, etc.) in its estuarine habitat (Killam et al. 1992). Because of the oyster's tolerance of these fluctuations, the environmental requirements of this species are not readily defined with precision.

Temperature - Eggs and Larvae: Normal egg development occurs between approximately 18° and 30°C (Loosanoff 1965). Larval development occurs generally at >20°C (Burrell 1986) with maximal growth occurring between 30° to 32.5°C at salinities ranging from 7.5 to 27‰ (Davis and Calabrese 1964, Loosanoff 1965).

Temperature - Juveniles and Adults: Adults exist within the range of -2°C in New England to 36°C in the Gulf of Mexico. During low tide, the American oyster can withstand temperatures below freezing and above 49°C, but it typically stops feeding at 6°-7°C, and at 42°C most bodily functions cease or are greatly reduced (Galtsoff 1964). Normal growth occurs at temperatures ranging from 10° to 30°C or greater (Burrell 1986). There may be as many as three races of American oyster based on temperature regimes (Ahmed 1975). Buroker et al. (1979) found all oysters to be genetically equivalent, and Groue and Lester (1982) found the Laguna Madre oysters to be genetically distinct from four other Gulf populations. These racial distinctions may be reflected in spawning temperatures determined by Stauber (1950): Gulf of Mexico oysters spawn around 25°C (water temperatures must be consistently over 20°C and above 25°C for mass spawnings); there are two races on the East Coast that spawn at 16 and 20°C. Cake (1983) reports that Gulf oysters are not as tolerant of freezing as the East Coast race.

Salinity - Eggs and Larvae: Normal egg cleavage in Virginia waters occurs between 7.5 and 34‰ (meso-euhaline) with optimum development between 10 and 22‰ (Castagna and Chanley 1973). The optimum salinity for proper egg and larval development may be related to the salinity at which the adult gonads complete gametogenesis (Davis 1958, Loosanoff 1965). Egg and larval development from mesohaline adult populations (9-10‰) are optimum at approximately 10 to 15‰ (Davis 1958), with an upper limit of about 22‰ (Loosanoff 1965). Development of spawn from adults in polyhaline areas (26-27‰) is best at 23‰ for the eggs and 18‰ for the larvae (Davis 1958) with a tolerance of 15 to 35‰. In general, larvae are meso- to euhaline tolerating salinities between 5 and 39‰ (Castagna and Chanley 1973). Larval growth is usually limited at lower salinities (10‰) (Chanley 1957) with optimums, in most cases, at higher salinities (25-29‰) (Castagna and Chanley 1973). Spat setting is usually less at low salinities, with consistent settling occurring from 16‰ to 22‰, and peaking at 20‰ to 22‰ (Menzel et al. 1966, Chatry et al. 1983). Metamorphosis occurs between 5.6‰ and 35‰, with best spat growth between 13 to 30‰ (Chanley 1957, Castagna and Chanley 1973).

Salinity - Juveniles and Adults: The salinity requirements of oysters vary depending on geographic location, life cycle stage, and environmental parameters (Killam et al. 1992). Adults are euryhaline, tolerating meso- to euhaline waters (Galtsoff 1964, Burrell 1986). In Gulf of Mexico estuaries, they normally occur at salinities from 10 to 30‰, tolerating a range from 2 to 43.5‰ (Gunter and Geyer 1955, Copeland and Hoese 1966). Low salinities (0‰) may be tolerated for short periods of time (Loosanoff 1965) with optimum adult growth occurring from 14 to 30‰ (Castagna and Chanley 1973). Gunter (1953) reported high mortalities during spring floods in Mississippi Sound and Louisiana. This has also been reported for Mobile Bay (May 1972) and the Santee River, South Carolina (Burrell 1977). Oysters from the Laguna Madre of Texas tolerate higher salinities, growing and spawning in salinities greater than 40‰ (Breuer 1962). Eleuterius (1977) found salinities from 2 to 22‰ from areas of productive reefs. Salinity tolerance is inversely correlated to the surrounding water temperature (Berrigan et al. 1991). Higher water temperatures generally result in reduced tolerance to salinity. At temperatures below 5° C, oysters are tolerant of low salinity conditions, but will die after only a few days at the same salinity when the temperature is 15° C.

pH: pH can influence oyster reproduction and development (Berrigan et al. 1991). Normal egg development and larval growth occur between a pH of 6.75 to 8.75, with an optimum pH for larval growth between 8.25 to 8.50 (Calabrese and Davis 1966, Calabrese 1972). Optimum pH for spawning is 7.80, and the pH must be greater than 6.75 for successful recruitment to occur.

Dissolved oxygen (DO): Information on the DO requirements for the American oyster is limited (Killam et al. 1992). Oysters are facultative anaerobes, enabling them to withstand daily periods of low or no oxygen, but an oxygen debt builds up (Berrigan et al. 1991). In a laboratory experiment, the hourly oxygen consumption for six whole animals (including shell) was 39 ml/kg or 303 ml/kg of wet tissue weight (Hammen 1969). Survival for up to five days has been noted in oysters kept in water with <1 ppm DO content (Sparks et al. 1958). Larvae appear able to cope well aerobically with most low oxygen conditions through simple diffusive processes (Mann and Rainer 1990). The consumption rate of oxygen is a function of water salinity and temperature (Berrigan et al. 1991). In Mobile Bay, low oxygen conditions killed oysters and reduced the setting of spat in 1971 (May 1972).

Migrations and Movements: Since adults are sessile, their distribution is determined by settlement of larvae and subsequent survival of the spat. The planktonic larval stages are transported by tides and migrate vertically through the water column. Larvae aggregate near the surface on rising tides and near the bottom on falling tides, thus ensuring their wide dispersion and diminishing their chances of being swept out to sea. Plantigrade larvae are capable of crawling on substrates to determine suitability (Burrell 1986, Stanley and Sellers 1986). Spat and adults from restricted waters are often moved to leased lots in approved waters for depuration and/or to increase the abundance in that area for future harvests.

**Reproduction**

Mode: Adults exhibit protandry and protogyny, but are gonochoristic (Andrews 1979). True functional hermaphrodites occur in less than 1% of a given population. Young oysters are predominantly male; subsequent sex inversion with age increases the proportion of females (Loosanoff 1965, Bahr and Lanier 1981, Burrell 1986). The male releases sperm and a pheromone into the water column that can be detected by the females at the inhalent siphon, triggering the release of eggs for external fertilization (Andrews 1979).

Spawning: The reproductive state is dependent upon a number of factors, the most important of which is water temperature. Water temperature triggers the time of spawning, and the critical temperature varies with geographical location (Burrell 1986, Gauthier and Soniat 1989). In the Gulf of Mexico, the temperature must be constantly above 20°C for spawning, and above 25°C for mass spawning (Hopkins 1931, Ingle 1951, Bahr and Lanier 1981, Burrell 1986, Stanley and Sellers 1986, Gauthier and Soniat 1989). Along the lower part of Florida's west coast, spawning probably occur during all months except during periods of high or low temperature extremes (Killam et al. 1992). Peak spawning in this area probably occurs in the spring and fall months, with the fall being the more successful. In the northern Gulf of Mexico, spawning occurs from March to November (Butler 1954). Peaks occur in Louisiana in late May-early June and September-October (Pollard 1973, Gauthier and Soniat 1989). In Mississippi, spawning occurs from May to October with a peak in June (MacKenzie 1977). In south Texas, spawning occurs in all months except July and August because of high temperature (Copeland and Hoese 1966).

Fecundity: A single female can produce 15 to 114.8 million eggs in a single spawn; fecundity is generally proportional to the size of the female. Females may spawn several times within a season (Davis and Chanley 1955, Galtsoff 1964, Loosanoff 1965, Gauthier and Soniat 1989).

**Growth and Development**

Egg Size and Embryonic Development: Egg development is oviparous. Fertilized eggs are pear shaped (55-75 µm long and 35-55 µm wide), and contain numerous oil droplets. These droplets are important for providing energy and nutrients to the developing embryo. The eggs hatch 6 hours after fertilization at a temperature of 24°C, and progress through blastula and gastrula stages, developing into a trochophore larvae in 6 to 9 hours (Galtsoff 1964, Loosanoff 1965, Bahr and Lanier 1981, Burrell 1986, Lee and Heffernan 1991).

Age and Size of Larvae: Larvae remain in the water column 2 to 3 weeks after hatching, passing through several developmental stages (trochophore, prodissoconch I, prodissoconch II or pediveliger). The final larval stage, the eyed pediveliger, is approximately 300 µm in length. At this stage the larval oyster uses its eyespot and foot to find a suitable substrate for settlement. In Galveston Bay, Texas, setting was first seen about 2 months after spawning when the larvae were approximately 0.2 mm in length (Hopkins 1931). Upon attachment, the larval foot and eyespot are lost and the newly settled, sessile juveniles are referred to as spat (Ritchie and Menzel 1969, Palmer 1976, Manzi et al. 1977). Spat-fall on the Gulf coast typically occurs from March until mid-November (Hopkins 1931, Ingle 1951, Hopkins 1955).

Juvenile Size Range: Juveniles (spat) develop when larvae cement themselves to the substrate. Growth of spat varies with location of settlement site with an average monthly growth rate of approximately 1 to 4 mm (Palmer 1976, Manzi et al. 1977). Fastest growth for juveniles occurs during the first 3 months, and decreases as they increase in size (Bahr 1976). Functional gonads may be present at 2-3 months of age and a size of only 1 cm (Bahr and Lanier 1981).

Age and Size of Adults: In the Gulf of Mexico, sexual maturity may be reached as soon as 4 weeks after attachment (Menzel 1951), but generally 18 to 24 months is normal (Quast et al. 1988). Butler (1954) reports growth for the Gulf oysters to be approximately 50 mm/year. Gunter (1951) gives growth rates of 0.26-0.30 mm/day in the first 3 months, 60 mm in the first year, 90 mm in the second year, and 115 mm in the third year. Growth coefficients in Louisiana are highly variable, fluctuating from 0.42 to 0.86 mm/day (Gillmore 1982). Growth is greatest in August and September, after spawning when glycogen reserves are restored (Loosanoff and Nomejko 1949, Price et al. 1975). Mortality rates for adult oysters generally increase with their size and age (Quast et al. 1988). In the absence of predation and fishing, 98% of all individuals die before they reach 6 years of age with the lowest mortality occurring in salinities below 15‰ and even 10‰ (Hopkins 1955, Mackin 1961, Quast et al. 1988). The maximum adult size is approximately 300 mm.

**Food and Feeding**

Trophic Mode: Larvae are planktivorous with large umbo stage larvae able to ingest particles from 0.2 to 30 µm (Davis 1953, Guillard 1957, Loosanoff 1965, Bahr and Lanier 1981, Burrell 1986, Baldwin et al. 1989). Juveniles and adults are suspension filter feeders that filter large quantities of brackish water, and are particularly effective at removing particles around the 3-4 µm range (Haven and Morales-Alamo 1970, Stanley and Sellers 1986). The rate of filtration varies with water temperature, with the volume filtered almost 1500 times the volume of the oyster's body (Stanley and Sellers 1986, Berrigan et al. 1991).

Food Items: Food is obtained from suspended particles entering through the ventral inhalent siphon and passed to the gills. The particles are sorted in the gills, and large particles are rejected. The rejected material is voided as pseudofeces through the inhalent siphon (Barnes 1980). Larvae feed on microscopic algae and naked flagellates (Davis 1953, Guillard 1957, Loosanoff 1965, Bahr and Lanier 1981, Burrell 1986, Stanley and Sellers 1986). Naked flagellates are preferred by adults. Bacteria are sometimes consumed, presumably because they are attached to detritus particles, but bacteria are generally a minor component of the diet. Oysters have variable uptake of carbon from *Spartina alterniflora* crude fiber ranging from less than 1% in Chesapeake area to over 20% in the southeast region, primarily due to differences in crude fiber concentrations in the seston (Crosby et al. 1989).

**Biological Interactions**

Predation: Larvae are susceptible prey to a variety of filter feeders such as ctenophores, coelenterates, tunicates, barnacles, molluscs, and and fishes (Hofstetter 1977, Berrigan et al. 1991). Ciliated protozoans also prey on larvae, and are able to ingest as many as six larvae at a time. Among sessile oysters, the predatory oyster drill, *Thais haemastoma*, is responsible for the majority of mortalities in Louisiana, Mississippi and Alabama (Chapman 1959, Gunter 1979). In Mississippi, rocksnails can destroy up to 50% of the oysters on a productive reef, and up to 100% of the oysters on a nonproductive reef. It is also a serious predator in high salinity areas of Texas bays (Hofstetter 1977, Soniat et al. 1989). All sizes of oysters are potential prey for the rocksnail, but spat are particularly vulnerable (Butler 1954, Chapman 1959). A single snail can consume up to 4 spat per hour, or up to one adult oyster every 8 days (Butler 1954, Gunter 1979). Rocksnails open oysters by a combination of chemical dissolution of the shell and drilling (radular rasping) (Stanley and

Sellers 1986). Stone crabs are also major oyster predators in the Gulf of Mexico (Menzel and Hopkins 1956, Berrigan et al. 1991). In Louisiana, it was estimated that one stone crab could kill up to 219 oysters per year. In addition, the blue crab and smaller mud crabs (Xanthidae), prey on oyster spat and young thin-shelled oysters. The black drum is an important predator of oysters as well (Pearson 1929, Cave 1978, Cave and Cake 1980, Berrigan et al. 1991). Black drum will attempt to crush and consume any oyster that will fit in their pharyngeal apparatus. Large black drum (>900 mm TL) can consume oysters up to 112 mm in length, while smaller drum (<900 mm TL) consume oysters less than 75 mm. It has been estimated that black drum consume up to two oysters per day for every kilogram of body weight, and a single large drum can consume an average of up to 48 oysters per day. Other predators include the oyster leech (*Stylochus frontalis*), the lightning whelk (*Busycon contrarium*), the crown conch (*Melongena corona*), echinoderms, flat worms, cownose ray (*Rhinoptera bonasus*), southern eagle ray (*Mylibatis goodei*), Atlantic croaker, spot, toad fish (*Opsanus* sp.), sheepshead, pinfish, and striped burrfish (*Chilomycterus schoepfi*) (Hopkins 1955, Menzel et al. 1966, Hofstetter 1977, Cake 1983, Stanley and Sellers 1986, Berrigan et al. 1991).

Factors Influencing Populations: Salinity is probably the single most important factor that influences the distribution and abundance of estuarine organisms (Copeland and Hoese 1966, Berrigan et al. 1991), and this is particularly important with respect to oysters. Droughts can increase salinities over oyster reefs and contribute to higher mortality due to increased numbers of high salinity, stenohaline oyster predators (Gunter 1955, Cake 1983, Lowery 1992). High mortality due to prolonged exposure to lowered salinities can occur during episodes of heavy flooding from storm events (Gunter 1953, May 1972, Burrell 1977, Hofstetter 1977, Soniat et al. 1989, Berrigan et al. 1991). Some flooding is beneficial because it maintains low levels of *Perkinsus marinus* infection (Soniat et al. 1989), and excludes marine predators and parasites (Hofstetter 1977) by keeping salinities low. Increased salinities in estuaries due to a reduction of freshwater inflow have caused oysters beds to relocate toward the headwaters of estuarine basins to more favorable salinities (Berrigan et al. 1991). Since this shift in location has occurred over a relatively short period of time, these areas lack extensive reefs for larval settlement. Oysters are also more prone to mortalities from freshwater flooding events in these areas. Another problem is that these locations are closer to areas of human habitation where sanitary conditions can become compromised, and other pollutant-related diseases and mortality will occur.

Hurricanes, tropical storms, and flooding can have both positive and negative effects on oyster populations in Gulf of Mexico estuaries (Berrigan et al. 1991, Lowery 1992). Hurricanes impact oyster production through several mechanisms. They can destroy reef integrity, remove live oysters and shell cultch, cause sedimentation that buries reefs, increase current velocity causing scouring and abrasion, and bring freshets into the estuary that drop salinities to lethal levels. The severity of the damage may be affected by local tidal conditions, proximity to the storm, wave surge, rainfall and other climatological factors. Runoff from storm events, along with dredge and fill activities and effluent discharges, can also increase turbidity and sedimentation in the aquatic environment (Killam et al. 1992). This can lead to silt settling out over oyster spat and inhibiting normal growth. This sedimentation also results in a soft muddy habitat that is undesirable for spat settlement. Currents are necessary for removal of feces and pseudofeces to prevent burial of the oyster reef. However, turbulent currents that carry sand or pebbles can damage oysters by eroding shell surfaces. Suspended solids may clog gills and interfere with filter feeding and respiration. If covered with sediment, oysters can die within a week (Stanley and Sellers 1986). Despite initial mortality resulting from hurricanes, long-term oyster production may be enhanced by the subsequent destruction of high-salinity predators and diseases, and the scouring of extant reefs making more clean shell available for spat settlement.

The loss of suitable habitat is probably the most important factor in the decline of oyster populations in the Gulf of Mexico (Berrigan et al. 1991). Reef substrate which is necessary for spat settlement is removed during harvest, and fossil reefs are mined for shell material. The continuing development of Gulf coastal areas is resulting in habitat areas being filled or dredged to accommodate human needs. Spoil banks from dredging projects modify the bottom morphology of bay bottoms and alter current patterns causing conditions that can result in mortality (Hoese and Ancelet 1987). Freshwater inflow into estuaries has been reduced due to the damming of rivers, leveeing of rivers preventing overflow into surrounding marshes, channelization, pumping for redistribution, and other construction projects that alter salinity regimes, reduce available nutrients, and allow the influx of predators. Development of coastal areas has also led to increased pollution and pollution-related mortality (Menzel et al. 1966, Berrigan et al. 1991). The development of power equipment for commercial oyster harvest has increased the potential for depleting and damaging oyster beds (Stanley and Sellers 1986).

Individuals of this species in high salinity areas are more susceptible to disease infection by the pathogenic protozoan, dermo (*Perkinsus marinus*) (Hofstetter 1977, Soniat et al. 1989, Berrigan et al. 1991, Killam et al. 1992). Dermo interferes with growth and reproduction, and is associated with, and primarily responsible for, annual losses of 10% to 50% of the market oysters. Water temperature is an important factor in controlling the occurrence and effects of this organism. Reproduction of dermo is drastically lowered in water temperatures below 20°C, and warm water temperatures during the summer months may promote it. The ectoparasitic gastropod, *Boonea impressa*, which infests the American oyster, is also capable of transmitting dermo from one oyster to another (White et al. 1987). Troublesome boring organisms reduce the market value, as well as consume energy in shell growth and repair. The most common of these are *Cliona*, the boring sponge, and *Diplothyra smithii*, the boring clam. Oysters infested with burrowing clams and sponges have been indicated to be much more susceptible to predation by black drum and possibly other predators because of weakened shells (Cave 1978). Intertidal oysters, because of their slower growth, thicker shells, and less relative time underwater, seem to be less susceptible to this predation than subtidal oysters. Blooms of red tide are another source of natural mortality. High concentrations (500 cells/ml) of this diatom, *Colchlodinium heterolobatum*, can kill oyster larvae (Killam et al. 1992). The oyster crab (*Pinnotheres* sp.) sometimes lives in the mantle cavity of the oyster where it may cause damage to the gills (Stanley and Sellers 1986).

The American oyster also competes for space and food with other organisms. Competitors include bryozoans (*Conopeum commensale*), barnacles (*Balanus* sp.), slipper shells (*Crepidula* sp.), hooked mussel (*Ischadium recurvum*), jingle shells (*Anomia* sp.), anemones, serpulid worms (*Eupomatus dianthus*), tunicates, and algae (Marshall 1954, Schlesselman 1955, MacKenzie 1970, Berrigan et al. 1991). The impact of competition for settlement space in the Gulf of Mexico has not been fully determined (Berrigan et al. 1991), but heavy sets of barnacles can seriously reduce the area of hard surface available to settling oysters (Ingle 1951). Young oysters can also be smothered by the excreta from polychaete worms (*Polydora* sp.) (Stanley and Sellers 1986). In some cases, these organisms have a purely commensal relationship with oysters, or do not seriously compete with them (Stanley and Sellers 1986, Berrigan et al. 1991).

**Personal communications**

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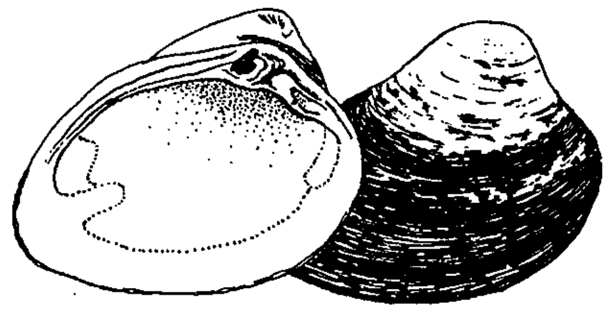
## Atlantic rangia

***Rangia cuneata***
**Adult**



2 cm

(from Fischer 1978)

**Common Name:** Atlantic rangia
**Scientific Name:** *Rangia cuneata*
**Other Common Names:** common rangia (Nelson et al. 1992); marsh clam (Burdon 1978); brackish water clam, road clam, wedge clam (LaSalle and de la Cruz 1985).
**Classification** (Turgeon et al. 1988)
Phylum: Mollusca
Class: Bivalvia
Order: Veneroida
Family: Mactridae

### Value

Commercial: The Atlantic rangia has been utilized for several thousand years along the Gulf coast, beginning with the Native Americans who made this clam a part of their diet (Tarver 1972, Tarver and Dugas 1973, LaSalle and de la Cruz 1985). The commercial value of this clam in now mainly in the use of its shell (both fresh and fossil) in the manufacture of cement, glass, chemicals, chicken and cattle feed, wallboard and other building products, agricultural lime, road construction and as fill in nearshore oil exploration (Tarver and Dugas 1973, Arndt 1976, Fischer 1978). Rangia shell is also used as substrate to enhance oyster settlement in Florida and Louisiana (MacKenzie 1996). Rangia are sometimes used for blue crab bait and some human consumption (Godcharles and Jaap 1973, LaSalle and de la Cruz 1985). Preparations include chopped clam dishes, chowders, soups, and either raw on the half shell, or steamed with rice dishes (Fischer 1978). It has also been canned occasionally for food products (Pfitzenmeyer and Drobeck 1964, Tarver and Dugas 1973). Hand-collected rangia are sometimes brought to cannery processors and added to hard clam catches (Fischer 1978).

Recreational: Recreational harvest of Atlantic rangia is not significant in Gulf of Mexico estuaries.

Indicator of Environmental Stress: The Atlantic rangia filter feeds on detritus, and is therefore susceptible to the accumulation of pollutants from the particles on which they feed. Because of this, they are commonly used for tests of toxicity and bioaccumulation of petroleum products and by-products (Neff et al. 1976, Morales-Alamo and Haven 1982, Ferrario et al. 1985, Jovanovich and Marion 1985, Bender et al. 1986), organochlorine insecticides (Lunsford and Blem 1982), dioxins and furans from pulp mill effluent (Harrel and McConnell 1995), and heavy metals (Olson and Harrel 1973, Lytle and Lytle 1982, McConnell and Harrel 1995). They have been used in the past to monitor radionuclides from radioactive debris resulting from atmospheric testing of nuclear weapons (Wolfe 1967, Wolfe and Schelske 1969).

Ecological: The Atlantic rangia is an important component of estuarine ecosystems, and can account for a large portion of the benthic biomass in estuaries (Cain 1975, LaSalle and de la Cruz 1985). This species is linked to primary producers and secondary consumers in estuarine areas, because they convert detritus and phytoplankton into biomass which can be utilized by many fishes, birds, and crustaceans (Tenore et al. 1968, Hopkins and Andrews 1970, Cain 1975, Olsen 1976a, LaSalle and de la Cruz 1985).

### Range

Overall: The Atlantic rangia occurs along the U.S. Atlantic coast and in the Gulf of Mexico. Although there is an extensive range for this species in the fossil record, the present day range is more limited. Along

Table 5.03. Relative abundance of Atlantic rangia in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | | | | | |
| Ten Thousand Islands | | | | | |
| Caloosahatchee River | ● | ● | ● | ● | ● |
| Charlotte Harbor | ● | ● | ● | ● | ● |
| Tampa Bay | ● | ● | ● | ● | ● |
| Suwannee River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Apalachee Bay | ○ | ○ | ○ | ○ | ○ |
| Apalachicola Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| St. Andrew Bay | ○ | ○ | ○ | ○ | ○ |
| Choctawhatchee Bay | ○ | ○ | ○ | ○ | ○ |
| Pensacola Bay | ○ | ○ | ○ | ○ | ○ |
| Perdido Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Mobile Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Mississippi Sound | ○ | ○ | ○ | ○ | ○ |
| Lake Borgne | ◉ | ◉ | ◉ | ◉ | ◉ |
| Lake Pontchartrain | ◉ | ◉ | ◉ | ◉ | ◉ |
| Breton/Chandeleur Sounds | ○ | ○ | ○ | ○ | ○ |
| Mississippi River | ○ | ○ | ○ | ○ | ○ |
| Barataria Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Terrebonne/Timbalier Bays | ◉ | ◉ | ◉ | ◉ | ◉ |
| Atchafalaya/Vermilion Bays | ○ | ○ | ○ | ○ | ○ |
| Calcasieu Lake | ○ | ○ | ○ | ○ | ○ |
| Sabine Lake | ● | ● | ● | ● | ● |
| Galveston Bay | ◉ | ◉ | ◉ | ◉ | ○ |
| Brazos River | na | na | na | na | na |
| Matagorda Bay | ○ | ○ | ○ | ○ | ○ |
| San Antonio Bay | √ | √ | √ | √ | √ |
| Aransas Bay | √ | √ | √ | √ | √ |
| Corpus Christi Bay | √ | √ | √ | √ | √ |
| Laguna Madre | | | | | |
| Baffin Bay | | | | | |
| | A | S | J | L | E |

*Life stage*

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present
- na No data available

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

the Atlantic coast, the Atlantic rangia is found from Chesapeake and Delaware Bays southward to Indian River, Florida. In the Gulf of Mexico, the Atlantic rangia is found from southwestern Florida to Texas, and to Alvarado, Veracruz, Mexico (Hopkins and Andrews 1970, Andrews 1981, Godcharles and Jaap 1973, Fischer 1978, Fritz et al. 1990).

Within Study Area: Along the U.S. Gulf coast, this species is found from the Corpus Christi Bay area to southwestern Florida, and is concentrated in brackish waters of Louisiana, particularly around Lake Pontchartrain, Maurepas, and Vermilion Bay (Table 5.03) (Tarver 1972, Tarver and Dugas 1973, Andrews 1981, LaSalle and de la Cruz 1985). It is not common in the south Florida and south Texas estuaries, which have relatively high salinities (Nelson et al. 1992).

**Life Mode**

Eggs and larvae are known to have a brief planktonic and pelagic existence (Fairbanks 1963, LaSalle and de la Cruz 1985). Juveniles and adults are semi-sessile estuarine benthic infauna capable of burrowing through sediments, and they typically have only a small portion of the shell protruding from the substrate. Juveniles and adults are generally restricted to shallower water along bay margins, presumably due to the concentration of free-swimming larvae by wave action where the metamorphosis to a benthic existence occurs.

**Habitat**

Type: All stages are found in river-influenced brackish water (riverine-oligohaline) and in subtidal oligohaline to polyhaline estuarine waters. This clam prefers a combination of low salinity, high turbidity, and a substrate of sand, mud and vegetation (LaSalle and de la Cruz 1985).

Substrate: Juvenile and adult stages occur in soft sediments of sand and mud (Tarver 1973, Godcharles and Jaap 1973, LaSalle and de la Cruz 1985). Larger sized Atlantic rangia tend to inhabit sandy bottom areas, suggesting that larger sized particles trap more food; sandy substrates facilitate burrowing, and excretory products do not accumulate (Tarver and Dugas 1972). Sandy sediments of high organic content and phosphate are more favorable for growth and survivorship than silt/clay sediments that are also high in organic matter and phosphate (Tenore et al. 1968). There is also evidence that larvae settle preferentially in sandy versus silty substrate, and that they prefer substrate with some organic content (Sundberg and Kennedy 1993). In the Trinity River delta, Texas, *Rangia* is found in soft mud-clay-silt substrates (Baldauf 1970). The sediments that *Rangia* resides in can result in shell erosion and ultimate mortality because of the presence of acids formed in the breakdown of detritus. Fairbanks (1963) noted substantial shell erosion of rangia along the north shore of Lake Pontchartrain, due to the presence of carbonic acids produced by carbon dioxide reacting with high concentrations of organic matter.

Physical/Chemical Characteristics:
Temperature: Optimum conditions for embryos studied in the laboratory are 18°-29°C (Cain 1973). The planktonic existence of larvae is greatly extended by low temperatures; larvae at survive 8° to 32°C, and growth is fastest at 20° to 32°C (Cain 1973, Cain 1974, LaSalle and de la Cruz 1985). Temperatures above 35°C are known to be lethal to larvae. Survival has been observed at temperatures as high as 40°C for small and medium sized animals acclimated to summer conditions (Lane 1986). The upper lethal limit (LT50) for large individuals was 38°C. A temperature of 36°C will begin causing mortalities after 3 days.

Salinity: Embryos and larvae cannot tolerate pure fresh water (0‰) (Cain 1972, Cain 1973, Cain 1974). Optimal salinities for embryos range from 6 to 10‰, with eggs surviving as low as 2‰. Larvae survive in salinities ranging from 2 to 20‰, and growth is fastest at 10 to 20‰. Juvenile and adult Atlantic rangia can tolerate a wide range of salinities, generally from 0 to 25‰, and have reported to be capable of living in fresh water (<0.3‰) for a period of at least 7 months (Hopkins and Andrews 1970) by osmoregulating with inorganic and intracellular free amino acids to control cell volumes (Anderson 1975, Otto and Pierce 1981). Uptake of osmotically active glycine from the environment increases as salinity increases, and when salinities drop below 5‰, the glycine is rapidly converted into protein. Spawning becomes physiologically impossible if salinities are <1‰ or >15‰ for long periods (Otto and Pierce 1981).

Dissolved Oxygen (DO): This species is tolerant of temporary anoxic conditions (LaSalle and de la Cruz 1985, Lane 1986). Individuals have survived a maximum of 6.5 days in waters with 0 ppm oxygen; however, they are intolerant of exposure to air.

Movements and Migrations: Planktonic egg and larval stages may be transported by tidal and river currents. Larvae are presumed to be negatively phototropic and are expected to be associated with the bottom of shallow bay margins. Juveniles and adults are sedentary with only the posterior end and siphons slightly exposed, and limited capability of vertical movement through the sediments. Captive specimens have been observed to only move toward the sediment surface when covered by sand (Fairbanks 1963). Attached organisms (barnacles, mussels and algae) indicate a stationary position for long periods of time (Fairbanks 1963, LaSalle and de la Cruz 1985). Although juveniles and adults do not migrate, they are easily transported by shifting water currents because of their small mass (LaSalle and de la Cruz 1985).

**Reproduction**
Mode: Reproduction is primarily sexual with separate sexes (gonochoristic), but there are rare cases of hermaphroditism (Olsen 1976b). Fertilization is external with the gametes released directly into the water.

Spawning: The initiation of gametogenesis in the spring and early summer is typically triggered by a rise in water temperature to approximately 10°-16°C (Cain 1975, Jovanovich and Marion 1985). Fairbanks (1963) identified two distinct periods of spawning per year in Louisiana; a spring spawn (March-May) and a less intense period from late summer to November. In most areas *Rangia* spawn from March to May and late summer to November, but it may be continuous from March to November. Wolfe and Petteway (1968) found spawning to occur from July to November with a peak in September in North Carolina. Ripe gametes have been reported July through November in Florida (Olsen 1976b) and from early summer through October with fall peaks in Alabama (Jovanovich and Marion 1985). Heavy spawning is associated with a rapid increase or decrease in salinity of approximately 5‰ (Cain 1975). Spawning has also been stimulated in the laboratory at other temperatures and salinities by adjusting water conditions and introducing male gametes (Chanley 1965, Cain 1973). Gametes are released through the exhalent siphon by both sexes (Sundberg and Kennedy 1992).

Fecundity: There is little available information on fecundity of Atlantic rangia (LaSalle and de la Cruz 1985).

**Growth and Development**
Egg Size and Embryonic Development: Egg development is oviparous. In laboratory studies, fertilized eggs (69 µm) have developed into ciliated blastulae 3 hours after fertilization (AF), and into pelagic trochophore larvae by 12 hours AF at 23° to 26°C (Fairbanks 1963, Sundberg and Kennedy 1992). A similar study by Fairbanks (1963) described these developmental stages as occurring in older larvae than Sundberg and Kennedy (1992) despite their being reared at the same temperature. This may have been due to his use of stripped eggs and sperm instead of naturally spawned gametes (Sundberg and Kennedy 1992).

Age and Size of Larvae: The length of the larval period is dependent on temperature and food, but generally is short lived (Fairbanks 1963). In a laboratory study, trochophore larvae developed to the veliger stage (93 µm) in 8 hours. Shelled larvae develop within 24 hours of fertilization (Chanley 1965, Sundberg and Kennedy 1992). Larval sizes range from 75-203 µm depending on the specific stage. These stages are extremely fragile and may not be picked up in normal larval sampling efforts.

Juvenile Size Range: In laboratory studies, larval settlement and metamorphosis to the juvenile stage occurred after 6 or 7 days at a size of 175-180 µm (Chanley 1965, Sundberg and Kennedy 1992, Sundberg and Kennedy 1993). Field studies, however, indicate a size at settlement of 300-400 µm (Fairbanks 1963, Cain 1975). Growth of juveniles is 15-20 mm in the first year, 5-9 in the second and 4-5 in the third year (Fairbanks 1963). The growth rate of Atlantic rangia can be significantly inhibited by suspended solids above the substratum, and suspended solids tend to influence growth more so than the actual substrate (Fairbanks 1963).

Age and Size of Adults: Size at sexual maturity ranges from 14 mm (Cain 1972) to 24 mm (Fairbanks 1963) in length, and is reached in 2-3 years (Fairbanks 1963). A maximum length of 7 cm has been recorded, and sizes to 5 cm are common (Fischer 1978). A confirmed life span for this species has not been determined (LaSalle and de la Cruz 1985). Estimates range from 4-5 years to a maximum of 15 years.

**Food and Feeding**

Trophic Mode: This species is a nonselective filter feeder. It controls food movement with the gill palps and ciliary currents over the gills (Darnell 1958, Olsen 1976a, LaSalle and de la Cruz 1985).

Food Items: Food of the Atlantic rangia consists of diatoms, algae and detritus, with detritus comprising the greatest portion (Darnell 1958, Olsen 1976a, LaSalle and de la Cruz 1985).

**Biological Interactions**

Predation: Atlantic rangia are preyed upon by fish, crustaceans, molluscs, and ducks (LaSalle and de la Cruz 1985). This species appears to be important to the diet of the migratory ducks, such as lesser scaup duck (*Aythya affinis*), greater scaup duck (*Aythya marila*), ring-neck duck (*Aythya collaris*), American black duck (*Anas rubripes*), mallard (*Anas platyrhynchos*), and the ruddy duck (*Oxyura jamaicensis*), and may be replaced in their diet under more saline conditions by the dwarf surfclam (*Mulinia lateralis*) (Tarver and Dugas 1973, LaSalle and de la Cruz 1985). Fishes that are known to prey on rangia include Atlantic stingray (*Dasyatis sabina*), spotted gar (*Lepisosteus oculatus*), alligator gar (*L. spatula*), longnose gar (*L. osseus*), gizzard shad, hardhead catfish, blue catfish (*Ictalurus furcatus*), freshwater drum (*Aplodinotus grunniens*), spot, Atlantic croaker, black drum, sheepshead, pinfish, striped blenny (*Chasmodes bosquianus*), southern flounder, and sand seatrout. Invertebrate predators include white shrimp, Ohio shrimp (*Macrobrachium ohione*), blue crab, Harris mud crab (*Rhithropanopeus harrisii*), moon snails (*Polinices* species), and oyster drill (*Thais haemastoma*) (Darnell 1958, Tarver and Dugas 1973, Levine 1980, LaSalle and de la Cruz 1985). A potential predator of Atlantic rangia larvae are ctenophores, such as *Mnemiopsis*, which sometimes are abundant in estuarine waters (LaSalle and de la Cruz 1985).

Factors Influencing Populations: Winter kills in the northern portion of the Atlantic rangia's range indicate that it has reached the limit of its temperature tolerance there (LaSalle and de la Cruz 1985). Sporocysts and cercarial larvae, intermediate trematode stages of the fish intestinal parasite *Cercaria rangiae*, have been described from *Rangia* in Galveston Bay, Texas (Wardle 1983); sporocysts concentrate in the gonadal tissue of the clam causing castration. Anthropogenic changes in river discharge patterns can result in flow regimes that can either enhance *Rangia* populations or cause their declines (Harrel 1993). Channelization of rivers may result in saltwater intrusions that produce favorable brackish water conditions in what was once a freshwater habitat. Increased reservoir discharges into a river can flush saltwater from an estuary, reducing *Rangia* abundance. Waste discharge into rivers can create toxic or anoxic conditions that also adversely affect *Rangia*.

**Personal communications**

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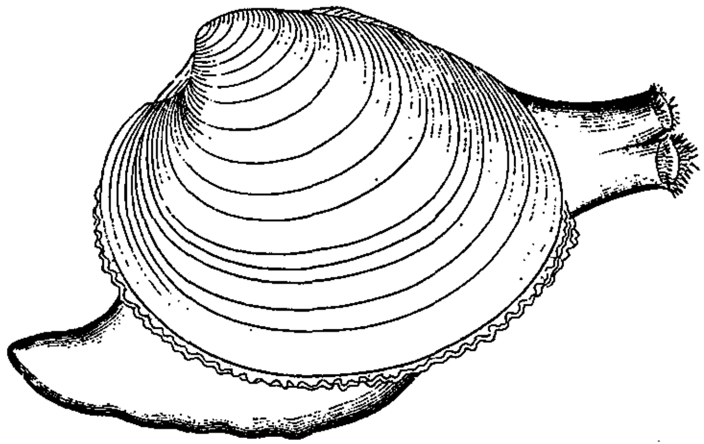
***Mercenaria* species**
**Adult**




(from Goode 1884)

**Common Name:** hard clam
**Scientific Name:** *Mercenaria* species
**Other Common Names:** Quahog, hard-shelled clam, littleneck, cherrystone clam, chowder clam (Stanley 1985); *praire du sud* (French), *almeja del sur* (Spanish) (Fischer 1978). *Mercenaria mercenaria* is known as northern quahog, and *M. campechiensis* as southern quahog (Turgeon et al. 1988). Andrews (1979) refers to *M. campechiensis* as southern quahog, and subspecies *M. campechiensis texana* as Texas quahog.
**Classification** (Turgeon et al. 1988)
Phylum: Mollusca
Class: Bivalvia
Order: Veneroida
Family: Veneridae

**Value**
Commercial: Although hard clams support a significant commercial fishery in the United States as a whole, the gulf coast of Florida supports only a very limited hard clam fishery (Schroeder 1924, Taylor and Saloman 1969). There was a substantial fishery in Florida's Ten Thousand Islands until the 1930's, and clams were taken to Key West for canning (Schroeder 1924, Marelli pers. comm.). During 1992, 27.7 metric tons (mt) of hard clam meat valued at $64,000 was landed on Florida's Gulf coast (Newlin 1993). No landings are reported for other Gulf coast states. The season for clams harvested in Florida is regulated, and harvest is restricted to approved shellfish areas (GSMFC 1993). Dredges can be used for harvest on private leases after posting a $3000 bond and securing a Special Activity License. The minimum allowable harvest size for clams is 7/8 inch (2.22 cm). In Texas, a commercial mussel and clam fisherman's license is required to commercially harvest hard clams (TPWD 1993). Harvest is open year-round, but only from water approved by the State Commissioner of Health. The traditional and most popular method of harvesting hard clams has been by rakes or tongs (Eversole 1987). In North Carolina, they are harvested by "kicking" which uses the wash from a boat propeller to dislodge clams from the substrate. An otter trawl is towed behind the boat to collect the clams.

Recreational: Hard clams are sometimes taken for home consumption by recreational fishermen. There is a significant recreational fishery for hard clams in the Tampa Bay area (Kunneke and Palik 1984, Killam et al. 1992). The bag limit in Florida is two bushels per person or boat (whichever is less) per day (GSMFC 1993, Arnold pers. comm). Harvesting is done mostly by hand picking or treading.

Indicator of Environmental Stress: Hard clams, like other bivalves, are used to study the uptake and bioaccumulation of heavy metals and toxic organic chemicals (Boehm and Quinn 1977, Moore 1985, Byrne 1989, Laughlin et al. 1989, Long et al. 1991). Because of their filter feeding life mode and benthic habitat, the presence of such compounds in clam tissues can be indicative of poor water quality and environmental stress (Eversole 1987). Evidence of past geologic events can be traced through fossil shell remains (Parker 1955, 1956).

Ecological: Hard clams provide a food source to bottom feeding fishes and invertebrates. Their larval stages also provide food for larval and early juvenile fishes. Through their suspension feeding activities hard clams help to transfer phytoplankton primary productivity to the higher trophic levels within the

Table 5.04. Relative abundance of hard clam in 31 Gulf of Mexico estuaries (Nelson et al. 1992, Marelli pers. comm.).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | | | | | |
| Ten Thousand Islands | O | O | O | O | O |
| Caloosahatchee River | | | | | |
| Charlotte Harbor | O | O | O | O | O |
| Tampa Bay | O | O | ◉ | O | O |
| Suwannee River | O | O | O | O | O |
| Apalachee Bay | O | O | O | O | O |
| Apalachicola Bay | | | | | |
| St. Andrew Bay | O | O | O | O | O |
| Choctawhatchee Bay | O | O | O | O | O |
| Pensacola Bay | | | | | |
| Perdido Bay | O | √ | √ | √ | √ |
| Mobile Bay | √ | √ | √ | √ | √ |
| Mississippi Sound | O | O | O | O | O |
| Lake Borgne | | | | | |
| Lake Pontchartrain | | | | | |
| Breton/Chandeleur Sounds | O | O | O | O | O |
| Mississippi River | | | | | |
| Barataria Bay | O | O | O | O | O |
| Terrebonne/Timbalier Bays | √ | √ | √ | √ | √ |
| Atchafalaya/Vermilion Bays | | | | | |
| Calcasieu Lake | | | | | |
| Sabine Lake | | | | | |
| Galveston Bay | O | O | O | O | O |
| Brazos River | na | na | na | na | na |
| Matagorda Bay | O | O | O | O | O |
| San Antonio Bay | O | O | O | O | O |
| Aransas Bay | O | O | O | O | O |
| Corpus Christi Bay | O | O | O | O | O |
| Laguna Madre | | | | | |
| Baffin Bay | | | | | |
| | A | S | J | L | E |

*Life stage* (columns)

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- O Common
- √ Rare
- blank Not present
- na No data available

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

estuarine food web (Eversole 1987).

**Range**

Overall: *Mercenaria campechiensis* occurs from Cape May, NJ, to the Yucatan Peninsula, most abundantly on Florida's Gulf coast. Populations inhabiting the muddier environments of the northern Gulf of Mexico are now recognized under the subspecific name *M. campechiensis texana* (Dillon and Manzi 1989b). *Mercenaria mercenaria* naturally ranges from Prince Edward Island, Canada, to the Atlantic coast of Florida, intertidally and subtidally to 15 m in estuaries and bays. It generally inhabits shallower waters of lower salinity than *M. campechiensis*. A hybrid zone between the two species occurs in the Indian River lagoon on Florida's Atlantic coast (Dillon and Manzi 1989a, Bert et al. 1993, Bert and Arnold 1995). Although probably not native to the Gulf of Mexico, *M. mercenaria* may have been locally introduced by aquaculture interests (Dillon pers. comm.). Populations of hard clams have also been introduced to the British Isles, parts of France, and California (Taylor and Saloman 1968, Abbott 1974, Kunneke and Palik 1984, Eversole 1987).

The most reliable physical character distinguishing *M. mercenaria* from *M. campechiensis* through most of their range is the strength of the ridges on their shells. *M. mercenaria* typically has thin, easily-eroded ridges, best adapted for life in silty mud. *M. campechiensis* has thick, resistant ridges, that seem adapted for coarse substrates, especially carbonate sands. A subspecies *M. campechiensis texana* has been described from the northern Gulf of Mexico, which unlike typical *M. campechiensis*, has thin ridges (Dillon pers. comm.). This makes sense, as the northern Gulf contains substantial areas of silty mud substrate. However, these clams are considered a subspecies of *M. campechiensis*, in spite of their external morphological similarities to *M. mercenaria*.

Within Study Area: Within U.S. estuaries of the Gulf of Mexico, *M. campechiensis* is found from south Florida to Texas. Hard clams are widely distributed, but not generally abundant in the nearshore waters of the Gulf coast states (Table 5.04).

**Life Mode**

Hard clam eggs and early larval stages are planktonic. The last larval stage (plantigrade) is semi-benthic alternating between swimming and crawling in search of a suitable settlement site. Juveniles and adults are semi-sessile benthic infauna capable of burrowing through sediments (Eversole 1987).

**Habitat**

Type: All life stages are estuarine or marine. Hard clams usually occur in dense groups in coastal bays, sounds, and estuaries from intertidal zones to a depth of 15 m or more. Although they occur in the open ocean, hard clams appear to prefer relatively shallow waters (Killam et al. 1992). They are typically found in waters less than 10 m deep (Sims and Stokes 1967, Taylor and Saloman 1970, Godcharles and Jaap 1973a, Godcharles and Jaap 1973b, Killam et al. 1992). Hard clams have been collected from grass flats on the shoreward side of barrier islands (Christmas and Langley 1973, Craig and Bright 1986), and near oyster reefs (Swingle 1971). In northern latitudes, *Mercenaria campechiensis* may generally occur in deeper waters with higher salinities (Eversole 1987) than does *M. mercenaria*.

Substrate: Substrate appears to play an important role in distribution and growth (Wells 1957, Craig and Bright 1986, Coen and Heck 1991). Late larval stages attach to hard substrates with byssal threads. If no hard substrate is available, they attach to sediment particles. Juvenile and adult clams occur primarily in soft bottom habitats of mud and sand. In one laboratory experiment, settling pediveligers were reported to prefer sand particles over mud (Keck et al. 1974). Highest natural densities of clams occur in sand with coarse shell sediments, which provide spatial refugia so that the juvenile clams are better protected from predation (Wells 1957, Walker et al. 1980, Craig and Bright 1986, Killam et al. 1992). Overall, hard clams can utilize a variety of unconsolidated substrates: firm sand, silty sand, sand/mud, sand/shell, sand/gravel, mud/sand/gravel, and frequently near seagrasses and algae. Hard clams are rare on fine silt and clay bottoms (Pratt 1953, Saloman and Taylor 1969, Taylor and Saloman 1970, Godcharles and Jaap 1973a, Godcharles and Jaap 1973b, Kunneke and Palik 1984).

Physical/Chemical Characteristics:
Temperature - Eggs and Larvae: Spawning occurs generally from 22° to 30°C, with maximum spawning activity found between 24° to 26°C (Loosanoff 1937c, Carriker 1961). Egg survival is high between 18° and 28°C (Kennedy et al. 1974, Wright et al. 1983). Egg mortality at low (15°C) and high (33°C) temperatures may be reduced through acclimation (Loosanoff et al. 1951). Larvae can tolerate temperatures ranging from approximately 13° to greater than 30°C with growth rates increasing with an increase in temperature (Loosanoff et al. 1951, Davis and Calabrese 1964, Wright et al. 1983). Maximum larval growth generally occurs between 22° and 33°C depending on the salinity (Davis and Calabrese 1964, Lough 1975). The range of temperatures tolerated by larvae is reduced as salinity decreases (Eversole 1987). As temperatures approach 40°C larval mortality increases (Wright et al. 1983).

Temperature - Juveniles and Adults: Juveniles and adults can tolerate temperature extremes ranging from <0° to greater then 35°C (Eversole 1987). The upper lethal temperature of the hard clam is 45.2°C (Henderson 1929), but temperatures above 30°C may alter clam behavior and physiology (Savage 1976, Van Winkle et al. 1976). Growth is negligible at <10°C and increases with rising temperatures to an optimum of about 20° to 23°C (Pratt and Campbell 1956). Optimum growth temperatures for *Mercenaria campechiensis texana* are from 15° to 35°C (Craig et al. 1988). In Florida, growth of *M. campechiensis* is optimal from 15° to 25°C, but is reduced at temperatures above 25°C.

Salinity - Eggs and Larvae: Egg development occurs at salinities of 20 to 33‰ (Davis 1958). The optimum salinity for egg development to the straight hinged larval stage is approximately 27 to 28‰ with metamorphosis occurring at a minimum of 17.5‰ (Davis 1958, Davis and Calabrese 1964, Castagna and Chanley 1973).

Salinity - Juveniles and Adults: Juveniles can tolerate salinities as low as 12 to 15‰, but death usually occurs at <10‰ within several weeks (Chanley 1958, Castagna and Chanley 1973). The optimum salinity for growth is approximately 24 to 28‰ (Chanley 1958). Optimum growth salinities for *Mercenaria mercenaria texana* are 22 to 33‰, probably with no growth occurring below 20‰ (Craig et al. 1988). In the Indian River, Florida, hard clams are reported to do well in salinities above 20‰ (Arnold et al. 1991, Arnold et al. 1996). During periods of stress, such as sudden extreme changes in water salinity, hard clams can close their shells tightly and respire anaerobically (Lutz and Rhoads 1977, Eversole 1987).

Turbidity: Hard clams prefer clear water in Tampa Bay (Kunneke and Palik 1984); secchi disc values range from 0.9 to 3.7 m in one study (Godcharles and Jaap 1973b). Reduced survival has been noted at high turbidity (Loosanoff 1962). Eggs and larvae develop normally at silt concentrations of <0.75 g/l, but no egg development occurs at silt concentrations of 3.0 to 4.0 g/l. Larval growth is retarded at 1.0 to 2.0 g/l and is negligible at 3.0 to 4.0 g/l (Davis 1960). Huntington and Miller (1989) found larval growth decreased only at the highest experimental levels of sediment load (2,200 mg/l), but survival remained unaffected. Silt concentrations can also influence growth of juvenile clams. Juveniles (9 mm) are not affected by sediment concentrations of 25 mg/l, but experience a 16% reduction in growth at 44 mg/l of silt (Bricelj et al. 1984). Water currents are important to the growth and survival of hard clams by removing silts that would otherwise accumulate and produce undesirable soft sediments

(Killam et al. 1992). In addition, currents are also important for providing food, maintaining acceptable water quality, removing biodeposits, and transporting eggs and larvae.

Dissolved oxygen (DO): One hundred percent egg mortality occurs at oxygen concentrations of 0.2 part per million (ppm). Embryos from Long Island Sound, New York develop normally at 0.5 ppm and above, and larval growth is lower at 2.4 ppm than at 4.2 ppm (Morrison 1971). However, larvae from Indian River Bay showed no significant differences in growth and survival when exposed to hypoxic conditions, but a decrease of growth was observed in larvae subjected to hyperoxic conditons (13.7 ppm) (Huntington and Miller 1989). In Tampa Bay hard clams were found in oxygen saturation conditions, while from Charlotte Harbor they are taken at 4.6 to 9.6 parts ppm (mean = 6.6 ppm), and at 4.0 to 7.8 ppm (mean = 5.8 ppm) from the Ten Thousand Island area (Taylor and Saloman 1970, Godcharles and Jaap 1973b).

pH: Normal development of embryos occurs between a pH of 7.00 and 8.50. Optimum larval growth occurs between pH 7.50 and 8.00 with a minimum of 6.25 and a maximum of 8.75. The pH must be greater than 7.0 for successful recruitment of juveniles to occur (Calabrese and Davis 1966, Calabrese 1972).

Migrations and Movements: Egg and larval stages are subject to tidal action and currents. Larvae are capable of migrating vertically throughout the water column to retain themselves in the estuary. Pediveliger larval stages crawl and swim in search of a settlement site. Juveniles and adults exhibit limited horizontal and vertical movement through the sediment, but do not migrate extensive distances (Eversole 1987). Upon removal from the sediment in Narragansett Bay, hard clams less than 83 mm in valve length (VL) are able to reburrow within a week (Rice et al. 1989). Hard clams exceeding 83 mm VL demonstrate the least capability of reburrowing.

**Reproduction**

Mode: Hard clams are protandrous hermaphrodites which release their gametes into the water column for external fertilization. *Mercenaria mercenaria* exhibit consecutive hermaphroditism, passing through a pre-adult sexual phase at around 6-7 mm shell length. Individuals usually function as males during the primary sexual phase, but their gonads have both male and female sex cells. The primary sex phase lasts throughout the first year. Following the primary sex phase, the clams experience a permanent sex change after which the male-female ratio changes to 50:50, and they will function primarily as male or female (Loosanoff 1937a, Merrill and Tubiash 1970, Walker and Stevens 1989). Subsequent reproductive efforts are sexual with separate male and female sexes (gonochoristic), with rare instances of hermaphroditism. *Mercenaria campechiensis* also tends to be protandric in its development (Dalton and Menzel 1983). Clams in the 60 mm size class have been reported as the most reproductively active (Belding 1912), but there appears to be no evidence of reproductive senescence in larger, older clams (Peterson 1983).

Spawning: Spawning occurs generally from 20° to 30°C, with maximum spawning activity found between 24° to 26°C (Loosanoff 1937c, Carriker 1961, Hesselman et al. 1989), in the marine and estuarine subtidal seawater zone (Dalton and Menzel 1983). Spawning activity has bimodal annual peaks in the more southern portion of the hard clam's range, such as the Gulf of Mexico (Eversole 1987). In Florida, these peaks occur in the spring (February-June) and fall (September-December) with spawning beginning in February-March and ending in October (Dalton and Menzel 1983). In the Tampa Bay area, spawning occurs during April and continues to August (Belding 1912, Kunneke and Palik 1984, Hesselman et al. 1989). Temperature influences gonadal development (Loosanoff 1937b, Porter 1964), and spawning may occasionally occur all year in warmer parts of the hard clam's range such as Florida (Dalton and Menzel 1983, Hesselman et al. 1989). When the water temperature averages ≥30°C gametogenesis is inhibited and spawning ceases (Hesselman et al. 1989). In addition to climatic influences, spawning frequency may also be differently influenced by genetic factors in different populations of hard clam (Knaub and Eversole 1988). Spawning appears to coincide with high algal concentrations during spring, fall and winter, allowing ample food resources for larval stages (Heffernan et al. 1989). Gametes are broadcast into the water column, and fertilization is external (Belding 1912, Loosanoff 1937b, Kunneke and Palik 1984, Eversole 1987).

Fecundity: Egg production estimates range from 2-3 million all the way up to 39.5 million per individual for an entire spawning season (Davis and Chanley 1956, Ansell 1967, Bricelj and Malouf 1980) with up to 24.3 million eggs reported in a single spawn (Davis and Chanley 1956). Fecundity is directly related to clam size (Bricelj and Malouf 1980, Peterson 1983), and reported differences may be due to clam size and condition at time of spawning.

**Growth and Development**

Egg Size and Embryonic Development: Hard clam eggs develop oviparously. Unfertilized eggs range 50-97 µm in diameter (Carriker 1961, Bricelj and Malouf 1980). A gelatinous envelope surrounds the egg bringing the egg diameter up to approximately 125 µm. The gelatinous envelope imbibes water causing the egg to swell, providing buoyancy to the egg and further increasing the diameter to 270 µm (Carriker 1961). Lipids stored in the egg provide energy and nutrients to the embryo, and are important to the embryo's development and survival (Lee and Heffernan 1991). Egg cleavage begins within 30 minutes of fertilization at 27°-30°C and after 10 hours a ciliated gastrula has developed. The ciliated blastula emerges from the gelatinous egg and becomes a trochophore larva (Carriker 1961).

<u>Age and Size of Larvae</u>: The first two larval stages, the trochophore and early veliger stages (85-90 µm), are non-shelled and possess a ciliated velum for propulsion (Carriker 1961, Eversole 1987). By day 1 the first shelled stage, the straight hinged veliger, develops ranging in size from 90-140 µm. By day 3 the second shelled stage, the umboed veliger, develops. The umboed veliger stage may last 3 to 20 days, depending on water temperature and food availability, and ranges in size from 140 to 220 µm in length. The pediveliger stage follows lasting 6 to 20 days with a size range of 170 to 220 µm. The pediveliger possesses a strong ciliated velum and foot that allow the larvae to swim and crawl in search of a suitable settlement site. At 200-230 µm the velum is lost, and the newly settled plantigrades are referred to as spat. The spat use byssal threads to attach and detach from various substrates. For approximately 2 weeks the spat alternate between crawling and attaching to substrates. By 7-9 mm the byssal gland is lost and the juvenile plantigrade settles permanently to its benthic existence (Carriker 1961, Eversole 1987).

<u>Juvenile Size Range</u>: Juvenile growth is influenced by temperature, food availability, siphon nipping, and type of substrate (Pratt 1953, Pratt and Campbell 1956, Loosanoff and Davis 1963, Coen and Heck 1991, Coen et al. 1994). Growth is more rapid in smaller hard clams, and most of it occurs during the initial several years of life, particularly the first year (Eversole et al. 1986, Jones et al. 1990). Thereafter, the growth rate declines progressively with age (Gustafson 1955). Growth may be affected by substrate and current regime more than increased exposure time at low tide (Walker 1989). In Florida, Menzel (1961) found that *Mercenaria campechiensis* grew most during the spring through fall months with little growth occurring during winter. In contrast, *M. mercenaria* grew in spring and fall with very little growth in summer or winter, which agrees with later work by Peterson et al. 1983, Peterson et al. 1985, and Jones et al. 1990. Growth rates of *M. mercenaria* imported into Texas remained different from native *M. campechiensis texana* which showed little growth occurring during summer (Craig et al. 1988). Growth rates in *M. campechiensis* exceed those of *M. mercenaria* and their hybrids. Taylor and Saloman (1968) reported average growth of Tampa Bay hard clams over a four year period as age I - 50 mm, age II - 73 mm, age III - 81 mm, and age IV - 90 mm. Growth is rapid and variable through the first three years and clams generally reach 50% of adult maximum size. *M. campechiensis* reaches a commercially marketable size of 45 mm within 1.5 to 2 years (Peterson et al. 1983, Kunneke and Palik 1984, Eversole et al. 1986, Eversole 1987). Juvenile *M. mercenaria* were found to reach marketable size faster at lower stocking densities than those stocked at higher densities (Rice et al. 1989, Eversole et al. 1990). Those planted in subtidal areas also grew faster than clams in intertidal areas. By five years *M. campechiensis* reach 70% of their maximum size (Taylor and Saloman 1969). Hybrid clams exhibit a growth rate greater than northern hard clams (Chestnut et al. 1956, Haven and Andrews 1957, Menzel 1964, Loosanoff and Davis 1963, Taylor and Saloman 1969). Overall growth rates of southern populations of hard clams are more rapid than those of northern populations; however, populations in the south do not appear to live as long (Jones et al. 1990). Size appears to determine sexual maturity more than age does (Quayle and Bourne 1972, Eversole 1987). Maturity is achieved at approximately 30-40 mm in length at an age of 1 to 2 years depending on environmental conditions (Eversole et al. 1980, Bricelj and Malouf 1980).

<u>Age and Size of Adults</u>: Hard clams in the Gulf of Mexico can live up to 28 years and maximum size can exceed 170 mm (Taylor and Saloman 1969, Kunneke and Palik 1984, Jones et al. 1990). On the Atlantic coast, two hard clams used in a growth experiment reached estimated ages of 33 and 36 years (Eversole 1987). The annual mortality for clams raised under laboratory conditions is about 4% (Eversole et al. 1986). The growth rate of hard clams decreases with increasing size and age (Eversole et al. 1986). Peterson's (1985) growth equation [length (in cm) = 3.176 + 1.819 *ln* (number of annual bands)] becomes a very poor predictor of age based on size after 4.5 years. Growth rates for the hard clam also vary with geographical area (Jones et al. 1990). Growth in Florida Gulf of Mexico sites is most rapid in the spring.

**Food and Feeding**

<u>Trophic Mode</u>: Hard clams are selective, omnivorous filter-feeders, utilizing a siphon system to take in suspended particles and dissolved organics carried along in bottom currents (Eversole 1987).

<u>Food Items</u>: Food is obtained from suspended particles entering through the ventral inhalant siphon and passed to the gills. The particles are sorted in the gills,

and large particles are rejected. The rejected material is voided as pseudofeces through the inhalant siphon. The size range of particles ingested changes as the hard clam grows (Riisgard 1988). Food items include: marine diatoms, naked flagellates and other phytoplankton, protozoans, micro-crustaceans, larvae of other mollusks, rotifers, bacteria, and other zooplankton (Belding 1912, Loosanoff and Davis 1963, Eversole 1987).

**Biological Interactions**

Predation: Predation is an important natural control of hard clam populations, and its impact is felt by all size classes (Killam et al. 1992). Blue crabs are a major predator of hard clams (Craig et al. 1988). Arnold (1984) demonstrated the effects of blue crab predation in different substrates, with predation rates being higher in sand and sand/mud substrates. Clams greater than 40 mm SL were not consumed, even by large crabs. Other predators include gastropods (oyster drills (*Thais* sp.), moon snails (*Polinices duplicatus* and *Lunatia heros*), and whelks (*Busycon* sp.)), starfish, stone crabs and other xanthid crabs, skates and rays, various bony fishes (sciaenids, puffers, flounders), and birds (Craig and Bright 1986, Craig et al. 1988, Bisker et al. 1989, Killam et al. 1992). The fish species feed on juvenile seed clams, and in localized areas, skates and rays may be important predators (Killam et al. 1992). The importance of fish predation is minor, however, when compared with that of invertebrate predators. Starfish prey on both juvenile and adult hard clams. Small clams are attacked by individual starfish, but larger clams (>50 mm shell length) are usually attacked by several starfish. Several species of shorebirds prey on clams and other bivalves, however, their influence is restricted to hard clams exposed in the intertidal area. Herring gulls have been observed capturing hard clams, flying them up, and dropping them onto hard surfaces to break them open. Grass beds may serve as refuges from predation (Craig and Bright 1986, Coen and Heck 1991), although it has been suggested these areas can have higher predation rates than bare areas (Coen and Heck 1991).

Factors Influencing Populations: Recruitment success and predation are two of the factors most limiting to large populations in the Gulf of Mexico. The sub-lethal effects of siphon nipping by predators is known to impact growth (Coen et al. 1994). The oyster toadfish (*Opsanus tau*) reduces predation on juvenile hard clams from xanthid and portunid crabs by preying on these species in field experiments (Bisker et al. 1989). Natural mortality decreases as clams reach sizes greater than 50 mm in length; however, fishing mortality can become significant at this point (Eversole 1987). It has been noted that the settlement and survival of juveniles is enhanced in beds where abundance of large clams is low due to fishing pressure (Rice et al. 1989). Possible reasons for this are the removal of competition and larviphagy from adults, and the disturbance of sediment from fishing activities forming a more suitable substrate for settlement. A parasitic copepod, *Ostrincola gracilis*, occurs in the mantle cavity of the hard clam (Humes 1953), but probably has little adverse impact on its host. Changes in the environment due to storm events can have either positive or negative effects on hard clam population (MacKenzie 1989). Storms can widen inlets that can lead to improved water circulation which can increase clam populations by increasing the water salinity. However, in some cases, wider inlets can cause swifter currents that sweep clam larvae out to sea or alter the sediment to a coaser less favorable texture. In the Indian River Lagoon of east central Florida, *M. mercenaria* x *M. campechiensis* hybrid clams have a high incidence of gonadal neoplasia, which may act as a barrier to gene flow, and reinforce reproductive isolation between the two species (Bert et al. 1993, Arnold pers. comm.).

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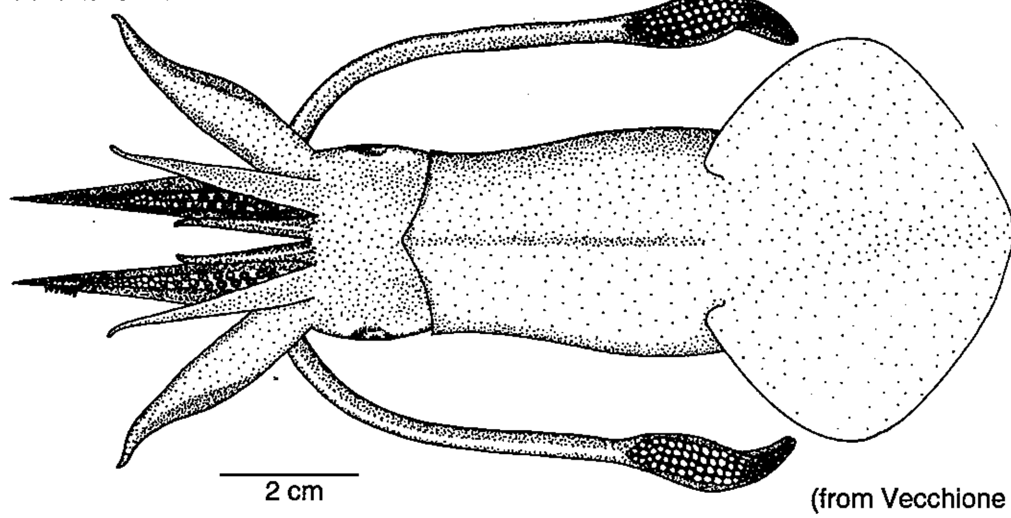
*Lolliguncula brevis*
**Adult**




(from Vecchione et al. 1989)

**Common Name:** bay squid
**Scientific Name:** *Lolliguncula brevis*
**Other Common Names**: Atlantic brief squid (Turgeon et al. 1988), thumbstall squid (Andrews 1981); brief squid, short squid, least squid (Bane et al. 1985); common gulf squid (Dillion and Dial 1962); *calmar doigtier* (French), *calamar dedal* (Spanish) (Fischer 1978).
**Classification** (Turgeon et al. 1988)

| | |
|---|---|
| Phylum: | Mollusca |
| Class: | Cephalopoda |
| Order: | Teuthoidea |
| Family: | Loliginidae |

**Value**
Commercial: The bay squid has been neglected as a fishery resource primarily because of its small size (Hixon 1980b). The low demand for squid and the high cost of capture makes a directed squid fishery in the U.S. Gulf of Mexico financially unfeasible (Hixon et al. 1980). Squid sold through commercial fisherman are typically acquired as incidental catch from trawling for shrimp and fish (Fischer 1978, Voss and Brakonieki 1984). The larger squid species (*Loligo pleii* and *L. pealeii*) are the ones usually taken. The bay squid is sometimes sold in Texas supermarkets, but, although edible, is not especially popular as a consumer food (Voss and Brakonieki 1984). This species is sometimes used in neurologic research because of the large axon characteristic of the cephalopod molluscs.

Recreational: Bay squid is often used as bait in offshore sport fishing (Bane et al. 1985).

Indicator of Environmental Stress: Bay squid is not typically used as an indicator species in studies of environmental stress.

Ecological: The bay squid is one of the few cephalopods that can tolerate estuarine salinities, and is often an abundant pelagic species in estuaries (Dragovich and Kelly 1967). It consumes shrimp and small fishes and is preyed upon by larger fishes.

**Range**
Overall: The range of the bay squid includes the western Atlantic Ocean from New Jersey, Delaware Bay southward to Florida, throughout the Gulf of Mexico and along the Caribbean mainland, and southward to Rio de la Plata in South America (Voss 1956, Fischer 1978, Hixon 1980a, Hixon 1980b, Andrews 1981). It is not known from the Bahamas and Caribbean Islands except Cuba and Curacao (Fischer 1978).

Within Study Area: Bay squid occur in U.S. Gulf of Mexico estuaries from Rio Grande, Texas, to Florida's Dry Tortugas, and are widely distributed along the Gulf coast during most of the year (Voss and Brakonieki 1984). They are common along the Texas coast during part of the year, but major concentrations determined by catch and observation are on both sides of the Mississippi River delta in waters of high productivity, off the Florida panhandle, and southwest Florida below Tampa (Table 5.05) (Voss and Brakonieki 1984).

**Life Mode**
This is a schooling, mobile, diurnally active species that occurs in near-shore waters and in estuaries (Hargis and Hanlon 1984, Vecchione and Roper 1991). Eggs are attached to submerged hard structures and substrate, but have also been collected on soft muddy bottoms (Hall 1970, Forsythe pers. comm.). Paralarvae,

Table 5.05. Relative abundance of bay squid in 31 Gulf of Mexico estuaries (Nelson et al. 1992, Vecchione pers. comm).

| *Estuary* | *Life stage* A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | √ | √ | √ | √ | √ |
| Ten Thousand Islands | √ | √ | √ | √ | √ |
| Caloosahatchee River | O | O | O | O | O |
| Charlotte Harbor | O | O | O | O | O |
| Tampa Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Suwannee River | O | O | O | O | O |
| Apalachee Bay | O | O | O | O | O |
| Apalachicola Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| St. Andrew Bay | ◉ | O | ◉ | O | O |
| Choctawhatchee Bay | O | O | O | O | O |
| Pensacola Bay | O | O | O | O | O |
| Perdido Bay | O | O | O | O | O |
| Mobile Bay | O | O | O | O | O |
| Mississippi Sound | ● | ● | ● | ● | ◉ |
| Lake Borgne | ◉ | | ◉ | | |
| Lake Pontchartrain | O | | O | | |
| Breton/Chandeleur Sounds | O | | O | | |
| Mississippi River | | | | | |
| Barataria Bay | O | | O | | |
| Terrebonne/Timbalier Bays | O | | O | | |
| Atchafalaya/Vermilion Bays | O | | O | | |
| Calcasieu Lake | O | | O | √ | |
| Sabine Lake | √ | | √ | | |
| Galveston Bay | O | O | O | O | O |
| Brazos River | O | na | O | na | na |
| Matagorda Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| San Antonio Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Aransas Bay | O | O | O | O | O |
| Corpus Christi Bay | O | O | O | O | O |
| Laguna Madre | O | O | O | O | O |
| Baffin Bay | O | | O | | |
| | A | S | J | L | E |

Relative abundance:

- ● Highly abundant
- ◉ Abundant
- O Common
- √ Rare
- blank Not present
- na No data available

Life stage:

- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae (paralarvae)
- E - Eggs

juveniles, and adults are pelagic.

**Habitat**

Type: The bay squid occurs in the upper salinity regions of estuaries around marsh grasses to the inshore continental shelf when the estuarine salinities are unfavorable. It is nektonic in the shallow waters of these areas with most specimens found in depths of <30 m. It has been observed as deep as 475 m on a steep rock face (Vecchione and Roper 1991), although this is probably not typical. In areas where salinities are favorable, squid are found in relatively deep passes and/or channels where current velocity is usually high (Dragovich and Kelly 1967, Hargis 1979a, Hargis 1979b, Laughlin and Livingston 1982, Hargis and Hanlon 1984, Vecchione and Roper 1991). This species is unique among the cephalopods in that it can withstand low salinity waters (down to 17.5‰) and become common inhabitants of bays (Hixon 1980a, Hixon 1980b). Paralarvae are much more abundant near the bottom than near the surface in both coastal and estuarine waters (Vecchione 1991b). Overall paralarval abundance is much greater in coastal rather than estuarine areas.

Substrate: Due to its pelagic life style, the bay squid occurs over a wide variety of bottom substrates, but appears to be found in association with soft mud bottoms (Dragovich and Kelly 1967, Hargis and Hanlon 1984).

Physical/Chemical Characteristics: Abundance is generally correlated with lower salinity and higher temperature (Hixon 1980a, Hixon 1980b).

Temperature - Paralarvae: The reported temperature range for paralarval bay squid taken in nearshore waters off Louisiana is 11-32°C, with the highest abundance occurring at 20-29°C (Bane et al. 1985).

Temperature - Adults and Juveniles: Temperature tolerance ranges from 11° to 33°C, and possibly as low as 7°C. Low temperatures exclude squid from bays during the winter months, usually December to February (Hixon 1980a, Hixon 1980b). Benson (1982) reports a range of 5-34.9°C, and a preference of 13-16°C.

Salinity - Paralarvae: Paralarval bay squid do not seem to be as euryhaline as the adults and were not found below 22‰ off of coastal Louisiana (Vecchione 1991b). In another study, salinities where paralarval bay squid were collected in nearshore Louisiana waters ranged from 20-36‰, with the highest abundance occurring at 32-33‰ (Bane et al. 1985). Tolerance of moderate salinities may develop ontogenetically late during paralarval development (Vecchione 1991b).

Salinity - Adults and Juveniles: Salinity ranges for juvenile and adult squid are 20-37‰, with the lower lethal limit being 17.5‰ (Hixon 1980a, Hixon 1980b, Hendrix et al. 1981, Laughlin and Livingston 1982). The salinity range reported by Benson (1982) for bay squid is 5-35.5‰, with a preference for >15‰. However, these lower reported salinities may have been taken at surface rather than bottom waters where the squid were collected. It is also considered possible that squid make forays into lower salinity surface waters to feed and then return to deeper waters where the salinity is higher (Hendrix et al. 1981).

Dissolved Oxygen: Evidence indicates that paralarval bay squid are capable of adjusting to low concentrations of dissolved oxygen (DO) (<2 mg/l), perhaps by increasing oxygen uptake rates (Vecchione 1991b). This may be an adaptation to survive the seasonally hypoxic bottom water where the the bay squid spawns. Adults have been observed in water with a DO content of 0.7 mg/l (Vecchione and Roper 1991).

<u>Migrations and Movements</u>: Bay squid migration and abundance are regulated by temperature and salinity (Benson 1982, Laughlin and Livingston 1982). Squid move out of bays to a few miles offshore during December and February to avoid the cooler temperatures. They move back to the bays in the spring when temperatures increase. The spring movement is also related to salinity, spawning, and feeding (Hixon 1980a, Hixon 1980b, Laughlin and Livingston 1982). Bay squid are able to move into bottom water layers which are higher in salinity due to stratification conditions that also result in hypoxic water layers (Vecchione 1991a). It is considered likely that the bay squid takes up oxygen in upper, more oxygenated water layers and then dives into the bottom waters facultatively. This could be a feeding or predator avoidance strategy (Vecchione 1991a), or possibly a behavioral mechanism for avoiding hypoosmotic stress in stratified waters (Hendrix et al. 1981).

**Reproduction**

<u>Mode</u>: The bay squid is gonochoristic, with separate sexes. Transfer of sperm to the female is accomplished by means of a spermatophore and specially adapted arms on the males.

<u>Mating/Spawning</u>: Bay squid perform head-to-mantle mating (Juanico 1983). A knob on the female mantle wall is reportedly formed for the attachment of spermatophores. However, it has also been suggested that this pad does not occur in virgin females, and is actually a tissue response to the implanted spermatophores (Vecchione pers. comm.). Duration of the spermatophore attachment and in what quality it can persist while attached to the female is unknown (Juanico 1983). In the northern Gulf of Mexico, spawning can occur year-round at depths of 2-18 m with major peaks from April to July and a lesser peak from October to November (Juanico 1983, Hargis and Hanlon 1984). In the northern Gulf of Mexico, bay squid eggs appear to hatch throughout the year except during the coldest months (Vecchione 1991b). Eggs are deposited on sandy bottoms, sometimes within estuaries (Benson 1982, Vecchione 1991b). In Galveston Harbor, Texas, egg capsules have been reported attached to crab traps so thickly as to make them useless (Vecchione 1991b).

<u>Fecundity</u>: As many as 2000 eggs have been produced in a single brood. With multiple broods, an estimated 1400-6350 can be produced by one female during a breeding season (Hixon 1980a). Eggs are enclosed in a capsule, the number per single capsule is limited by size of individual eggs and the size of the spawning female's nidamental apparatus (Boletzky 1986).

**Growth and Development**

<u>Egg Size and Embryonic Development</u>: Eggs are contained in clavate egg capsules that are between 10 and 13 cm long (Hall 1970). One end of the capsule is bulbous and contains most of the embryos, and the opposite end is narrow and appears to be an attachment stalk. Capsules are not joined together, and are apparently attached directly to bottom sediments. The average number of eggs and embryos in a capsule is 69. Eggs, on the average, measure 1.8 mm long by 1.3 mm wide and are enveloped in a clear jelly-like matrix. Total embryonic lifespan is estimated as 35 to 40 days based on observed growth rates. Detailed descriptions of embryonic development can be found in the literature (Hall 1970, Hunter and Simon 1975).

<u>Age and Size of Larvae</u>: The total length of a newly hatched bay squid is about 3.8 mm. Morphology and development of planktonic "paralarvae" are discussed by Vecchione (1982). Due to the ambiguity of the term "larva" when applied to cephalopods, a new designation has been proposed (Young and Harman 1988). Cephalopods in the first post-hatching growth stage that are pelagic in near-surface waters during the day, and that have a distinctively different mode of life from that of older conspecific individuals are defined as "paralarvae." Paralarvae appear to exist only in the Teuthoidea and Octopoda groups of cephalopod molluscs.

<u>Juvenile Size Range</u>: Hixon (1980) found growth among individuals to be highly variable with averages in nature of 8.6 and 7.9 mm/month for males and females respectively. There was no significant differences in growth rates recorded from nature and laboratory or between sexes.

Age and Size of Adults: The life cycle of this species is approximately one year (Hargis and Hanlon 1984). Males are sexually mature in about 6 months at a mantle length (ML) of about 40-60 mm (≈13 g); females at 8 months when they are about 70-80 mm ML (≈30 g) (Hixon 1980a, Hixon 1980b, Hargis and Hanlon 1984). Males appear to mature at slightly smaller sizes (32 mm ML) than females (63 mm ML) (Benson 1982). Adults have been collected with ML's up to 85 mm for males and 110 mm for females (Fischer 1978). Growth morphometry of bay squid in Delaware Bay is described by Haefner (1964).

**Food and Feeding**

Trophic mode: Juveniles and adults are carnivores, consuming a variety of fish and crustaceans. Their high feeding and growth rates make this species an important predator in coastal estuaries (Hargis and Hanlon 1984). Preferred prey species typically seem to be highly visible nektonic species (Hargis 1979a, Hargis 1979b). The bay squid and cephalopods possess a sophisticated receptor system analogous to the lateral line system in fishes and amphibians for the detection of small water movements (Budelmann and Bleckmann 1988). This sensory apparatus could allow the normally visually oriented bay squid to locate prey under low visibility conditions (e.g. murky or deep water, or night). Feeding methods of this species are typical of loliginid squid (Hanlon et al. 1983, Turk pers. comm.). Prey are seized with the squid's tentacles that are thrust quickly forward by means of an internal hydraulic mechanism. The captured animal is then "reeled in" and positioned near the mouth by retracting the tentacles. Prey items (e.g. fish) are injected with venom usually through bites behind the head with the squid's parrot-like beak. The venom acts as a tranquilizer that paralyzes the prey. Once fish prey are paralyzed, the squid consumes the viscera, and then strips the flesh from the animal by means of perforating bites down the animal's sides. Shrimp prey are completely eaten except for the head and the exoskeleton. A typical meal is cleared through the digestive system in approximately 30 minutes.

Food Items: Planktonic copepods are likely the natural prey for paralarval bay squid (Vecchione 1991). Juveniles and adults feed on larger prey, mostly nektonic fishes and shrimps. Juveniles have a slight preference for crustaceans, while adults seem to prefer fish (Hargis and Hanlon 1984). Adults feed primarily on juvenile striped mullet, tidewater silversides, and Atlantic croaker in the upper regions of the water column. They also show some preference for white shrimp. If prey move to the bottom without being detected they are not pursued. Juvenile bay squid prefer fish and shrimp equal to or smaller than their own size. Tidewater silversides, sheepshead minnows, and sailfin mollies have been observed as natural foods (Hargis 1979a, Hargis 1979b, Hixon 1980a). Seagrass has also been reported as a food item (Benson 1982). Polychaetes have also been reported as occurring in bay squid stomach contents (Vecchione 1991a).

**Biological Interactions**

Predation: The bay squid is preyed upon by larger fishes.

Factors Influencing Populations: Greater abundances of bay squid are correlated with lower salinities and higher temperatures with respect to other squid species in the Gulf of Mexico (Hixon 1980). This species is most numerous in waters <30 m deep.

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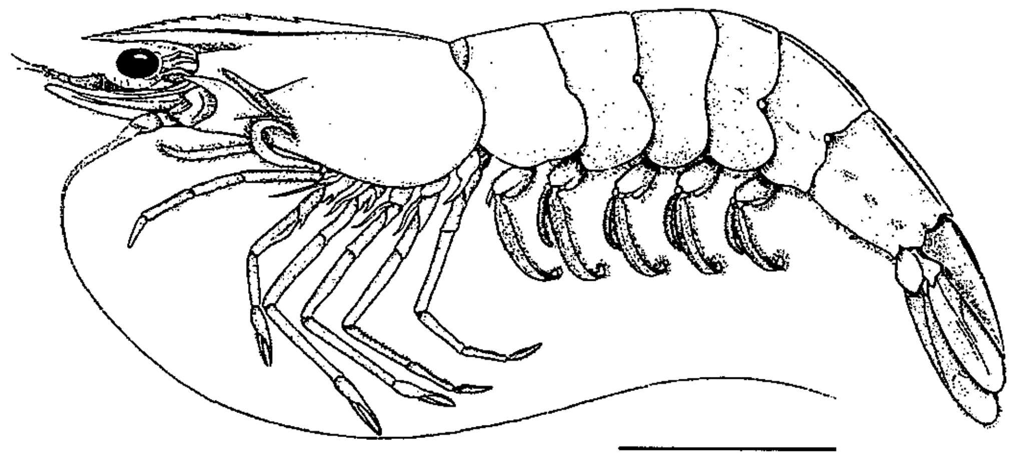
## Brown shrimp

***Penaeus aztecus***
**Adult**




(from Pérez-Farfante 1969)

**Common Name**: brown shrimp
**Scientific Name**: *Penaeus aztecus*
**Other Common Names**: brownies, golden shrimp, green lake shrimp, native shrimp, red or red tail shrimp (Motoh 1977); *crevette royale grise* (French), *camarón café norteño* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Williams et al. 1989)

| | |
|---|---|
| Phylum: | Arthropoda |
| Class: | Crustacea |
| Order: | Decapoda |
| Family: | Penaeidae |

### Value

Commercial: Shrimping has been ranked as the second most valuable commercial fishery in the U.S., and seventh in quantity (NMFS 1993). U.S. landings of all shrimp species combined in the Gulf of Mexico were 100.7 thousand mt in 1992, and were valued at $316.6 million. Total U.S. brown shrimp harvest in the Gulf of Mexico was 64,075 mt in 1991, and brown shrimp typically comprise 57% of the total Gulf of Mexico shrimp landings (NOAA 1993). The fishery for Gulf of Mexico brown shrimp is considered to be fully exploited at this time (Nance and Nichols 1988, Nance 1989), and a longterm potential annual yield of 63,001 mt has been estimated (NOAA 1993). In 1991 an estimated 5,000 offshore vessels were participating in the fishery with an unknown number of smaller boats fishing in the inshore and nearshore waters. The season begins in May, peaks from June to July and gradually declines through April. Major fishing grounds are off the coasts of Texas and Louisiana. Federal regulations have annually closed the offshore fishery along the coast of Texas from around mid-May to mid-July not more than 55 days to allow shrimp to grow to larger sizes (Klima et al. 1982, Klima et al. 1987, Nance et al. 1990). The majority of the brown shrimp are harvested for human consumption. In addition, a smaller bait shrimp fishery also exists (Swingle 1972, Klima et al. 1987, Nance et al. 1991).

Recreational: Recreational shrimping has become increasingly popular along the Gulf coast in recent years (Christmas and Etzold 1977). Fishermen use small trawls for the most part, but seines, cast nets, and push nets are used as well. Approximately 4,000 mt (heads on) of total shrimp (brown, pink, and white) were taken by recreational shrimpers in 1979 in Texas and Louisiana. Regulations pertaining to licensing and gear type vary among the Gulf states, and catches are limited by location and season of fishing (GMFMC 1981).

Indicator of Environmental Stress: An experiment conducted by Miligan (1983) indicated dredge material free of significant concentrations of heavy metals, pesticides, and waste metabolites was non-toxic to brown shrimp. A second experiment demonstrated better growth for shrimp in rearing ponds treated with dredge material. Ward et al. (1981) determined a concentration of 1.2 mg/l selenium (96 hours LC50) to be toxic to brown shrimp. Wofford et al. (1981) observed the bioaccumulation of phthalate esters (plasticizers) and demonstrated brown shrimp were better biodegraders of the ester than oysters. A study of the impact of production water from offshore oil platform found toxic effects occurred in the immediate outfall area on larval brown shrimp (Gallaway 1980). Population studies conducted around brine disposal sites found no effects by brine on brown shrimp distribution (Reitsema et al. 1982). Studies in areas treated with aerial insecticides have found varying degrees of shrimp mortality (Christmas and Etzold 1977). Couch (1978)

Table 5.06. Relative abundance of brown shrimp in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | √ | | √ | √ | |
| Ten Thousand Islands | √ | | √ | √ | |
| Caloosahatchee River | | | √ | | |
| Charlotte Harbor | √ | | √ | √ | |
| Tampa Bay | | | | | |
| Suwannee River | | | | | |
| Apalachee Bay | | | | | |
| Apalachicola Bay | ◉ | | ◉ | ◉ | |
| St. Andrew Bay | ◉ | | ◉ | ◉ | |
| Choctawhatchee Bay | ◉ | | ◉ | ◉ | |
| Pensacola Bay | ● | | ● | ● | |
| Perdido Bay | ● | | ● | √ | |
| Mobile Bay | ● | | ● | ● | |
| Mississippi Sound | ● | ○ | ● | ● | ◉ |
| Lake Borgne | ◉ | | ● | ● | |
| Lake Pontchartrain | ○ | | ◉ | ○ | |
| Breton/Chandeleur Sounds | | | ◉ | | |
| Mississippi River | | | ○ | | |
| Barataria Bay | | | ● | ● | |
| Terrebonne/Timbalier Bays | | | ● | | |
| Atchafalaya/Vermilion Bays | | | ● | ◉ | |
| Calcasieu Lake | | | ● | ◉ | |
| Sabine Lake | √ | | ◉ | ◉ | |
| Galveston Bay | | | ● | ● | |
| Brazos River | | | ◉ | ◉ | |
| Matagorda Bay | ● | | ● | ● | |
| San Antonio Bay | ◉ | | ● | ● | |
| Aransas Bay | | | ● | ◉ | |
| Corpus Christi Bay | | | ● | ○ | |
| Laguna Madre | ○ | | ◉ | √ | |
| Baffin Bay | | | ● | | |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae/postlarvae
- E - Eggs

has compiled a comprehensive review of the toxic responses of penaeid shrimp.

Ecological: The brown shrimp is consumed by many finfish species and by large crustaceans. Large juvenile stocks of these and other penaeid shrimp appear to be important in supporting large populations of certain juvenile fish species (Hettler 1989). The loss of marsh habitat and reduction in freshwater inflow into the bays have come under scrutiny as major factors influencing shrimp production (Kutkuhn 1966, Minello and Zimmerman 1983, Minello and Zimmerman 1984).

### Range

Overall: The brown shrimp extends farther north than any of the other western Atlantic species of *Penaeus* (Fischer 1978). It is distributed from Martha's Vinyard, Massachusetts, around the tip of Florida and throughout the Gulf of Mexico to the northwestern Yucatan Peninsula.

Within Study Area: In U.S. waters of the Gulf of Mexico, the brown shrimp is distributed throughout bays, estuaries and coastal waters (Table 5.06). For the purposes of Table 5.06, all larval and postlarval stages of brown shrimp are considered together as "larvae" (L). However, the brown shrimp is uncommon in Florida Bay and is conspicuously absent along the western Florida coast from the Sanibel grounds to Apalachicola Bay. Its maximum density occurs along the coasts of Texas, Louisiana, and Mississippi (Allen et al. 1980, Williams 1984, NOAA 1985).

### Life Mode

This species is found in neritic to estuarine habitats and is pelagic to demersal, depending on life stage. Eggs are denser than seawater and are demersal (Kutkuhn 1966). Larval stages are planktonic, their position in the water column is dependent on time of day, water temperature and clarity (Temple and Fischer 1965, 1967, Kutkuhn, et al. 1969). Nauplii are demersal, becoming pelagic as they develop through the protozoeae and mysis stages (Lassuy 1983). Postlarvae spawned in the fall may burrow into the sediments to escape cooler temperatures and overwinter (St. Amant et al. 1966, Aldrich et al. 1968). Postlarvae move into estuaries and transform into juveniles (Cook and Lindner 1970). Adults generally inhabit offshore waters ranging from 14 to 110 m in depth (Renfro and Brusher 1982). The brown shrimp is most abundant from March to December with optimum catches occurring from March to September (Copeland and Bechtel 1974). This species typically seems to have an annual life cycle; however, captive individuals have survived for over two years (Perez-Farfante 1969, Zein-Eldin pers. comm.).

**Habitat**

Type: Eggs occur offshore and are demersal. Larvae occur offshore and begin to immigrate to estuaries as postlarvae around 8 to 14 mm total length (TL) (Cook and Lindner 1970, Zein-Eldin pers. comm.). In estuaries, postlarvae and small juveniles are associated with shallow vegetated habitats, but are also found over silty sand and non-vegetated mud bottoms. Juveniles and subadults are found from secondary estuarine channels out to the continental shelf, but prefer shallow marsh areas and estuarine bays, showing a preference for vegetated habitats. Adults occur in neritic Gulf waters (Perez-Farfante 1969, Copeland and Bechtel 1974, Williams 1984, Minello et al. 1990, Zimmerman et al. 1990).

Substrate: Substrate suitable for burrowing activity generally seems to be preferred (Minello et al. 1990). Postlarvae and juveniles inhabit soft, muddy areas, especially in association with plant-water interfaces. Adults are associated with terrigenous silt, muddy sand, and sandy substrates (Hildebrand 1954, Ward et al. 1980, Lassuy 1983, Williams 1984).

Physical/Chemical Characteristics:
Temperature: Eggs will not hatch at temperatures below 24°C (Cook and Lindner 1970). Postlarvae have been collected from temperatures of 12.6° to 30.6°C. Aldrich et al. (1968) demonstrated postlarval burrowing in temperatures below 18°C. Extended exposure to temperatures below 20°C may be detrimental to population survival (Zein-Eldin and Renaud 1986). Brown shrimp greater than 75 mm tolerate temperatures between 4° and 36°C, with a preferred range of 14.9° to 31.0°C (Ward et al. 1980, Copeland and Bechtel 1974). Estuarine water temperature appears to affect growth more than salinity does (Herke et al. 1987). Maximum growth, survival, and conversion efficiency occurs at 26°C (Ward et al. 1980, Copeland and Bechtel 1974). No growth occurs below 16°C and growth is reduced above 32.2°C (Ward et al. 1980, Lassuy 1983).

Salinity: Brown shrimp are euryhaline to stenohaline depending on life stage. Larvae tolerate salinities ranging from 24.1 to 36‰ (Cook and Murphy 1966). Postlarvae have been collected from salinities of 0.1 to 69‰, and have good growth at 2 to 40‰. Juvenile brown shrimp are distributed over 0 to 45‰, but have been reported to prefer 10 to 20‰ (Cook and Murphy 1966, Copeland and Bechtel 1974, Zimmerman et al. 1990). Adults tolerate salinities of 0.8 to 45‰, but their optimum range is 24 to 38.9‰ (Cook and Murphy 1966). Salinity tolerance is significantly narrowed below 20°C (Copeland and Bechtel 1974). Salinity and temperature effects are more conspicuous at either extremes (Ward et al. 1980, Zein-Eldin and Renaud 1986).

Dissolved Oxygen: In one field study, abundance levels were lower in areas that had been altered by development where dissolved oxygen content had dropped below 3 ppm (Trent et al. 1976). Detailed laboratory studies of brown shrimp oxygen consumption and its interactions with temperature, salinity, and body size are presented by Bishop et al. (1980).

Turbidity: The effects of turbidity on shrimp distribution and abundance are not well known (Kutkuhn 1966). General observations indicate that turbid water areas tend to have higher concentrations of young shrimp than clear water areas. Water turbidity has also been observed to strongly affect the brown shrimp's habitat selection preference for structure in laboratory experiments (Minello et al. 1990). Significant reductions in abundance occurred in habitats with structure when turbidity levels were high.

Migrations and Movements: Brown shrimp postlarvae (10-15 mm TL) move into estuaries from February to April with the incoming tides and migrate to shallow and often vegetated nursery areas (Copeland and Truitt 1966, King 1971, Minello et al. 1989b). In the northern Gulf of Mexico, estuarine recruitment may occur all year (Baxter and Renfro 1967). Rogers et al. (1993) hypothesized that the estuarine recruitment is enhanced by downward migration of brown shrimp postlarvae as northerly cold fronts force out estuarine water, and upward migration into the tidal water column as waters is forced back into the estuary. When juveniles reach a size generally greater than 55-60 mm, they move out into open bays. The sub-adults then migrate into the coastal waters (Minello et al. 1989b). Emigration to offshore spawning grounds occurs from May through August, coinciding with full moons and ebb tides (Copeland 1965). Some tagging studies in the northern Gulf indicate a west and southward movement of the adults with the prevailing currents (Cook and Lindner 1970, Hollaway and Baxter 1981); but other studies do not indicate a net movement in any direction when fishing effort is taken into account (Sheridan et al. 1989, Sheridan pers. comm.).

**Reproduction**

Mode: Brown shrimp reproduce sexually by external fertilization in offshore Gulf of Mexico waters (Cook and Lindner 1970, Lassuy 1983). This species has separate male and female sexes (gonochoristic).

Mating/Spawning: Mating probably occurs soon after the female molts and before the exoskeleton hardens (Cook and Lindner 1970). A spermatophore is placed inside the thelycum of the female by the male before her eggs are spawned. Spawning occurs offshore usually between depths of 46 to 91 m, but can range from 18 to 137 m (Renfro and Brusher 1982). The major spawning season is September through May; however, spawning may occur throughout the year at depths greater than 46 meters. In the northern Gulf of Mexico, there are two spawning peaks: September - November, and April - May. In waters off Texas, spawning occurs in spring and fall at depths greater than 14 m, and throughout the year at depths of 64 to 110 m. In shallower water, peaks of spawning are during late spring and in the fall (Renfro and Brusher 1982). Brown shrimp may spawn more than once during a season (Perez-Farfante 1969), and usually spawn at night (Henley and Rauschuber 1981).

Fecundity: Reitsema et al. (1982) found brown shrimp that averaged 192 mm TL released an average of 246,000 viable eggs, of which 15 % hatched.

**Growth and Development**

Egg Size and Embryonic Development: Eggs are round, golden brown, and translucent measuring approximately 0.26 mm in diameter (Cook and Murphy 1971). They are demersal and hatch within 24 hours after release into the water column (Kutkuhn 1966, Christmas and Etzold 1977).

Age and Size of Larvae: Larvae transform through 5 naupliar stages with average total lengths of 0.35, 0.39, 0.40, 0.44 and 0.50 mm respectively; 3 protozoeal stages, average total lengths of 0.96, 1.71, and 2.59 mm; and 3 mysis stages, average total lengths of 3.3, 3.8 and 4.3 mm, to become postlarvae at an average total length of 4.6 mm, in a period of 10 to 25 days (Cook and Murphy 1969, Cook and Murphy 1971). Postlarvae enter the estuaries and transform into juveniles around 25 mm TL. Larval growth rate estimates are: nauplii, 0.1-0.2 mm/day; protozoeae 0.3-0.35 mm/day; myses 0.4-0.5 mm/day (Ward et al. 1980). Postlarval growth is at a maximum between 25 to 27° C, greater than 0.5 mm/day.

Juvenile Size Range: Estuarine juveniles range from 25 to 90 mm. The shrimp spend about 3 months on the nursery grounds, and then move back offshore at sizes ranging from 80 to 100 mm TL (Copeland 1965, Cook and Lindner 1970, Parker 1970). Growth rates are temperature dependent and tend to decrease after maturity. Juveniles have grown 3.3 mm/day at temperatures above 25°C; growth decreases from 29 to 33°C (Zein-Eldin and Renaud 1986).

Age and Size of Adults: Growth of offshore adults has not been studied in detail. Females usually reach sexual maturity at about 140 mm TL (Henley and Rauschuber 1981). Brown shrimp have lived over two years in captivity (Zein-Eldin pers. comm.).

**Food and Feeding**

Trophic Mode: Larvae are omnivorous, and feeding begins with the first protozoeal stage (Cook and Murphy 1969). Juveniles and adults forage nocturnally on available food, and are more carnivorous, progressing from "encounter-feeders" to selective omnivore-predators (GMFMC 1981, Zein-Eldin and Renaud 1986, Minello and Zimmerman 1991).

Food Items: Larval stages feed on phytoplankton and zooplankton. Postlarvae feed on epiphytes, phytoplankton and detritus, but faster growth is attained on animal food (e.g. *Artemia*, fish meal, shrimp meal, and squid meal) (Gleason and Zimmerman 1984, Zein-Eldin and Renaud 1986, Zein-Eldin pers. comm.). Juveniles and adults prey on polychaetes, amphipods, and chironomid larvae, but also detritus and algae (GMFMC 1981, Zein-Eldin and Renaud 1986). Optimal growth of juveniles in a laboratory feeding study was obtained using a diet that consisted of a mixture of animal and plant material (McTigue and Zimmerman 1991). Brown shrimp were found to rely more heavily on animal material in their diet than white shrimp, and this may be the result of interspecific competition.

**Biological Interactions**

Predation: Predation is probably the most usual direct cause of brown shrimp mortality in estuarine nurseries in the northern Gulf of Mexico (Minello et al. 1989b). Habitat location may affect the degree of predation with such factors as differences in vegetation, substrate, and water turbidity altering mortality rates (Minello et al. 1989a). A wide variety of predators, including carnivorous fishes and crustaceans feed on this species. In estuarine waters, the southern flounder is considered the major predator of juvenile brown shrimp especially during the spring, but spotted seatrout, sand seatrout, and inshore lizard fish also prey heavily on penaeid shrimp (Stokes 1977, Minello et al. 1989a, Minello et al. 1989b). Other piscine predators include: sand tiger shark, bull shark, dusky shark, ladyfish, gafftopsail catfish, hardhead catfish, sheepshead, rock sea bass, bluefish, comon snook, silver seatrout, pinfish, pigfish, gulf killifish, red snapper, lane snapper, southern kingfish, spot, silver perch, black drum, red drum, Atlantic croaker, crevalle jack, cobia, code goby, Spanish mackerel, gulf flounder (Gunter 1945, Kemp 1949, Miles 1949, Springer and Woodburn 1960, Harris and Rose 1968, Boothby and Avault 1971, Odum 1971, Carr and Adams 1973, Diener et al. 1974, Bass and Avault 1975, Stokes 1977, Overstreet and Heard 1978a, Overstreet and Heard 1978b, Danker 1979, Overstreet and Heard 1982, Divita et al. 1983, Saloman and Naughton 1984, Sheridan et al. 1984, Minello et al. 1989a, Minello et al. 1989b). Penaeid shrimp are an important link in the energy flow of food webs by feeding on benthic organisms, detritus, and other organic material found in sediments (Odum 1971, Carr and Adams 1973).

Factors Influencing Populations: Disease is second only to predation and periodic physical catastrophes in limiting numbers of penaeid shrimps in nature (Couch 1978). A high proportion (up to 40%) of postlarval and juvenile brown shrimp in Mississippi waters may be infected with the *Baculovirus penaei* (BP) virus (Overstreet 1994, Stuck pers. comm.), which may be highly pathogenic to these life stages (Couch et al. 1975, Lightner and Redman 1991). The commercial fishery has a major impact on parental stock during a given year, but does not seem to affect production of young for recruitment into the next year's fishery. Environmental conditions, habitat alteration, food availability and substrate type may also affect brown shrimp abundance and distribution (Christmas and Etzold 1977, Herke et al. 1987, Minello et al. 1989b, Minello et al. 1990). Salinity, turbidity, and light conditions can interact with the brown shrimp's preference for vegetated areas, causing it to inhabit non-vegetated areas where it may be more vulnerable to predation (Minello et al. 1989b, Minello et al. 1990).

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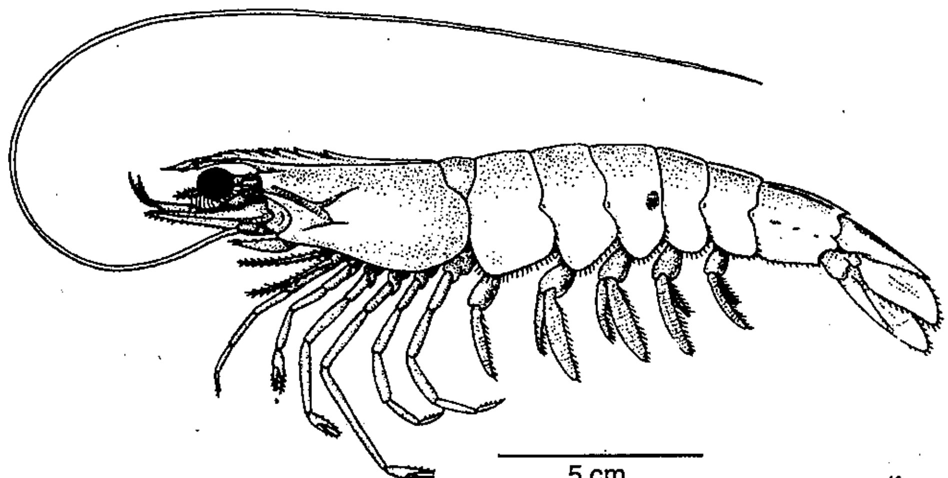
## Pink shrimp

*Penaeus duorarum*
**Adult**




(from Fischer 1978)

**Common Name:** Pink shrimp
**Scientific Name:** *Penaeus duorarum*
**Other Common Names**
Brown spotted shrimp; Green shrimp, grooved shrimp, hopper, pink spotted shrimp, pink night shrimp, pushed shrimp, red shrimp, skipper, spotted shrimp (Costello and Allen 1970, Motoh 1977, McKenzie 1981, Bielsa et al. 1983, Williams 1984); *crevette roché du nord* (French), *camarón rosado norteño* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Williams et al. 1989)

| | |
|---|---|
| Phylum: | Arthropoda |
| Class: | Crustacea |
| Order: | Decapoda |
| Family: | Penaeidae |

### Value

Commercial: Shrimping is the second most valuable commercial fishery in the U.S., and ranks seventh in quantity (NMFS 1993). U.S. landings of all shrimp species combined in the Gulf of Mexico were 100.7 thousand mt in 1992, and were valued at $316.6 million. Total U.S. pink shrimp harvest in the Gulf of Mexico was 4,785 mt in 1991, and pink shrimp typically comprise 8% of the total Gulf of Mexico shrimp landings (NOAA 1993). The pink shrimp is a commercially important species throughout the Gulf of Mexico, and its stocks have historically been considered quite stable compared to those of white and brown shrimp (Nance and Nichols 1988). However, the Tortugas pink shrimp fishery has had considerable fluctuation in landings and effort since 1986 (Nance 1994, Sheridan 1996, Steele pers. comm.). Most of the commercial catch is taken by otter and roller-frame trawls, but other methods include haul seines, cast, butterfly, drop, push, and channel nets (Costello and Allen 1970, Eldridge and Goldstein 1975, Eldridge and Goldstein 1977, Steele pers. comm.). Federal and some state laws may require the use of Turtle Excluder Devices (TEDs) year-round on shrimp trawls, but bait shrimpers (catch ≤16 kg/day, trawl <10.7 m) may be exempt from this rule (Nance pers. comm.). The major pink shrimp fishery is in the Tortuga and Sanibel grounds of southwest Florida. In Texas there is also a major fishery, but the pink shrimp is often difficult to distinguish from the brown shrimp, and is usually included with the brown shrimp fishery statistics. The pink shrimp fishery probably does not contribute more than 10% of the total catch off Texas (Klima et al. 1982), and catches are minor in Louisiana as well (Christmas and Etzold 1977). The pink shrimp helps support an substantial bait shrimp industry that is mainly in western Florida from Tampa Bay north to Apalachee Bay (Christmas and Etzold 1977). Bait harvests also occur in Biscayne Bay, along the Florida Keys, and along the east coast of Florida (Costello and Allen 1966, Joyce and Eldred 1966, Steele pers. comm.). Bait harvest is prohibited in the Everglades National Park portion of Florida Bay (Schmidt pers. comm.). Bait shrimpers in Alabama and south Texas also utilize this species, but catches are small compared to those of brown and white shrimp (Swingle 1972, Sheridan pers. comm.).

Recreational: Recreational shrimping has become increasingly popular along the Gulf coast in recent years (Christmas and Etzold 1977). Fishermen use small trawls for the most part, but seines, dip-nets, cast nets, and push nets are used as well (Christmas and Etzold 1977, Killam et al. 1992). Regulations pertaining to licensing and gear type vary among the Gulf states, and catches are limited by location and season of fishing (GMFMC 1981). In Tampa Bay, fishing effort is

Table 5.07. Relative abundance of pink shrimp in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| | | | *Life stage* | | |
| Florida Bay | ○ | | ● | ● | |
| Ten Thousand Islands | | | ● | ● | |
| Caloosahatchee River | | | ◉ | | |
| Charlotte Harbor | ○ | | ◉ | | |
| Tampa Bay | ○ | | ● | ● | |
| Suwannee River | | | ● | ○ | |
| Apalachee Bay | | | ◉ | ○ | |
| Apalachicola Bay | √ | | ◉ | ○ | |
| St. Andrew Bay | ◉ | | ◉ | √ | |
| Choctawhatchee Bay | √ | | ◉ | √ | |
| Pensacola Bay | √ | | ○ | ○ | |
| Perdido Bay | ○ | | ○ | √ | |
| Mobile Bay | √ | | ○ | √ | |
| Mississippi Sound | ○ | ○ | ○ | ○ | ○ |
| Lake Borgne | | | √ | | |
| Lake Pontchartrain | | | √ | | |
| Breton/Chandeleur Sounds | ○ | | ◉ | | |
| Mississippi River | | | | | |
| Barataria Bay | | | ○ | ○ | |
| Terrebonne/Timbalier Bays | | | √ | | |
| Atchafalaya/Vermilion Bays | | | √ | | |
| Calcasieu Lake | | | | | |
| Sabine Lake | | | | | |
| Galveston Bay | √ | | √ | | |
| Brazos River | | | ○ | | |
| Matagorda Bay | ○ | | √ | | |
| San Antonio Bay | ○ | | ○ | | |
| Aransas Bay | ○ | | ○ | | |
| Corpus Christi Bay | | | ○ | | |
| Laguna Madre | ○ | | ◉ | | |
| Baffin Bay | √ | | ○ | | |
| | A | S | J | L | E |

| Relative abundance: | | Life stage: |
|---|---|---|
| ● | Highly abundant | A - Adults |
| ◉ | Abundant | S - Spawning |
| ○ | Common | J - Juveniles |
| √ | Rare | L - Larvae/postlarvae |
| blank | Not present | E - Eggs |

highest during the fall (Christmas and Etzold 1977) when pink shrimp are moving from the estuaries into deeper waters (Costello and Allen 1970).

Indicator of Environmental Stress: Penaeid shrimps are known to be very sensitive to certain classes of chemical pollutants (Couch 1978). Pesticides and other organic chemicals have been found to cause mortality in pink shrimp (Christmas and Etzold 1977, Couch 1978). Heavy metals have also been found to be detrimental. All of these compounds can enter estuarine systems as surface runoff, point source discharges, or atmospheric deposition. This species has been used by National Oceanic and Atmospheric Administration (NOAA), Technology Resources, Inc. and the Environmental Protection Agency (EPA) to study the effects of bioaccumulation of heavy metals, chlorinated hydrocarbons, and toxic substances from bottom sediments and dredge materials (Heitmuller and Clark 1989, Parrish et al. 1989, Long et al. 1991).

Ecological: Pink shrimp distribution seems to be correlated with seagrasses in general and shoalgrass (*Halodule wrighti*) in particular, and postlarvae may actively select this habitat (Costello et al. 1986, Sheridan pers. comm.). Large populations of juvenile penaeid shrimp appear to be important in supporting large populations of certain juvenile fish species (Hettler 1989). Penaeid shrimp also provide an important link in the estuarine food web by converting detritus into available biomass for fishes, birds, and other predators many of which are commercially or recreationally important (Bielsa et al. 1983, Robblee et al. 1991).

**Range**

Overall: The pink shrimp ranges from lower Chesapeake Bay to southern Florida, through the Gulf of Mexico to Cape Catoche and the Isla Mujeres at the tip of the Yucatan Peninsula. Maximum densities in the Gulf of Mexico occur along the coast of southwestern Florida and in the Gulf of Campeche (Perez-Farfante 1969).

Within Study Area: The primary nursery ground is the Florida Bay region within Everglades National Park. This area is known as the "Tortugas Shrimp Sanctuary", and is closed to most commercial shrimping (Steele pers. comm.). However, it supports the fisheries of the Tortugas fishing grounds (Beardsley 1970, Bielsa et al. 1983, Robblee et al. 1991). Highly productive fishery areas also occur at the Sanibel grounds, supported by the Charlotte Harbor-Pine Island Sound and Tampa Bay nurseries, and the Big Bend grounds which receives stock from Apalachicola Bay and nearby estuarine areas (Bielsa et al. 1983). Other areas of high abundance are in the Laguna Madre, Texas, and offshore from Brownsville and

Galveston, often associated with coarse substrate (Sheridan pers. comm.) (Table 5.07). For the purposes of Table 5.07, all larval and postlarval stages of pink shrimp are considered together as "larvae" (L).

**Life Mode**
Eggs and adults are demersal; larvae are planktonic to the postlarval stage (Costello and Allen 1970). Postlarval and juvenile stages are demersal in estuaries and coastal bays (Perez-Farfante 1969, Costello and Allen 1970, Williams 1984). Juvenile pink shrimp burrow during the day and are active nocturnally. The nocturnal activity is most obvious during new and full moons (Hughes 1967, Williams 1984). In the Florida Bay region juvenile pink shrimp are most abundant between September and December (Robblee et al. 1991, Schmidt 1993).

**Habitat**
Type: Eggs and early planktonic larval stages are oceanic. Postlarval and juvenile stages occur in oligohaline to euhaline estuarine waters and bays, and adults occur in estuaries and nearshore waters to 64 m depth. Mature pink shrimp inhabit deep offshore marine waters with the highest concentrations in depths of 9 to 44 m. Largest numbers of pink shrimp occur where shallow bays and estuaries border on a broad shallow shelf (Perez-Farfante 1969, Costello and Allen 1970, McKenzie 1981, Bielsa et al. 1983, Williams 1984). Costello et al. (1986) indicate optimum habitats have daily tidal flushing with marine water and large seagrass beds with high blade densities. Protozoeal and mysis stage larvae on the Tortugas Shelf were found in depths of 14.6 to 47.6 m (Jones et al. 1970). Larvae most generally occurred at depths of 18.3 to 36.6 m. Older pink shrimp occurred almost entirely in inshore waters, and in Florida Bay appeared to be most abundant in shallow water habitats (Jones et al. 1970, Robblee et al. 1991). Optimum catches in Texas occur in secondary bays, but this species occurs from secondary estuarine channels out to the continental shelf (Copeland and Bechtel 1974)

Substrate: Pink shrimp inhabit a range of bottom substrates including shell-sand, sand, coral-mud, and mud. Immature pink shrimp prefer shell-sand or loose peat, and adults prefer shell-sand over loose peat (Williams 1958, Williams 1984). Juvenile shrimp are also commonly found in estuarine areas with seagrass where they burrow into the substrate by day and emerge and are active by night (Perez-Farfante 1969, Costello and Allen 1970, Williams 1984). Juveniles have been frequently associated with seagrasses, and it has been suggested that the distribution of seagrasses may influence the geographic distribution of pink shrimp populations (Costello and Allen 1970). In inshore Florida waters, small juveniles were found close to shore in beds of shoal grass, *Halodule wrightii*, while large juveniles occurred in deeper waters in turtle grass, *Thalassia testudinum* (Robblee et al. 1991, Schmidt 1993). Turtle grass has also been found to provide a suitable habitat for many organisms that penaeids and other species utilize as food (Moore 1963).

Physical/Chemical Characteristics:
Temperature: One laboratory study found larvae showed normal growth at 21° and 26°C, but died at temperatures exceeding 31°C (Williams 1955a). While larval development may be restricted to a narrower range, juveniles may be fairly tolerant of a wide range of temperatures (Williams 1955a). Juveniles tolerate temperatures between 4° to 38°C, but extended periods of low water temperatures may result in death. In Texas, they become more abundant with increasing temperature, and optimal catches occur between 20° and 38°C (Copeland and Bechtel 1974). Adult pink shrimp tolerate temperatures between 10° to 35.5°C (Williams 1955a), and temperature may be a limiting factor in the northern part of their range (Hettler 1992).

Salinity: Pink shrimp show different degrees of salinity preference at different life stages (Bielsa et al. 1983). Postlarvae have been observed in salinities ranging from 12 to 43‰ with little apparent differences in their growth (Williams 1955a). At a constant temperature of 24°C postlarvae showed no difference in growth at salinities ranging from 2 to 40‰ (Zein-Eldin 1963). Juveniles have been observed between <1 to 47‰ although they prefer salinities greater than 20‰ (Costello and Allen 1970, Copeland and Bechtel 1974). Optimum catches in Texas occur between 20 and 35‰ (Copeland and Bechtel 1974). Salinity does not appear to be a major factor in the distribution of adults or in controlling spawning activity (Roessler et al. 1969). Adults are generally found in 25 to 45‰, although they have been found in salinities as high as 69‰. Abundances are reduced above 45‰. At their lower salinity tolerance, pink shrimp have been observed in 2.7‰ in the western Gulf of Mexico; and close to 1‰ in the Caloosahatchee estuary and Ten Thousand Islands of Florida. One study indicates a possible positive relationship with freshwater runoff in the Everglades and landings in the Tortugas shrimping grounds (Browder 1985). Salinity requirements or preferences vary with geographic area and shrimp size (Costello and Allen 1970). The pink shrimp appears to have superior osmoregulatory capabilities to those of the brown shrimp during periods of low water temperature, and thus shows a greater capability for overwintering in estuaries in the northern part of its range (Williams 1955a).

Migrations and Movements: Larval stages are capable of vertical migration to control their position in the water column (Costello and Allen 1970, Allen et al. 1980). Both larval and juvenile stages show phototaxic responses in their movements (Ewald 1965, Costello and Allen 1970, Jones et al. 1970). Larvae migrate vertically away from the water surface during the day, and juveniles move to the water surface during full moon tides. Pink shrimp postlarvae enter estuarine nursery areas during the summer months after 21 to 28 days of larval and postlarval development and remain there for 2 to 6 months (Costello and Allen 1970, Jones et al. 1970, Copeland and Bechtel 1974, Allen et al. 1980). Entry into estuaries may be facilitated by net inflows of sea water after periods of low water levels. The annual rise in sea level that occurs during the warmer months when spawning is occurring may facilitate current-borne movement of postlarvae from the continental shelf into these nursery areas (Allen et al. 1980). Late juveniles and early adults (95-100 mm total length (TL)) migrate to deeper offshore waters as they grow, often migrating 150 nautical miles (Joyce 1965, Costello and Allen 1970). There is no evidence that adults from different spawning stocks migrate to different spawning grounds (Costello and Allen 1966). The intensity of the migrations at the surface appears to be associated with moon phase, with greater numbers captured during full moon tides compared to captures during new and quarter moon tides (Beardsley 1970, Costello and Allen 1970). Although emigration occurs throughout the year, the main activity peak occurs in the fall with a secondary peak in the spring. Decreasing water temperature triggers the pink shrimp to move into deeper waters (Joyce 1965, Costello and Allen 1970, Copeland and Bechtel 1974). In Florida during this time, maturing juveniles move from Florida Bay westward into the Tortugas fishery area (Costello and Allen 1966, Allen et al. 1980, Gitschlag 1986). Western Gulf of Mexico pink shrimp typically move southward as they mature into adults, but some movement to the north has been observed (Klima et al. 1987). Movement patterns are influenced by patterns in fishing effort (Sheridan et al. 1989, Sheridan pers. comm.). Shrimp stocks in northern Mexico and south Texas cross the U.S.-Mexico border and probably comprise a single management entity. The pink shrimp may also overwinter in estuaries by burrowing into sediment (Williams 1955b, Joyce and Eldred 1966, Costello and Allen 1970, Copeland and Bechtel 1974, Bielsa et al. 1983).

**Reproduction**

Mode: Sexual reproduction occurs through external fertilization by sexually dimorphic (gonochoristic) male and female individuals (Costello and Allen 1970, McKenzie 1981).

Mating/Spawning: Spawning occurs in sea water at depths of 4 to 48 m and probably in deeper waters as well (Perez-Farfante 1969). Mating may occur several times during a female's growth and development and is not always associated with spawning. Mating occurs between midnight and early morning between a hard-shell male and a soft-shell female (Eldred 1958). A spermatophore is placed on the female's abdomen during mating. When the female releases eggs the spermatophore releases sperm and fertilization occurs externally (Costello and Allen 1970, McKenzie 1981, Williams 1984). In one study, the smallest impregnated female observed was 89 mm, and the smallest ripe female was 101 mm. In the Gulf of Mexico, the two principal spawning grounds are the Sanibel and Tortuga shelf regions between depths of 15 to 48 m. The Tortugas shrimp grounds receives emigrants from nursery areas between Florida Bay and Indian Key, and the Sanibel grounds receives shrimp from nursery areas between Indian Key and Pine Island Sound. Although ripening females and postlarvae have been observed throughout the year, the number of larvae indicates the height of spawning activity occurs from April through September in the Florida Bay region (Costello and Allen 1970, Roessler and Rehrer 1971, McKenzie 1981, Williams 1984). Similar but seasonally more abbreviated patterns are seen in areas to the west and north of south Florida. Spawning occurs as water temperatures rise, and water temperature is apparently critical to reproductive development (Cummings 1961, Costello and Allen 1966, Jones et al. 1970, Allen et al. 1980, Bielsa et al. 1983). Most spawning activity in the Florida Tortugas grounds is during the waning moon (Costello and Allen 1970, Roessler and Rehrer 1971), and occurs between 20° to 31°C with maximum activity between 27° and 30.8°C (Roessler et al. 1969, Jones et al. 1970).

Fecundity: Shrimp with a weight of 10.1-66.8 g contain 44,000 to 534,000 developing ova (Martosubroto 1974).

**Growth and Development**

Egg Size and Embryonic Development: The average egg diameter is 0.31-0.33 mm. At 27-29°C, nauplii emerge 13-14 hours after the eggs are spawned (Dobkin 1961).

Age and Size of Larvae: Pink shrimp larvae undergo 5 naupliar stages with length ranges of 0.35-0.40, 0.40-0.45, 0.45-0.49, 0.48-0.55, and 0.53-0.61 mm. There are 3 protozoeal stages with length ranges of 0.86-1.02, 1.5-1.9, and 2.2-2.7 mm. There are 3 mysis stages with length ranges of 2.9-3.4, 3.3-3.9, and 3.7-4.4 mm. Two postlarval stages have been described, with length ranges of 3.8 to 4.8 mm, and 4.7 to nearly 10.0 mm (Ewald 1965, Costello and Allen 1970, Allen et al. 1980). The pink shrimp grows from nauplius to postlarva in 2 to 3 weeks depending on the temperature and location. Metamorphosis from protozoea to postlarva occurs in 15 days at 26°C, and in 25 days at 21°C (Ewald 1965).

Juvenile Size Range: Reported juvenile growth rates vary from 7 to 52 mm/month (Williams 1955a, Eldred et al. 1961, Iversen and Jones 1961), and subadults and adults grow approximately 0 to 22 mm/month (Costello and Allen 1960, Iversen and Jones 1961, McCoy and Brown 1967). Sexual maturity occurs at 85 mm TL for females and 74 mm TL for males (Dobkin 1961, Bielsa et al. 1983).

Age and Size of Adults: The average sizes of large male and female pink shrimp are 170 mm and 210 mm TL, respectively. The average maximum age is 83 weeks with an absolute maximum age of 2 years (Bielsa et al. 1983).

**Food and Feeding**

Trophic Mode: Pink shrimp are omnivorous consumers in marine and estuarine systems (Bielsa et al. 1983). Larvae in the naupliar stages do not feed, but first protozoea were observed to begin feeding immediately when food became available (Ewald 1965). Larvae and postlarvae feed on various plankton species. Juveniles and adults are opportunistic and forage primarily at night, on benthic prey, in shallow grass beds (Bielsa et al. 1983, Williams 1984, Nelson and Capone 1990, Schmidt 1993).

Food Items: Larvae raised in hatchery conditions are fed various cultures of algae initially, and increasing amounts of brine shrimp nauplii as they became older (Ewald 1965). Typical juvenile and adult prey includes nematodes, polychaetes, ostracods, copepods, dinoflagellates, annelids, gastropods, mollusks, filamentous green and blue-green algae, vascular detritus, and inorganic material (Bielsa et al. 1983, Williams 1984, Nelson and Capone 1990, Schmidt 1993).

**Biological Interactions**

Predation: Many inshore fish species utilize the pink shrimp in their diet. Sport fishes such as snook, spotted seatrout, and gray snapper feed heavily on this species, but it is found in varying amounts in the diets of other fishes. These include lemon shark (*Negaprion brevirostris*), hardhead catfish, gafftopsail catfish (*Bagre marinus*), pinfish, pigfish (*Orthopristis chrysoptera*), sheepshead, crevalle jack, red drum, code goby, Spanish mackerel, and red snapper (*Lutjanus campechanus*) (Kemp 1949, Miles 1949, Springer and Woodburn 1960, Odum 1971, Carr and Adams 1973, Overstreet and Heard 1978, Overstreet and Heard 1982, Saloman and Naughton 1984, Sheridan et al. 1984, Schmidt 1986, Harrigan et al. 1989, Hettler 1989). Many reef species, such as mutton snapper (*Lutjanus analis*), red grouper (*Epinephelus morio*), black grouper (*Mycteroperca bonaci*), and even pelagic species such as king mackerel (*Scomberomorus cavalla*) have been found to prey on pink shrimp (Bielsa et al. 1983). In addition, several birds prey on this species. These include wading birds, feeding opportunistically in coastal areas and seabirds foraging in mixed species flocks on concentrations of prey. Pink shrimp are probably an easy target for diving seabirds during periods of congregated movement. This species has also been found in the stomachs of some marine mammals (*Tursiops truncatus* and *Stenella coeruleoalba*), and may possibly be a prey item of marine reptiles (Bielsa et al. 1983). The bay squid (*Lolliguncula brevis*) is known to consume penaeid shrimp, and may include the pink shrimp as a prey item (Hargis 1979).

Factors Influencing Populations: Disease is second only to predation and periodic physical catastrophes in limiting numbers of penaeid shrimps in nature (Couch 1978). A significant number of pink and brown shrimp in the Gulf of Mexico may be infected with the *Baculovirus penaei* (BP) virus (Overstreet 1994, Stuck pers. comm.). This virus is highly pathogenic to the early life stages of penaeid shrimp (Lightner and Redman 1991), and it may be responsible for epizootic mortalities of pink shrimp (Couch et al. 1975). Penaeid shrimp infected with symbiotic organisms may be weakened and more susceptible to mortality in waters with low DO (Overstreet 1978). Distribution, abundance, and recruitment of the pink shrimp may be limited by salinity, freshwater runoff, temperature, seagrass habitat, and substrate (Williams 1965, Bielsa 1983, Browder 1985, Hettler 1992, Schmidt 1993). Recruitment overfishing by commercial shrimpers does not appear to be a problem for this species, but annual catch is managed to prevent the parent stock from falling below the level considered necessary to maintain recruitment (Nance 1989, Klima et al. 1990). Environmental changes may cause variable recruitment (Klima et al. 1990, Sheridan 1996). The pink shrimp may compete for or be displaced by brown shrimp from habitats. This species can be difficult to distinguish from the brown shrimp, often resulting in unreliable data (Sheridan pers. comm.).

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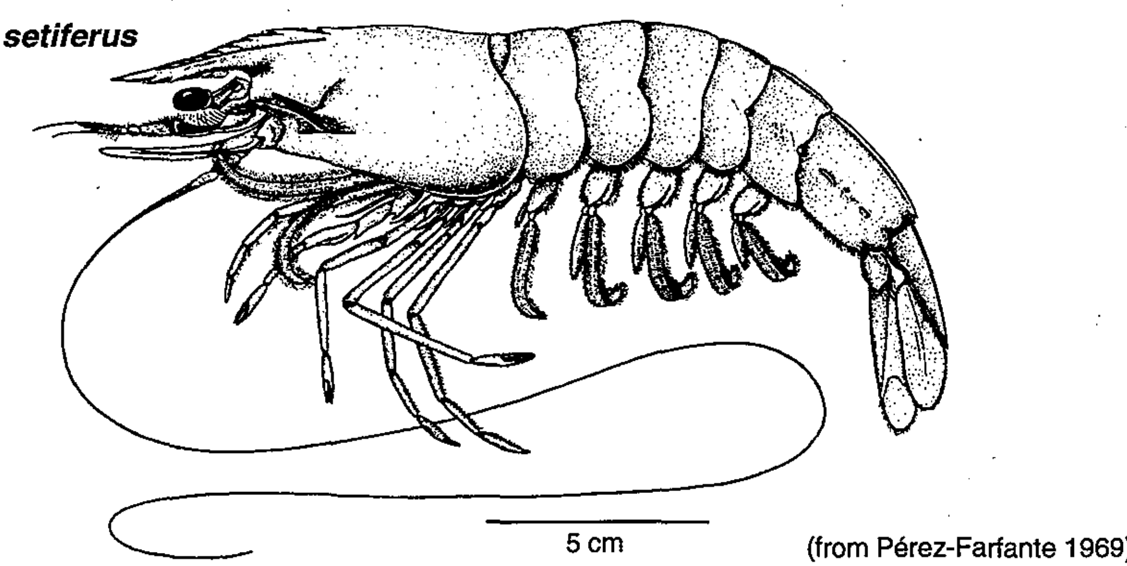
# White shrimp



(from Pérez-Farfante 1969)

**Common Name:** white shrimp
**Scientific Name:** *Penaeus setiferus*
**Other Common Names:** Blue shrimp, blue-tailed shrimp, common shrimp, Daytona shrimp; gray shrimp, green shrimp, green-tailed shrimp, lake shrimp, rainbow shrimp, southern shrimp (Pérez-Farfante 1969, Lindner and Cook 1970, Motoh 1977, McKenzie 1981, Muncy 1984); *crevette ligubam du nord* (French), *camarón blanco norteño* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Williams et al. 1989)

| | |
|---|---|
| Phylum: | Arthropoda |
| Class: | Crustacea |
| Order: | Decapoda |
| Family: | Penaeidae |

**Value**

Commercial: Shrimping has been ranked as the second most valuable commercial fishery in the U.S., and seventh in quantity (NMFS 1993). U.S. landings of all shrimp species combined in the Gulf of Mexico were 100.7 thousand mt in 1992, and were valued at $316.6 million. Total U.S. white shrimp harvest in the Gulf of Mexico was 32,012 mt in 1991, and white shrimp typically comprise 31% of the total Gulf of Mexico shrimp landings (NOAA 1993). White shrimp were the targeted species in the U.S. shrimp fishery until the mid-1930's; other species were darker and not as marketable. The species is fished for throughout the nearshore Gulf of Mexico and along the southeast U.S Atlantic coast. Maximum catches in the Gulf occur along the Louisiana coast west of the Mississippi Delta (Christmas and Etzold 1977). Catches of young-of-the-year shrimp occur almost entirely during summer and fall, while the spring white shrimp fishery consists of adults that have overwintered in the estuaries (Christmas and Etzold 1977, Nance et al. 1991). The Gulf of Mexico white shrimp fishery is considered fully exploited, and a longterm potential annual yield of 34,403 mt has been estimated (NOAA 1993). It has been suggested that commercial harvest has reached a point at which overfishing can occur (Nance and Nichols 1988, Nance 1989). There is also a bait fishery for white shrimp throughout the bays and nearshore waters from June to October. This catch, as well as most of the commercial catch, is obtained using otter trawls. Federal and some state laws may require the use of Turtle Excluder Devices (TEDs) on shrimp trawls, but bait shrimpers (catch ≤16 kg/day, trawl <10.7 m) may be exempt from these regulations (Nance pers. comm.). Other methods include haul seines and cast, butterfly, drop, push, and channel nets (Eldridge and Goldstein 1975, Eldridge and Goldstein 1977). White shrimp form the mainstay for the Texas commercial bay fishery (Christmas and Etzold 1977). They also form an important part of the catch in Alabama where it is one of the primary species harvested for bait (Swingle 1972). Highest catches occur in fall months using otter trawls.

Recreational: Recreational shrimping has become increasingly popular along the Gulf coast in recent years (Christmas and Etzold 1977). Fishermen use small trawls for the most part, but seines, cast nets, and push nets are used as well. Approximately 4,000 mt (heads on) of total shrimp (brown, pink, and white) were taken by recreational shrimpers in 1979 in Texas and Louisiana. Regulations pertaining to licensing and gear type vary among the Gulf states, and catches are limited by location and season of fishing (GMFMC 1981).

Table 5.08. Relative abundance of white shrimp in 31 Gulf of Mexico estuaries (from *Volume I*).

| | *Life stage* | | | | |
|---|---|---|---|---|---|
| | A | S | J | L | E |
| Florida Bay | | | | | |
| Ten Thousand Islands | | | | | |
| Caloosahatchee River | | | | | |
| Charlotte Harbor | | | | | |
| Tampa Bay | | | | | |
| Suwannee River | √ | | √ | √ | |
| Apalachee Bay | ◉ | | ● | | |
| Apalachicola Bay | ◉ | | ● | √ | |
| St. Andrew Bay | O | | O | | |
| Choctawhatchee Bay | O | | ◉ | | |
| Pensacola Bay | O | | ◉ | | |
| Perdido Bay | O | | O | | |
| Mobile Bay | O | | ● | | |
| Mississippi Sound | ● | O | ● | ◉ | O |
| Lake Borgne | ◉ | | ● | | |
| Lake Pontchartrain | ◉ | | ● | | |
| Breton/Chandeleur Sounds | O | O | O | O | O |
| Mississippi River | | | O | O | |
| Barataria Bay | ◉ | | ● | ● | √ |
| Terrebonne/Timbalier Bays | O | | ◉ | O | |
| Atchafalaya/Vermilion Bays | ◉ | | ● | ◉ | |
| Calcasieu Lake | O | | ● | ● | |
| Sabine Lake | ● | | ● | ● | |
| Galveston Bay | O | | ● | ● | |
| Brazos River | O | | ● | ◉ | |
| Matagorda Bay | ◉ | | ● | ● | |
| San Antonio Bay | ● | | ● | ● | |
| Aransas Bay | O | | ◉ | O | |
| Corpus Christi Bay | ◉ | | ◉ | | |
| Laguna Madre | O | | ◉ | √ | |
| Baffin Bay | √ | | √ | | |
| | A | S | J | L | E |

| Relative abundance: | | Life stage: |
|---|---|---|
| ● | Highly abundant | A - Adults |
| ◉ | Abundant | S - Spawning |
| O | Common | J - Juveniles |
| √ | Rare | L - Larvae/postlarvae |
| blank | Not present | E - Eggs |

Indicator of Environmental Stress: Pesticides have been found to have adverse effects on shrimp populations along the coast of the Gulf of Mexico (Christmas and Etzold 1977, Couch 1978). White shrimp at locations in Galveston treated by aerial sprays of Malathion have experienced mortalities of up to 80%. The use of this pesticide has increased to the point that currently much of the Gulf coast uses some form of it in mosquito control programs. Other pesticides, as well as industrial and agricultural discharges, pose serious threats when used or discharged in drainage areas where they can enter water systems. The effects of petroleum products on penaeid shrimp is not well known. Mortality and pathological conditions have been induced in species exposed to different concentrations of these chemicals. Penaeid shrimp are sensitive to heavy metals (Couch 1978). Jackson (1975) found mercury to be two orders of magnitude more toxic than zinc for juvenile white shrimp, with higher mortalities occurring at higher temperatures. Mortalities were also higher during spring compared to winter.

Ecological: Penaeid shrimp provide an important link in the estuarine food web by converting detritus and plankton into available biomass for fishes and other predators. White shrimp are preyed on by many species of estuarine and coastal finfish. Abundant juvenile penaeid shrimp appear to be important in supporting large populations of certain fish species (Hettler 1989). The postlarvae and juveniles are more tolerant of lower salinities than other *Penaeus* species (Williams 1984, Zein-Eldin and Renaud 1986), and may venture further into brackish marshes. White shrimp remain in estuaries longer and grow larger than brown shrimp (Christmas and Etzold 1977). They may be displaced by brown shrimp from *Spartina* marshes to nearby mud substrates in areas where they are sympatric (Giles and Zamora 1973, Zimmerman and Minello 1984).

**Range**

Overall: The white shrimp ranges from Fire Island, New York, to the St. Lucie Inlet, Florida, on the Atlantic coast. In the Gulf of Mexico, it is found from Ochlockonee River, Florida, to Campeche, Mexico. It is rarely found near the Dry Tortugas, Florida, and is absent around the southernmost portion of the Florida peninsula. The centers of abundance occur off Georgia and northeastern Florida for the Atlantic coast; and Louisiana, Texas and Tabasco for the Gulf of Mexico (Williams 1984, Klima et al. 1987), but greatest densities occur off the coast of Louisiana (Klima et al. 1982). NOAA (1985) reports the range within the Gulf of Mexico from Apalachee Bay, Florida, to northeast Campeche Bay, Mexico. Pérez-Farfante (1969) distinguishes the area of Ciudad, Mexico as the southern limit in the Gulf of Mexico.

Within Study Area: Postlarval to subadult white shrimp are well established throughout the Texas, Louisiana, and Mississippi estuaries and nearshore Gulf waters, utilizing the nursery habitat generally from June/July through October/November (Christmas and Etzold 1977) (Table 5.08). For the purposes of Table 5.08, all larval and postlarval stages of white shrimp are considered together as "larvae" (L).

**Life Mode**
Eggs are spawned from spring through fall in offshore waters, where they hatch and develop into larvae (Etzold and Christmas 1977, Klima et al. 1982). Eggs are demersal and larval stages are planktonic. Postlarvae become benthic upon reaching the nursery areas of estuaries, and begin development into the juvenile stage (Pérez-Farfante 1969, Lindner and Cook 1970, McKenzie 1981, Muncy 1984, Williams 1984). As juveniles approach adulthood, they move out of estuaries into coastal waters where they mature and spawn. Both juveniles and adults are demersal in estuarine and coastal waters, and are usually found at depths of <30 m (Pérez-Farfante 1969, Lindner and Cook 1970, Etzold and Christmas 1977, McKenzie 1981, Muncy 1984, Williams 1984).

**Habitat**
Type: The white shrimp is neritic to estuarine, and pelagic to demersal, depending on the life stage. Eggs and early planktonic larval stages occur in nearshore marine waters. Postlarvae seek estuarine habitats of shallow water with muddy/sand bottoms high in organic detritus, or abundant in marsh grass in oligohaline to euhaline salinities. Juveniles prefer lower salinity waters, and are frequently found in tidal rivers and tributaries throughout their range (Christmas and Etzold 1977). Juveniles and sub-adults move into offshore waters during fall and winter. Adults generally inhabit nearshore waters of the Gulf in depths less than 27 m, and are usually more abundant at a depth of 14 m (Pérez-Farfante 1969, Lindner and Cook 1970, Renfro and Brusher 1982, Muncy 1984, Williams 1984).

Substrate: Postlarvae and juveniles inhabit mostly mud or peat bottoms with large quantities of decaying organic matter or vegetative cover (Williams 1955b, Williams 1958). Adults are found on bottoms of soft mud or silt in offshore waters (Pérez-Farfante 1969, Lindner and Cook 1970, Muncy 1984, Williams 1984). It has been suggested that white shrimp densities are related to the amount of marsh vegetation available in intertidal estuarine habitats (Turner 1977), but other studies have found abundances to be quite variable in relationship to vegetation (Minello et al. 1990, Zimmerman et al. 1990, Zimmerman pers. comm.).

Physical/Chemical Characteristics:
Temperature: This species is tolerant of temperatures ranging from approximately 7° to 38°C (Williams 1955b, Joyce 1965, Zein-Eldin and Griffith 1969). Sudden changes in temperature, however, can be detrimental. White shrimp are more tolerant of high temperatures and less tolerant of low temperatures than brown or pink shrimp (Christmas and Etzold 1977). Postlarval white shrimp have been collected in temperatures from 12.6° to 30.6°C. Juveniles have been collected in temperatures ranging from 6.5° to 39.0°C, with peaks in abundance between 15° and 33°C (Zein-Eldin and Renaud 1986). Normal growth of juveniles occurs between 15°-16° and 25°-30°C with growth rates decreasing as temperatures approach > 35°C (Zein-Eldin and Griffith 1969) or drop below 15°C (Christmas and Etzold 1977, St. Amant and Lindner 1966).

Salinity: White shrimp can be considered euryhaline since most life stages tolerate fairly wide salinity ranges (Gunter 1961, Zein-Eldin and Griffith 1969, Lindner and Cook 1970, Copeland and Bechtel 1974). This species is apparently more tolerant of lower salinities than brown shrimp (Gunter 1961), and does not appear to be affected by sudden salinity drops as the brown shrimp is (Minello et al. 1990). White shrimp postlarvae have been collected in salinities ranging from 0.4 to 37.4‰. Juveniles seem to prefer or tolerate lower salinities than do other penaeid species (Williams 1955a). They prefer salinities less than 10‰ (Zein-Eldin and Renaud 1986), and have been found several kilometers upstream in rivers and tributaries (Christmas and Etzold 1977). Collections of juveniles have occurred in salinities from 0.3‰ in Florida to as high as 41.3‰ in the Laguna Madre of Texas (Gunter 1961, Joyce 1965). Adults are usually found offshore in waters with salinities greater than 27‰ (Muncy 1984). Size appears to be related to salinity tolerance (Williams 1955a, Joyce1965). In laboratory studies no growth differences were detected over a salinity range from 2 to 40‰ (Zein-Eldin and Griffith 1969).

Migrations and Movements: White shrimp postlarvae migrate into the estuarine nurseries through passes from May to November, with peaks in June and a second peak in September for the northwest Gulf of Mexico (Baxter and Renfro 1967, Klima et al. 1982). Juveniles migrate farther up the estuary into less saline water than brown or pink shrimp (Pérez-Farfante 1969). As shrimp grow and mature they leave the marsh habitat for deeper, higher salinity parts of the estuary prior to their emigration to Gulf waters (Lindner and Cook 1970). The emigration of juveniles and subadults from estuaries usually occurs in late August and September, and appears to be related to the size of the shrimp and the environmental conditions within the estuarine system (Klima et al. 1982). One factor that may influence this emigration is sharp drops in water temperature occurring during the fall and winter (Pullen and Trent 1969). After leaving the estuaries, there is a general westward movement of adult white shrimp in offshore waters combined with movement to deeper waters (Baxter and Hollaway 1981, Hollaway and Sullivan 1982, Lyon and Boudreaux 1983). In April to mid-May, white shrimp move back to nearshore and inshore waters (Hollaway and Sullivan 1982).

**Reproduction**

Mode: Reproduction is by external fertilization between sexually dimorphic male and female individuals (Pérez-Farfante 1969, Lindner and Cook 1970, Muncy 1984). Although this species has separate male and female sexes (gonochoristic), hermaphroditism has been reported in white shrimp parasitized by *Thelohania* sp. (Rigdon et al. 1975).

Mating/Spawning: The external genital organ (thelycum) in female white shrimp is open, unlike those in brown shrimp, making copulation possible between two hard-shelled individuals (Overstreet 1978, Muncy 1984). The male places a spermatophore on the female's abdomen, and when eggs are released the spermatophore releases sperm fertilizing the eggs externally (Pérez-Farfante 1969). Spawning along the Atlantic coast probably begins in May and extends through September (Lindner and Anderson 1956, Williams 1984); in the Gulf, the season probably extends from March to September or October (spring to late fall) (Franks et al. 1972). Spawning occurs offshore at depths of 9 to 34 m deep and peaks in the summer (June-July). There is also some suggestion of limited spawning within estuaries and bays (Lindner and Cook 1970, Whitaker pers. comm.). Females that spawn early may spawn a second time in late summer or fall, and possibly up to 4 times in a season (Lindner and Anderson 1956, Lindner and Cook 1970, Whitaker pers. comm.). The ability of shrimp over one year old to spawn is unknown, but considered possible (Lindner and Cook 1970, Zein-Eldin pers. comm.). Other shrimp species with similar methods of reproduction have been found to spawn again in their second year. Rapid temperature changes, such as the sudden increases and decreases that occur in the summer and fall, seem to trigger spawning (Henley and Rauschuber 1981).

Fecundity: A large female is estimated to produce 0.5 to 1.0 million eggs at a single spawning (Anderson et al. 1949, Lindner and Cook 1970, Williams 1984).

**Growth and Development**

Egg Size and Embryonic Development: Egg development is oviparous. Fertilized eggs are demersal, nonadhesive, spherical, and are approximately 0.28 mm in diameter (Lindner and Cook 1970). Ripe eggs are 0.2 to 0.3 mm in diameter and hatch in 10 to 12 hours after fertilization (Klima et al. 1982).

Age and Size of Larvae: Eggs hatch into planktonic nauplii approximately 0.3 mm TL (Klima et al. 1982). Larvae transform through 5 naupliar stages, 3 protozoeal stages and 3 mysis stages (Pérez-Farfante 1969). The length of larval life is from 10 to 12 days, depending on local food, habitat, and environmental conditions. They enter the estuaries as postlarvae at total lengths (TL) of approximately 7 mm. Rapid growth rates of 20-40 mm/month occur in nursery areas (Williams 1955a, Lindner and Anderson 1956, Pérez-Farfante 1969, Lindner and Cook 1970). Growth is far more strongly affected by changes in temperature than salinity (Zein-Eldin and Griffith 1969), with little or no growth occuring below 18°C (Zein-Eldin and Renaud 1986). Postlarvae develop into juveniles at about 25 mm TL (Christmas et al. 1976).

Juvenile Size Range: Juveniles can attain lengths of 98 to 146 mm TL in 4 to 6 weeks after entering estuarine areas (Zein-Eldin and Renaud 1986). Emigration of subadults occurs through the summer and fall at a size of 100 to 120 mm TL. Sexual maturity is generally reached at 140 mm TL in the northern Gulf of Mexico (Pérez-Farfante 1969, Lindner and Cook 1970).

Age and Size of Adults: The white shrimp has a life expectancy of 18 months, although some have been maintained in the laboratory for 3 to 4 years (Klima et al. 1982). Females become sexually mature at about 165 mm TL and ripe sperm first appears in males at about 119 mm TL (Burkenroad 1939, Lindner and Cook 1970).

**Food and Feeding**

Trophic Mode: White shrimp are omnivorous at all life stages, but may depend more heavily on plant matter than animal matter (McTigue and Zimmerman 1991). Larval white shrimp are planktivorous, while adults and juveniles are scavengers.

Food Items: Penaeid larvae subsist on egg yolk until the Protozoea I stage when active feeding begins (Lindner and Cook 1970). Larvae are reported to feed on plankton and suspended detrital material, and in the laboratory, they have been successfully fed microscopic green algae and brine shrimp nauplii. Both juveniles and adults are omnivorous. Juveniles combine detrital feeding with scavenging on the bottom sediment. As they mature, they combine predation with detrital feeding. Foods consist of detritus,insects, annelids, gastropods, and fish, and copepods, bryozoans, sponges, corals, filamentous algae, and vascular plant stems and roots (Darnell 1958, Pérez-Farfante 1969, Christmas and Etzold 1977).

**Biological Interactions**

Predation: Finfish prey heavily on this species. Known predators include tiger shark (*Galeocerdo cuvier*), Atlantic sharpnose shark (*Rhizoprionodon terraenovae*), bull shark, ladyfish (*Elops saurus*), hardhead catfish, crevalle jack, red snapper (*Lutjanus campechanus*), southern kingfish (*Menticirrhus americanus*), spotted seatrout, sand seatrout, red drum, black drum, cobia (*Rachycentron canadum*), code goby, Spanish mackerel, southern flounder, and gulf flounder (Gunter 1945, Kemp 1949, Miles 1949, Darnell 1958, Springer and Woodburn 1960, Boothby and Avault 1971, Stokes 1977, Overstreet and Heard 1978a, Overstreet and Heard 1978b, Danker 1979, Creel and Divita 1982, Overstreet and Heard 1982, Saloman and Naughton 1984, Sheridan et al. 1984). Some predation by bay squid (*Lolliguncula brevis*) is possible (Hargis 1979). Penaeid shrimp are an important link in the energy flow of food webs by feeding on benthic organisms, detritus, and other organic material found in sediments (Odum 1971, Carr and Adams 1973).

Factors Influencing Populations: The commercial shrimp fishery may be impacting the white shrimp population (Nance and Nichols 1988, Nance 1989, Nance et al. 1989). Catch statistics indicate that current harvest levels may be over-exploiting the resource, causing a decline in adult recruitment. Pathogens also affect the white shrimp. It is susceptible to diseases and parasites, but the extent of resultant mortality is largely unknown (Couch 1978, Muncy 1984). Predation and episodic catastrophes probably play more important roles as limiting factors of natural populations. Penaeid shrimp infected with biosymbionts may be weakened and die in low oxygen situations (Overstreet 1978). In the Mississippi Sound, adult white shrimp are infected with a cestode which invades the hepatopancreas (Muncy 1984). White shrimp tend to aggregate, forming a patchy distribution pattern in estuaries. The environmental factors that govern this type of distribution are not known (Zimmerman et al. 1990, Zimmerman pers. comm.). Suitable estuarine habitat is critical to survival and recruitment of juveniles (Turner 1977, Nance et al. 1989). However, development has destroyed or altered large portions of these estuarine areas to a point of low productivity (Christmas and Etzold 1977). Continued loss of this habitat may result in declines in recruitment and harvest (Christmas and Etzold 1977, Nance et al. 1989). Episodic weather events such as hurricanes and freezes also impact white shrimp populations (Kutkuhn 1962, Barrett and Gillespie 1973). Hurricanes can result in high mortality of a spawning class by causing adverse environmental conditions. Such conditions include high tides and extensive flooding, higher salinities, excessive turbulence, turbidity, and habitat destruction. Freezes can cause mass mortalities by reducing the water temperature to lethal levels. Other factors felt to be related to penaeid shrimp population dynamics are productivity of estuarine nursery areas, food availability and content, refuge from predation, amount of freshwater inflow, light intensity, tide, and rainfall (Christmas and Etzold 1977, Gracia 1991).

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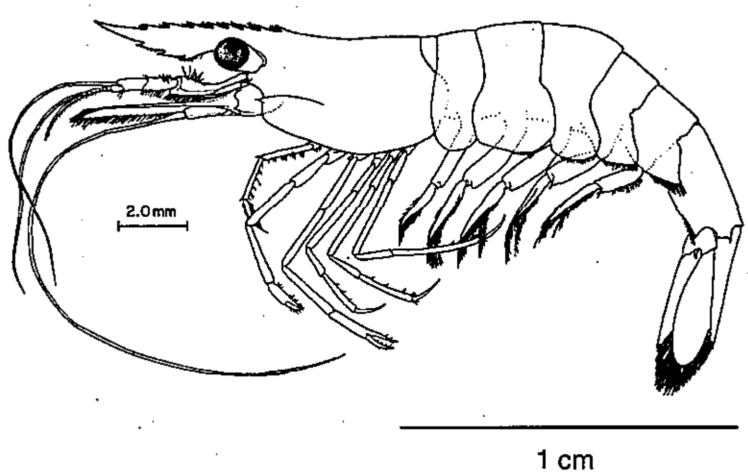
***Palaemonetes pugio***
**Adult**




(from Heard 1979)

**Common Name**: grass shrimp
**Scientific Name**: *Palaemonetes pugio*
**Other Common Names**: daggerblade grass shrimp (Williams et al. 1989), glass shrimp
**Classification** (Williams et al. 1989)

| | |
|---|---|
| Phylum: | Arthropoda |
| Class: | Crustacea |
| Order: | Decapoda |
| Family: | Palaemonidae |

There are several *Palaemonetes* species in U.S. estuarine waters, which are known collectively as "grass shrimp" (Camp pers. comm.). For the purposes of this life history summary, "grass shrimp" refers specifically to *P. pugio*, also known as "daggerblade grass shrimp" (Williams et al. 1989). Closely related "sister species" include *P. vulgaris* (marsh grass shrimp), *P. intermedius* (brackish grass shrimp), *P. kadiakensis* (Mississippi grass shrimp), and *P. paludosus* (riverine grass shrimp) (Hedgepeth 1966, Williams et al. 1989).

**Value:**
Commercial: The grass shrimp has little commercial value. It is available for sale through commercial biological suppliers for use in toxicity testing (Buikema et al. 1980). It is also sometimes sold in pet stores as live food for aquarium fish (Anderson 1985).

Recreational: The grass shrimp has little recreational value (Anderson 1985). Anglers catch grass shrimp to use as live bait for game fish (Huner 1979). In Louisiana, preserved grass shrimp are also sold as bait in some fishing shops.

Indicator of Environmental Stress: This species is often used for LD50 bioassays for petroleum hydrocarbons because it is usually a common inhabitant of estuarine systems. It has also been used to study toxicity and bioaccumulation of heavy metals, insecticides, petroleum hydrocarbons, and suspended particulate sediments (Schimmel and Wilson 1977, Anderson 1985, Khan et al. 1989, Moore 1989, Rice et al. 1989, Thorpe and Costlow 1989, Burton and Fisher 1990, Fisher and Clark 1990, Lindsay and Sanders 1990, Rule and Alden 1990, Long et al. 1991).

Ecological: This grass shrimp and other members of its genus are among the most widely distributed and abundant shallow water benthic macroinvertebrates in Gulf of Mexico estuaries (Odum and Heald 1972, Anderson 1985, Zimmerman et al. 1990). Its abundance in estuaries can enable it to have a substantial impact on the dominant energy sources of these systems while channeling significant quantities of that energy through its own population (Welsh 1975). The grass shrimp's importance as a prey item in the diet of many estuarine fishes and as a link in the marine food web makes this a valuable species ecologically. It is also important in estuarine trophic dynamics in speeding detrital breakdown by breaking up large detrital particles during its feeding activities. This serves to prevent blockages or accumulations from occurring due to pulses of detrital material into the environment. The grass shrimp also transfers refractory organic matter and detritus to higher trophic levels by repackaging this material into feces, heterogeneous fragments, dissolved organic material, and shrimp biomass, thus making this food source more available to a variety of trophic levels (Welsh 1975, Anderson 1985, Killam et al. 1992).

Table 5.09. Relative abundance of grass shrimp in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| | *Life stage* | | | | |
| Florida Bay | ○ | ○ | ○ | ○ | ○ |
| Ten Thousand Islands | ○ | ○ | ○ | ○ | ○ |
| Caloosahatchee River | ● | ● | ● | ● | ● |
| Charlotte Harbor | ● | ● | ● | ● | ● |
| Tampa Bay | ● | ● | ● | ● | ● |
| Suwannee River | ● | ● | ● | ● | ● |
| Apalachee Bay | ● | ● | ● | ● | ● |
| Apalachicola Bay | ● | ● | ● | ● | ● |
| St. Andrew Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Choctawhatchee Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Pensacola Bay | ● | ● | ● | ● | ● |
| Perdido Bay | | | | | |
| Mobile Bay | ● | ● | ● | ● | ● |
| Mississippi Sound | ● | ● | ● | ● | ● |
| Lake Borgne | ● | ● | ● | ● | ● |
| Lake Pontchartrain | ○ | ○ | ○ | ○ | ○ |
| Breton/Chandeleur Sounds | ◉ | ◉ | ◉ | ◉ | ◉ |
| Mississippi River | ○ | ○ | ○ | ○ | ○ |
| Barataria Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Terrebonne/Timbalier Bays | ◉ | ◉ | ◉ | ◉ | ◉ |
| Atchafalaya/Vermilion Bays | ● | ● | ● | ● | ● |
| Calcasieu Lake | ● | ● | ● | ● | ● |
| Sabine Lake | ● | ● | ● | ● | ● |
| Galveston Bay | ● | ● | ● | ● | ● |
| Brazos River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Matagorda Bay | ● | ● | ● | ● | ● |
| San Antonio Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Aransas Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Corpus Christi Bay | ● | ● | ● | ● | ● |
| Laguna Madre | ● | ● | ● | ● | ● |
| Baffin Bay | ● | ● | ● | ● | ● |
| | A | S | J | L | E |

| Relative abundance: | | Life stage: |
|---|---|---|
| ● | Highly abundant | A - Adults |
| ◉ | Abundant | S - Spawning |
| ○ | Common | J - Juveniles |
| √ | Rare | L - Larvae/postlarvae |
| blank | Not present | E - Eggs |

**Range**

Overall: The range of the grass shrimp is probably discontinuous from Quebec to Nova Scotia, and Maine to Texas (Williams 1984).

Within Study Area: This is a ubiquitous species, along with its congeners, throughout the estuaries of the Gulf coast from Florida Bay, Florida, to the Laguna Madre, Texas (Table 5.09). It is often replaced in higher salinities by *Palaemonetes vulgaris* and/or *P. intermedius*, and by *P. kadiakensis* and *P. paludosus* in fresh water (Hedgepeth 1966).

**Life Mode**

Eggs are carried by the female, and the larvae are planktonic. Juveniles and adults are littoral or estuarine and benthic, appearing to prefer vegetated areas (Williams 1984). In Georgia salt marshes, juveniles and adults are segregated by habitat (Kneib 1987a). Movements and distribution patterns may be influenced by both photoperiod and tidal cycles (Anderson 1985, Kneib 1987a). Juveniles and adults are omnivorous in their feeding habits.

**Habitat**

Type: The grass shrimp occupies habitats ranging from estuarine to riverine (Knowlton and Williams 1970). It is usually found near the water's edge in shallows of bays and creeks, or in marshes, submerged vegetation and oyster reefs (Williams 1984, Anderson 1985). Although most common in shallow waters, it has been collected in waters as deep as 17 m. During periods of extreme heat or cold it retreats to deeper channel areas. It is often abundant in turbid waters possibly to avoid predators, but turbidity is not a necessary habitat requirement (Anderson 1985, Killam et al. 1992). It also uses seagrass and other aquatic vegetation as refuge from predation and as foraging areas (Killam et al. 1992). Juveniles are found primarily on vegetated marsh surfaces in the intertidal region, while adults inhabit subtidal areas (Anderson 1985, Kneib 1987a).

Substrate: Vegetated or oyster shell substrate is preferred (Williams 1984, Anderson 1985).

Physical/Chemical Characteristics:

Temperature: The grass shrimp is eurythermal and both juveniles and adults can tolerate from 5° to 38°C, depending on geographic location (Wood 1967, Christmas and Langley 1973, Anderson 1985). In laboratory studies an estimated 80% of larvae completed metamorphosis to postlarval stages at temperatures of 20°C to 30°C at salinities ranging from 11 to 33‰, with optimum development occurring at 20° to 27°C and 17 to 27‰ (Sastry and Vargo 1977, McKenney and Neff 1979). Juveniles and adults have optimum survival at temperatures ranging from 18° to 25°C in salinities of

4 to 16‰ (Wood 1967). Growth of juveniles is greatest at temperatures between 25° and 32°C and salinities between 16 and 22‰. Below 14°C growth decreases, and is negligible at 11°C (Wood 1967). Breeding temperatures vary with geographic location of the study, and range between 17° to 38°C (Sastry and Vargo 1977, Wood 1967).

Salinity: The effects of salinity on larval growth and development are unclear and may vary with geographic location and individual populations. Larval survival, however, is generally poor at salinities of less than 15‰ (Kirby and Knowlton 1976, McKenney and Neff 1979). The upper and lower 96 hour LC50 values for larval grass shrimp in laboratory studies occurred at 16 and 46‰ respectively (Kirby and Knowlton 1976). The optimum salinity for complete larval development is reportedly from 20 to 25‰ (McKenney and Neff 1979, Knowlton and Kirby 1984). Larval and juvenile grass shrimp are more tolerant of low salinities and high temperatures than of high salinities and high temperatures (Wood 1967). Juveniles and adults are capable of tolerating salinities ranging from 0 to 55‰ (freshwater to hypersaline), but are most common in oligohaline to euhaline salinities of 2 to 36‰ (Wood 1967, Kirby and Knowlton 1976, Williams 1984, Anderson 1985). In southwestern Florida, they were most common from 10 to 15‰ in one study (Rouse 1969), and in waters with salinities of <20‰ in another (Odum and Heald 1972). Salinity appears to affect maturation and spawning age, with individuals from higher salinity waters reaching maturity faster than those in lower salinity waters (Alon and Stancyk 1982). The 96 hour LC50 values for adults is 0.5‰ and 44‰ (Kirby and Knowlton 1976).

Dissolved Oxygen (DO): Data on the DO requirements of the grass shrimp are limited (Killam et al. 1992). It is apparently well adapted to low oxygen conditons, and collections have been made in waters with DO levels that ranged from 2.8 to 11 ppm (Welsh 1975, Barrett et al. 1978, Rozas and Hackney 1984). In laboratory tests, it is able to tolerate DO levels less than 1.0 ppm (Anderson 1985). Grass shrimp can cope with brief periods of low DO by climbing out of water on *Spartina* stalks for a few hours, particularly during warm summer nights (Wiegert and Pomeroy 1981). This species is also able to tolerate anoxic conditions by decreasing its oxygen consumption as DO declines (Welsh 1975).

Migrations and Movements: There is little indication of extensive migrations. The grass shrimp does, however, move to deeper waters with the onset of especially high or low temperatures. The extent of its movements among various depths may be related to the distribution of oyster shell substrates. It tends to migrate in the direction of tidal currents, but avoids fast currents (Thorp 1976, Anderson 1985). There is some evidence that grass shrimp may be more active at night (Rozas and Hackney 1984).

**Reproduction**

Mode: Sexes in the grass shrimp are separate (gonochoristic). This species is sexually dimorphic and has external fertilization (Burkenroad 1947, Knowlton and Williams 1970). Eggs develop oviparously.

Mating and Spawning: When females become sexually mature, they molt into breeding-form and become receptive to males (Burkenroad 1947, Anderson 1985, Killam et al. 1992). The breeding-form is characterized by extra setae on the pleopods, enlargement of the abdominal brood pouch, and development of periodic chromatophores and is recognized by males through antennal contact on some part of the female's body (Burkenroad 1947). Mating must occur within 7 hours of the female's molting, and oviposition must occur within 7 hours after transfer of sperm. Spawning usually occurs a few hours after mating (Burkenroad 1947). Fertilization is external and occurs with dissolution of the spermatophore as eggs are released by the female (Burkenroad 1947, Anderson 1985). Eggs are extruded onto the female's pleopods and are held there until they hatch, usually in 12 to 60 days, depending on temperature. A new brood of eggs is deposited 1 to 2 days after hatching of the previous brood (Knowlton and Williams 1970). The spawning season is from February to October, but may vary with geographic location. Two spawning peaks have been noted in Galveston Bay, Texas, one in the early summer and the other in early fall (Wood 1967). The presence of ovigerous females suggests that spawning occurs throughout the year in southwest Florida (Rouse 1969, Williams 1984, Anderson 1985).

Fecundity: The number of eggs produced increases as the female grows. Fecundity estimates range from <100 to >700 eggs per female (Welsh 1975, Wood 1967, Sikora 1977), but eggs probably number from 300 to 500 most commonly (Anderson 1985, Killam et al. 1992). Females can molt again within a few days after spawning and produce a second brood (Knowlton and Williams 1970, Anderson 1985). Peak egg production occurs in May and is continuous through the summer months, but begins to wane in September (Knowlton and Williams 1970).

**Growth and Development**

Egg Size and Embryonic Development: Eggs are 0.6 to 0.9 mm in diameter (Holthius 1952, Broad 1957) and develop oviparously (Anderson 1985). Hatching occurs in 12 to 60 days depending on geographical location. The period of incubation is usually shorter in areas with warmer water than in cooler locations.

Age and Size of Larvae: Newly hatched larvae are 2.6 mm. They go through 3-11 zoeal stages (molts), ending at about 6.3 mm. The zoeal stages last from 11 days to several months depending on environmental conditions including the amount of food (Broad 1957). In a study conducted in Georgia, it was suggested that settlement from the plankton by advanced zoeal stages and metamorphosis to the postlarva stage is triggered when larvae enter vegetated habitats (Kneib 1987b).

Juvenile Size Range: Growth to maturity in Texas is reported to take 2 to 3 months in summer and 4 to 6 months in winter. Females are mature at a size of approximately 18-24 mm TL (total length) and males at approximately 15 mm TL (Broad 1957, Wood 1967, Knowlton and Williams 1970, Alon and Stancyk 1982).

Age and Size of Adults: The life span of this species is 6 to 13 months. The older overwintering shrimp usually spawn early in the year as adults, and postlarvae that survive the winter spawn the following spring. In South Carolina, habitats with consistently higher salinities (>20‰) may provide more optimal conditions, resulting in faster growth and earlier spawning, than fluctuating, lower salinity habitats (<20‰) (Alon and Stancyk 1982). Reported maximum sizes for males and females are 33 mm and 50 mm TL, repectively (Holthuis 1952).

**Food and Feeding**

Trophic mode: This species is an opportunistic, omnivorous feeder (Anderson 1985, Kneib 1987a, Nelson and Capone 1990). It probably uses tactile cues and/or chemoreceptors on its legs in order to find relatively sedentary benthic prey, but may rely on the sensitivity of its compound eyes to detect nektonic prey (Kneib 1987a).

Food Items: Planktonic larvae feed on zooplankton, algae, and detritus. Juveniles and adults eat a variety of animal and plant matter including detritus, polychaetes, meiofauna, blue crab megalopae, larval fish, algae and dead animal matter (Heard 1979, Anderson 1985, Kneib 1987a, Nelson and Capone 1990, Olmi 1990). Grass shrimp are known to consume the epiphytic organisms attached to seagrasses while living in this habitat (Morgan 1980). When epiphyte abundance is high, grass shrimp are capable of using them to completely satisfy their dietary needs.

**Biological Interactions**

Predation: Wading birds such as the clapper rail (*Rallus longirostris*) utilize the grass shrimp as food (Heard 1982). It has also been found in the stomach contents of juvenile American alligators (Platt et al. 1990). Piscine predators include: longnose gar (*Lepisosteus osseus*), blue catfish (*Ictalurus furcatus*), gafftopsail catfish (*Bagre marinus*), hardhead catfish, gulf killifish, yellow bass (*Morone mississippiensis*), largemouth bass (*Micropterus salmoides*), snook, gray snapper, silver perch, Atlantic croaker, spotted seatrout, sand seatrout, red drum, black drum, pinfish, sheepshead, bighead searobin (*Prionotus tribulus*), Spanish mackerel, king mackerel (*S. cavalla*), and southern flounder (Gunter 1945, Kemp 1949, Miles 1949, Darnell 1958, Harrington and Harrington 1961, Linton and Rickards 1965, Boothby and Avault 1971, Diener et al. 1974, Bass and Avault 1975, Danker 1979, Levine 1980, Overstreet and Heard 1982, Rozas and Hackney 1984, Perschbacher and Strawn 1986, Morales and Dardeau 1987, Peters and McMichael 1987, Hettler 1989). Penaeid shrimp may also prey upon juvenile grass shrimp (Kneib 1987b). Blue crabs in Florida are known to occasionally prey on grass shrimp during the winter (Laughlin 1982), and small juvenile blue crabs have been observed capturing and consuming grass shrimp when both were held in aquaria set up with marsh habitats (Pattillo pers. obs.).

Factors Influencing Populations: Temperature and salinity are considered to be the major factors affecting the distribution of grass shrimp (Wood 1967, Killam et al. 1992). Although this species can tolerate wide ranges of these two parameters, reproduction, optimal growth, and survival can be negatively affected by extreme conditions. Grass shrimp abundance can be affected by habitat alterations that destroy vegetation on which this species depends (Trent et al. 1976, Anderson 1985). The loss of vegetation also results in a reduction of detrital input into surrounding systems which can cause a decrease in grass shrimp abundance. *Palaemonetes pugio* is not as tolerent to higher salinities as some of its sister species, and this may contribute to its replacement in high salinity waters by *P. vulgaris* and/or *P. intermedius* (Williams 1985). Predation by fishes can have a major influence in the distribution and longevity of grass shrimp (Alon and Stancyk 1982, Kneib 1987b). Displacement of grass shrimp from their preferred habitats of submerged macrophytes makes them more vulnerable to predation (Anderson 1985). Adult grass shrimp prey on the larvae of killifish (*Fundulus* sp.) and, by so doing, contribute to the control of one of their principal predators (Kneib 1987a). Diseases and parasites do not appear to have any major effect on the abundance and growth of grass shrimp in the Gulf of Mexico (Anderson 1985).

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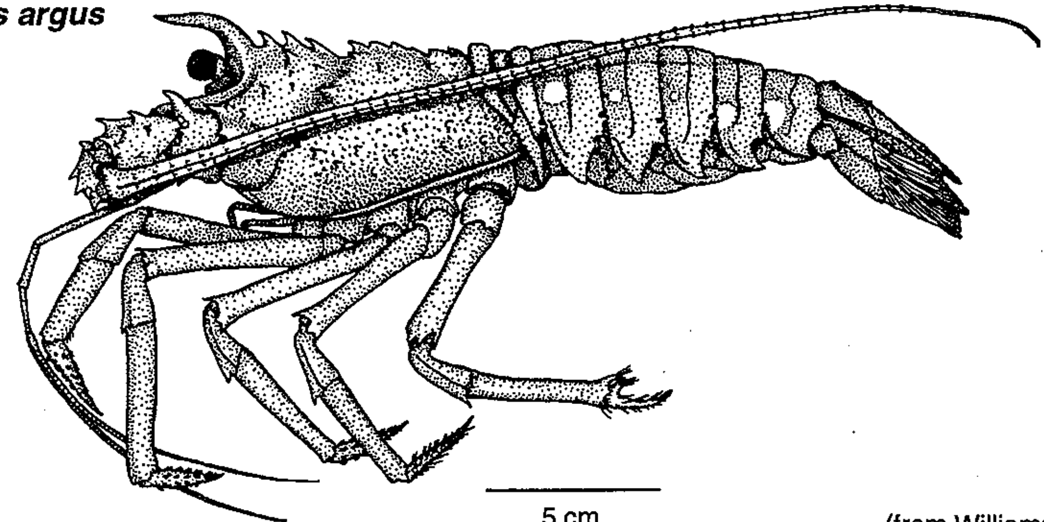
## Spiny lobster

***Panulirus argus* Adult**



5 cm (from Williams 1965)

**Common Name**: spiny lobster
**Scientific Name**: *Panulirus argus*
**Other Common Names**: crawfish, Florida spiny lobster, western Atlantic spiny lobster, Caribbean spiny lobster, rock lobster, bug, *langouste blanche* (French), *langosta común* (Spanish) (Fischer 1978, NOAA 1985, Williams et al. 1989).
**Classification** (Williams et al. 1989)

| | |
|---|---|
| Phylum: | Arthropoda |
| Class: | Crustacea |
| Order: | Decapoda |
| Family: | Palinuridae |

**Value**
Commercial: Spiny lobster are typically marketed as tails either fresh or frozen (Fischer 1978). U.S. landings in 1992 were 2,222.6 mt valued at $20.2 million (NMFS 1993). Florida, with landings of 1,814.4 mt valued at 14.6 million, accounted for 81% of the total catch and 73% of the value. In 1992, all reported Gulf landings were from the west coast of Florida (Newlin 1993), mostly from the Florida Keys in Monroe County (Lyons pers. comm.). Reported landings for Florida's 1995-96 fishing season were considerably higher at 3,186 mt (Matthews pers. comm.). Fishermen use top-entry wood-slat traps and juvenile lobsters to attract adults into the trap (Lyons 1986, Marx and Herrnkind 1986). A few are harvested by divers and as incidental catch by shrimp trawlers (Hunt 1994). Florida issues a special permit required for the commercial harvest of this species (GMFMC 1987). Spiny lobster is a valuable commercial species and supports Florida's second most valuable shellfishery (Schomer and Drew 1982, Marx and Herrnkind 1986). In Florida state waters, lobsters must measure at least three inches (76 mm) carapace length (CL) and tails must be at least 140 mm in length to be legal for harvest (Hunt pers. comm.). Florida has maintained a closed harvest season since 1919 (Lyons 1986). Dates for the closure have changed several times, but have always occurred during the spring-summer spawning season. Similar regulations apply in offshore federal waters of the Gulf of Mexico as well (GMFMC 1996a). The fishery appears to be fully exploited in the U.S. and may be overexploited in Puerto Rico (NOAA 1992). Capitalization of the fishery is considered to be excessive. Current regulations have reduced the number of traps in the Florida fishery from 939,000 to approximately 613,000, while landings have remained high (Matthews pers. comm.). Although there is interest in mariculture of palinurid lobsters, successful rearing of the larval stages has been problematic (Van Olst et al. 1980).

Recreational: Divers, using either skin- or SCUBA-diving gear catch lobsters recreationally using gloves and small hand held nets (Marx and Herrnkind 1986). The recreational harvest is typically about 20% of the commercial landings (Bertelson and Hunt 1991), and most of this fishery is in the Florida Keys. Recreational diving can substantially impact local spiny lobster populations when divers congregate in specific areas (Blonder et al. 1990). Recreational fishing is typically closed in Florida from early April to early August (GMFMC 1982, NOAA 1992), although there has been a special two-day non-trap recreational season in late July (Hunt pers. comm.). Lobsters must measure at least three inches (76 mm) CL and tails must be at least 140 mm in length, and possession limits are enforced. Similar recreational regulations apply in offshore federal waters of the Gulf of Mexico as well (GMFMC 1996b). In Florida state waters, a special lobster stamp must be purchased in addition to a recreational saltwa-

Table 5.10. Relative abundance of spiny lobster in 31 Gulf of Mexico estuaries (Nelson et al. 1992, Hunt, Lyons pers. comm.).

| *Estuary* | A | M | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | √ | √ | ◉ | | |
| Ten Thousand Islands | | | √ | | |
| Caloosahatchee River | | | | | |
| Charlotte Harbor | √ | | √ | | |
| Tampa Bay | √ | | √ | | |
| Suwannee River | | | | | |
| Apalachee Bay | √ | | √ | | |
| Apalachicola Bay | | | | | |
| St. Andrew Bay | √ | | √ | | |
| Choctawhatchee Bay | | | | | |
| Pensacola Bay | | | | | |
| Perdido Bay | | | | | |
| Mobile Bay | | | | | |
| Mississippi Sound | | | √ | | |
| Lake Borgne | | | | | |
| Lake Pontchartrain | | | | | |
| Breton/Chandeleur Sounds | | | | | |
| Mississippi River | | | | | |
| Barataria Bay | | | | | |
| Terrebonne/Timbalier Bays | | | | | |
| Atchafalaya/Vermilion Bays | | | | | |
| Calcasieu Lake | | | | | |
| Sabine Lake | | | | | |
| Galveston Bay | | | | | |
| Brazos River | | | | | |
| Matagorda Bay | | | | | |
| San Antonio Bay | | | | | |
| Aransas Bay | | | | | |
| Corpus Christi Bay | | | | | |
| Laguna Madre | √ | | √ | | |
| Baffin Bay | | | | | |
| | A | M | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- M - Mating
- J - Juveniles
- L - Larvae
- E - Eggs

ter fishing license.

Indicator of Environmental Stress: The spiny lobster is not typically used in studies of environmental stress.

Ecological: Spiny lobsters are frequently the dominant carnivores in their habitat and have important ecological effects on marine benthic communities (Marx and Herrnkind 1986). The loss of spiny lobster from habitats through overfishing could have serious consequences. Removal of such a large sized and abundant carnivore may result in loss of diversity and significant shift in food webs in simpler ecosystems (Davis 1977).

**Range**

Overall: The spiny lobster is found in coastal and shallow continental shelf waters along the western Atlantic coast from North Carolina to Brazil, including Bermuda, and throughout the Gulf of Mexico. Genetic studies indicate that spiny lobsters throughout the Caribbean are genetically similar, suggesting a single population (Silberman and Walsh 1994, Silberman et al. 1994). A few specimens have been collected in the Gulf of Guinea, West Africa (Lewis 1951, Williams 1984, NOAA 1985, Marx and Herrnkind 1986).

Within Study area: The species is abundant off the southern Florida coast from Florida Bay to Dry Tortugas and is found throughout the Gulf of Mexico in warm offshore waters. The southern edge of Florida Bay is the major nursery area for juvenile spiny lobster in South Florida (Field and Butler 1994, Herrnkind and Butler 1994). Rare collections are made in inshore waters of south Texas (Moore 1962, Marx and Herrnkind 1986, Tunnell pers. comm., Hockeday pers. comm.). (Table 5.10).

**Life Mode**

Eggs are carried on the female's pleopods. Egg bearing females are found in reef areas at approximately 24 to 30°C. Larvae (phyllosoma stage) are planktonic and their distribution is regulated by ocean currents. Larvae metamorphose to the puerulus stage offshore, and move shoreward at the water's surface (Acosta et al. in press). Benthic juveniles show a combination of crepuscular and nocturnal activity. Juveniles reside in shallow nearshore waters in seagrass, mangrove, or hardbottom nursery areas until they approach maturity, and then move out to reef habitats (Moe 1991, Herrnkind et al. 1994, Acosta et al. in press). Lobsters found offshore are principally adult stage (Witham et al. 1968, Williams 1984, Marx and Herrnkind 1986). Adults also have a combined pattern of crepuscular and nocturnal activity (Andree 1981).

**Habitat**

Type: Spiny lobster phyllosome larvae are planktonic and inhabit oceanic waters (Lyons 1986). They are found in the epipelagic zone of the Caribbean Sea, Gulf of Mexico, and the Straits of Florida (GMFMC 1987). The postlarval swimming puerulus stage enters estuarine nursery areas. After pueruli molt into juveniles, they become demersal and littoral, and utilize the coastal waters of bays, lagoons, and reef flats, seeking shelter associated with the substrate (Moore 1962, Witham et al. 1968, Herrnkind et al. 1994). They are solitary and reside in algal clumps for about 3 months (Witham et al. 1964, Andree 1981, Marx and Herrnkind 1985a, Butler and Herrnkind 1991, Butler et al. in press). These clumps provide an epifaunal food source, and protection from predation and physical disturbance (Marx and Herrnkind 1985b). When they reach 15-16 mm CL, they begin to enter holes and crevices in rocks, corals, and sponges and start associating with similar-sized juveniles (Marx and Herrnkind 1985a, Lyons 1986). Juveniles become gregarious at about 20-25 mm CL and congregate in rocky dens (Childress and Herrnkind 1994, Childress and Herrnkind 1996). Larger dens are occasionally shared with stone crabs, spider crabs, small grouper, and other fishes (Davis and Dodrill 1989). Juveniles can use these areas for 15 months to 3 years (Lyons 1986, Davis and Dodrill 1989, Forcucci et al. 1994). They spend this time foraging and seeking dens appropriate for their increasing size (Lyons 1986). Appropriate sized dens appear to be an important defense against predation (Eggleston et al. 1992). As juveniles become older they move from inshore nursery areas to begin adult life in seaward waters. Adults occur on reefs and rubble areas from shore to 80 m (Moore 1962, Eldred et al. 1972, Williams 1984, NOAA 1985, Lyons 1986, Marx and Herrnkind 1986).

Substrate: Adults are found among reefs, jetties, offshore oil platforms, and rubble, while young pueruli and juveniles occur among seagrasses, algal beds (especially the red algae *Laurencia*), sponges, tidal channels, and holes and crevices among jetties, rocky outcrops, and corals (Khandker 1964, Schomer and Drew 1982, Williams 1984, NOAA 1985, Marx and Herrnkind 1985a, Davis and Dodrill 1989, Tunnell pers. comm., Hockeday pers. comm.).

Physical/Chemical Characteristics:

Temperature: The spiny lobster can survive exposure to 13°C, but generally inhabits areas with an annual minimum temperature of at least 20°C (Marx and Herrnkind 1986). Temperature tolerance may vary with developmental stage, location, and salinity. Temperature and salinity interact in their effect on postlarval survival, time to metamorphosis, and size at metamorphosis (Field and Butler 1994). Temperature has been found to significantly affect all measured aspects of juvenile growth, including survival, intermolt period, postmolt size change, feeding, and weight gain (Lellis and Russell 1990). Early juveniles do not generally survive below 10°C, nor above 35°C (Witham 1974, GMFMC 1982). Growth of juveniles and adults is optimal at 26 to 28°C, and spawning activity is related to temperature.

Salinity: In a factorial experiment, survival of postlarvae to the first benthic juvenile stage was found to be highest at 22°C and 35‰, and declined markedly at temperatures and salinities above and below those values (Field and Butler 1994). Juveniles and adults are known to occur in mesohaline to euhaline salinities (5-40‰) (Witham et al. 1968, Witham 1974, GMFMC 1982, Lellis and Russell 1990). Older juveniles are able to use marginal inshore habitats because they are highly mobile and can retreat from unsuitable conditions (Marx and Herrnkind 1986).

Movements and Migrations: Local movements are reported in response to temperature, salinity, currents, wave surge, turbulence, and food availability. Adults sometimes move to offshore water to mate. Males return to shallower water after mating, followed by females after their larvae have been released. Larvae are dispersed by oceanic currents. Pueruli swim shoreward at night during dark lunar phases, moving from the open ocean into shallow nearshore waters, and are aided in movements into nursery areas by wind driven and tidal currents (Calinski and Lyons 1983, Acosta et al. in press). Peak influxes occur from December through April (Acosta et al. in press). Juveniles residing in algal clumps may move to different clumps depending on food abundance, presence of other juveniles, and the quality of shelter provided by their original clump (Marx and Herrnkind 1985b, Butler et al. in press). As juveniles approach maturity, they move to deeper offshore waters, traveling as much as 210 km in the process. Adult movement patterns are not fully understood. They may occupy particular reefs or dens for several years, or move many kilometers for unknown reasons (Hunt et al. 1991). Offshore movement during autumn is prompted by periods of cold temperatures and possibly photoperiod. Mass migrations during this period can involve thousands of lobsters moving in separate single-file queues of up to 50 individuals. Movement in this type of formation may conserve energy during locomotion (Davis 1977, Herrnkind 1980, Lyons et al. 1981, Schomer and Drew 1982, NOAA 1985, Marx 1986, Marx and Herrnkind 1986, Davis and Dodrill 1989, Yeung and McGowan 1991, Lozano-Alvarez et al. 1991).

## Reproduction

Mode: Reproduction is sexual, sexes are separate (gonochoristic), and fertilization is external. Hermaphroditism has not been reported (GMFMC 1982).

Mating and Spawning: Mating may occur up to a month prior to spawning, and consists of placement of a spermatophore by the male onto the female's sternum. In Florida, the mating season is principally from March to August, but some may occur throughout the year (Hunt et al. 1991). After mating, the spermatophore adheres to the female's sternum; at spawning she scratches it to initiate and achieve fertilization. Spawning occurs offshore in open waters and is principally associated with reef habitats. The season extends from March to July with some spawning occurring in August. In the Florida Keys, it peaks in May and June. Some spawning throughout the year has been reported (Little 1977, Warner et al. 1977, Lyons 1981, Lyons et al. 1981, GMFMC 1982, Gregory et al. 1982, Williams 1984, NOAA 1985, Marx and Herrnkind 1986).

Fecundity: Fecundity is proportional to size (Mora-Alves and Bezerra 1968). Recent Florida fecundity studies show that a 76 mm CL female lobster can lay 320,000 eggs, an 87 mm CL female 500,000 eggs, a 113 mm CL female 1,000,000 eggs, and a 141 mm CL female was observed with 1,952,000 eggs (Matthews pers. comm.). A second and potentially a third mating and spawning may occur during the season, increasing the spawning potential two or three fold (Hunt et al. 1991). It has been estimated that nearly half of the egg pool is contributed by females in the 75-85 mm CL size class (Gregory et al. 1982).

## Growth and Development

Egg Size and Embryonic Development: Eggs are spherical and about 0.5 mm in diameter. Embryonic development lasts about 3 weeks. During this time the eggs adhere to pleopodal setae on the underside of the female's abdomen. The phyllosome larvae emerge from the egg membrane and disperse in the water column (Marx and Herrnkind 1986).

Age and Size of Larvae: Phyllosome larvae develop through about 11 stages increasing in size from 2 mm total length at hatching to nearly 34 mm before metamorphosis. Duration of the phyllosome stages is about 6 to 12 months (Richards and Potthoff 1981, Marx and Herrnkind 1986, Acosta et al. in press).

Juvenile Size Range: The phyllosome larvae metamorphose into a transparent swimming stage called a puerulus which may last several weeks. They begin to acquire reddish-brown pigment within 3 to 6 days after arriving in nursery areas, and within days molt into the first juvenile stage. Juveniles are 6 mm CL when they first settle out of the water column beginning the spiny lobster's benthic juvenile phase (Eldred et al. 1972, Andree 1981, Marx and Herrnkind 1986, Butler and Herrnkind 1991). Growth of juveniles is estimated at 5 mm carapace length (CL) per month (Eldred et al. 1972). Other estimates are 12 mm in first year of benthic existence (GMFMC 1982), from 6 mm to 90 mm CL in the first three years of life (Sutcliffe 1957), 5.4 mm per molt (Warner et al. 1977), 0.46 mm CL/ week (23.9 mm CL/year) (Hunt and Lyons 1986), 0.76 mm CL/week (Davis and Dodrill 1989), and 0.95 mm CL/ week (Forcucci et al. 1994). In general, there are 4 molts per year (GMFMC 1982). Growth decreases dramatically between 74 mm CL (0.46 mm CL/week) and 76 mm CL (0.23 CL/week) signifying a shift in energy use from growth to the onset of maturation (Hunt and Lyons 1986). Difference of sex does not appear to affect growth rates in juveniles (Davis and Dodrill 1989, Forcucci et al. 1994). Injury appears to have the greatest effect on growth rates in lobsters less than 60 mm CL, and confinement of juveniles in traps may also affect growth (Hunt and Lyons 1986, Forcucci et al. 1994).

Age and Size of Adults: Onset of maturation begins near 70 mm CL in south Florida, but a few are reproductively functional at 66 mm CL (Warner et al. 1977, Gregory et al. 1982, Hunt and Lyons 1986). Histological examination of ovaries, however, indicates that most south Florida spiny lobsters are not reproductively active until reaching 90-95 mm CL (Lyons 1986). Injury does not affect growth rate in adults as much as in juveniles (GMFMC 1982, Hunt and Lyons 1986). Adult males grow faster than adult females, and growth rates during the summer are faster than in the winter (Davis and Dodrill 1989). Intermolt periods range from 3 to 6 months for subadults and adults (Andree 1981).

## Food and Feeding

Trophic Mode: Throughout their benthic juvenile and adult stage, spiny lobsters are nocturnal predators, locating their food by means of antennae and chemoreceptive filaments that line the antennules and dactyls of the legs (Marx and Herrnkind 1986). The lobster's mandibles are used to crush the shells of molluscs, crustaceans, and urchins. Spiny lobsters are probably the dominant carnivores in their habitat and have important ecological effects on the marine benthic commuinity (Marx and Herrnkind 1986).

Food Items: Spiny lobster phyllosome larvae are presumed to feed on plankton; laboratory-reared phyllosomes fed on chaetognaths, euphasiids, fish larvae, medusae and ctenophores (Marx and Herrnkind 1986). Pueruli stage lobsters are not known to feed at all. The spiny lobster is a nocturnal forager throughout the benthic juvenile and adult stages (Cox et al. 1997).

It preys on a wide variety of slow-moving and sedentary animals such as molluscs, crustaceans, and echinoderms. Young juveniles can be considered general opportunistic feeders that consume a large variety of organisms (Andree 1981, Herrnkind et al. 1988). The only major difference between the diets of younger and older juveniles is the size of the prey; smaller lobsters feed on smaller species of gastropods, bivalves, and crustaceans as well as smaller size classes of commonly eaten larger species. Small quantities of algae, sea grass, detritus, foraminiferans, polychaetes, and sponges have also been found in fecal samples. Older juveniles were found to feed on molluscs, crustaceans, and other fauna that exist on the algal clumps in which they reside (GMFMC 1982, Marx and Herrnkind 1985a). Larger juveniles and adults are higher trophic level carnivores that forage considerable distances from their dens in search of prey, principally bivalves, snails, hermit crabs, other crustaceans, and fish (Crawford and DeSmidt 1923, Davis 1977, GMFMC 1982, Schomer and Drew 1982, Marx and Herrnkind 1986).

**Biological Interactions**

Predation: Larvae are preyed on by a number of pelagic fishes, including skipjack tuna (*Katsuwonus pelanus*) and blackfin tuna (*Thunnus atlanticus*) (GMFMC 1982). Postlarvae are preyed on most heavily as they cross the reef track (Acosta 1997). Blue crabs and octopuses have been observed eating early juveniles (Andree 1981). Juveniles are presumably subject to predation by numerous fishes while occupying the mangrove and grass flat habitats (GMFMC 1982). Major predators of adult and sub-adult stages include skates (*Dasyatis* species), sharks (especially nurse shark, *Ginglymostoma cirratum*), various snappers (*Lutjanus* species), grouper (*Mycteroperca* and *Epinephelus* species), jewfish, grunts, barracudas, and octopus (Andree 1981, GMFMC 1982, Smith and Herrnkind 1992). Dolphins (*Tursiops*) and loggerhead turtles (*Caretta caretta*) also prey on lobster. A small snail, *Murex pomum*, is known to kill lobsters in traps by boring through the carapace (GMFMC 1982). The degree of predation risk in an area appears to influence the distribution and abundance of lobsters present there (Eggleston and Lipcius 1992, Mintz et al. 1994).

Factors Influencing Populations: Extreme temperatures and salinities (Field and Butler 1994) and sedimentation (Herrnkind et al. 1988) reduce survival of postlarvae and juveniles. The cascading effects of environmental disturbance can result in declines in lobster populations (Butler et al. 1995). Although Florida Bay is a major nursery area for juvenile spiny lobster, recruitment within the northern portion of the bay may be limited by physical hydrology, and by seasonal extremes of temperature and salinity (Field and Butler 1994). Illegal harvest out-of-season and of undersize lobsters (shorts) are no longer'considered serious problems in the now-limited entry fishery (Lyons pers. comm.). The widespread use of shorts as trap attractants by commercial fishermen may have an adverse impact on recruitment to the adult population due to increased mortality of the shorts (GMFMC 1982, Lyons 1986). However, this impact may diminish as the number of traps in the fishery is reduced considerably by limited entry (Lyons pers. comm.). Ocean dumping of dredged material creates silt that settles over larvae and suffocates them (GMFMC 1982). Oil and tar pollution of marine waters can potentially impact the open ocean epipelagic habitat of larvae (GMFMC 1982). Shallow water mangrove and grass flat nursery areas are subject to abuses of dredge and fill, modified discharges, and coastal development, all of which destroy necessary habitat needed to sustain spiny lobster population levels (Herrnkind et al. 1988). Damage to reef areas from pollution, ship groundings, anchors, and collectors also remove habitat necessary for sustaining this species (Andree 1981, GMFMC 1982). Large amounts of rainfall that significantly lower the salinity of estuarine nursery areas can cause mortality in postlarval lobsters, affecting their recruitment to these areas (Witham et al. 1968, Field and Butler 1994). Loss or degradation of inshore nursery habitat could have a serious effect on continued lobster recruitment and production (Little 1977, Butler et al. 1995, Butler and Herrnkind 1997). However, artificial habitats that mimic mimic natural shelters are useful in mitigating loss of shelter (Herrnkind et al. 1997). The inability of lobsters to survive low temperatures (<10° C) probably limits latitudinal and depth distribution of this species and prevents its spread northward and across deep ocean basins (Witham 1974, Marx and Herrnkind 1986). The density of lobsters in a given habitat can enhance gregariousness, which in turn can influence the relative impact of lobster size, shelter size, and predation risk upon den choice (Eggleston and Lipcius 1992).

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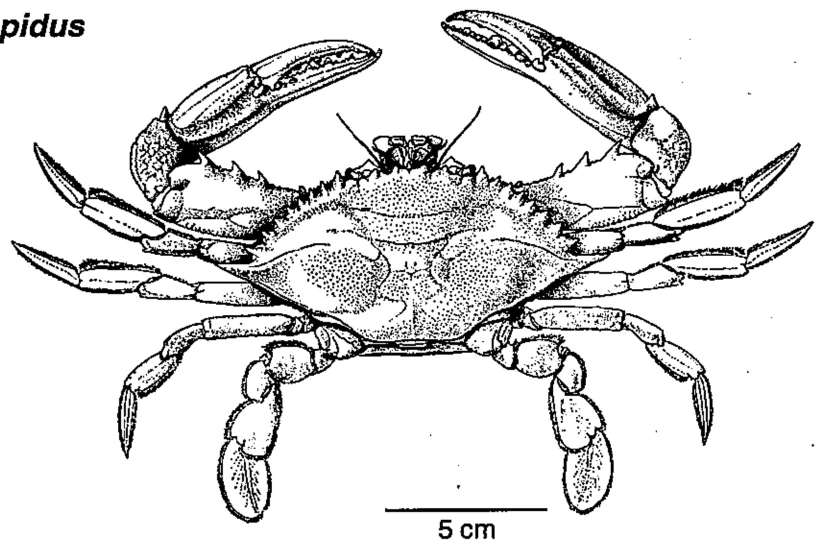
# Blue crab

***Callinectes sapidus***
**Adult**



5 cm

(from Goode 1884)

**Common Name:** blue crab
**Scientific Name:** *Callinectes sapidus*
**Other Common Names:** jimmies (males), sooks (adult females), common edible crab, sallies, spongers, sponge crab, berry crab, soft shell, soft shelled crab, hard crab; *crabe bleu* (French), *cangrejo azul, jaiba azul* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Williams et al. 1989)
Phylum: Arthropoda
Class: Crustacea
Order: Decapoda
Family: Portunidae

**Value**
Commercial: Commercial blue crab landings have been reported from the Gulf of Mexico since 1880, although the data are not continuous prior to 1948 (Steele and Perry 1990). With the introduction of the wire crab trap and improved shipping methods came an increased availablility of fresh raw product, which stimulated processing capacity, market development, and consumer demand. Since 1984, Gulf landings have increased greatly, at least partially as a result of increased fishing effort. Declining catches and increased regulation of other fisheries may have prompted many fishermen to turn to crabbing to supplement their income.

The commercial value of the Gulf of Mexico blue crab fishery is difficult to estimate. Many blue crab fishermen use unsurveyed market channels which lead to under-reporting of landings (Roberts and Thompson 1982, Keithly et al. 1988). In additon, large numbers of blue crabs are harvested as incidental catch during shrimping operations (Adkins 1972b, Steele and Perry 1990). These crabs are sold, eaten, given away, or swapped for supplies and thus not reported as landings. With this under-reporting noted, the following landings are presented. In 1994, 24,123 mt of blue crab, valued at $32.5 million, were reported in the Gulf region (NMFS 1997). The contribution of the Gulf of Mexico to total U.S. blue crab landings reached a peak of 38% in 1987, but has remained below 30% since 1990. The annual proportional contribution of each Gulf State to harvest is variable (Perry pers. comm.). However, since 1972, Louisiana has consistently contributed the highest proportion of Gulf landings, followed by Florida (Steele and Perry 1990). The proportional contribution of each state to the total Gulf harvest from 1980 to 1994 is Louisiana 59.9%, Florida 18.0%, Texas 15.0%, Alabama 4.9%, and Mississippi 2.2% (Perry pers. comm.). In 1994, 98.9% of the Gulf of Mexico blue crab harvest was by crab pots (traps), whereas only 1.1% was by trawl (Perry pers. comm.), and these proportions are consistent with previous years (Perry et al. 1984). The seasonal variation in harvest is similar among the Gulf States. Highest catches usually occur from May through August, with peaks in June and July.

There is a tremendous domestic consumer demand for blue crab, and the landings are believed to be totally consumed by the domestic market. The main commercial outlets for blue crab are seafood restaurants and retail seafood markets. Approximately 75% of the hard crab landings are sold as processed product, the other 25% are assumed to be sold live for boiling or steaming (Perry et al. 1984). There is also a small soft shell crab fishery, which supports local demand for fresh soft shell crabs. Soft shell crabs demand a higher price, and are most abundant during the late spring, summer, and fall, when crabs are actively molting (Perry pers.

Table 5.11. Relative abundance of blue crab in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | M | J | L | E |
|---|---|---|---|---|---|
| | Life stage | | | | |
| Florida Bay | ◉ | ◉ | ◉ | ◉ | √ |
| Ten Thousand Islands | ◉ | ◉ | ◉ | ◉ | √ |
| Caloosahatchee River | ◉ | ◉ | ● | | |
| Charlotte Harbor | ◉ | ◉ | ◉ | ◉ | ◉ |
| Tampa Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Suwannee River | ● | ● | ● | ● | ◉ |
| Apalachee Bay | ● | ● | ● | ● | ◉ |
| Apalachicola Bay | ● | ● | ● | ● | ◉ |
| St. Andrew Bay | ● | ◉ | ● | ◉ | ○ |
| Choctawhatchee Bay | ◉ | ◉ | ◉ | ◉ | √ |
| Pensacola Bay | ◉ | ◉ | ◉ | ◉ | √ |
| Perdido Bay | ◉ | ○ | ◉ | ○ | ○ |
| Mobile Bay | ● | ● | ● | ● | √ |
| Mississippi Sound | ● | ● | ● | ● | ● |
| Lake Borgne | ● | ● | ● | ● | ● |
| Lake Pontchartrain | ◉ | ○ | ○ | √ | |
| Breton/Chandeleur Sounds | ◉ | ◉ | ◉ | ◉ | ◉ |
| Mississippi River | ○ | ○ | ○ | ○ | ○ |
| Barataria Bay | ◉ | ○ | ◉ | ◉ | ◉ |
| Terrebonne/Timbalier Bays | ◉ | ◉ | ◉ | ● | ◉ |
| Atchafalaya/Vermilion Bays | ◉ | ◉ | ◉ | ◉ | |
| Calcasieu Lake | ● | ○ | ● | ○ | |
| Sabine Lake | ● | ◉ | ◉ | ◉ | |
| Galveston Bay | ◉ | ○ | ◉ | ◉ | ◉ |
| Brazos River | ○ | ○ | ○ | ○ | ○ |
| Matagorda Bay | ◉ | ○ | ◉ | ● | ○ |
| San Antonio Bay | ● | ○ | ● | ● | ● |
| Aransas Bay | ◉ | ○ | ● | ○ | ○ |
| Corpus Christi Bay | ◉ | ○ | ● | ◉ | ◉ |
| Laguna Madre | ◉ | ○ | ◉ | ◉ | ◉ |
| Baffin Bay | ◉ | | ◉ | ○ | ○ |
| | A | M | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- M - Mating
- J - Juveniles
- L - Larvae (zoeae and megalopae)
- E - Eggs

comm.). The soft shell crab fishery is primarily in Louisiana and Florida (NMFS 1997), and actual landings are probably greater than reported (Perry pers. comm.).

Since the commercial harvest of blue crabs is primarily in state, not federal, territorial waters, the fisheries are managed by the state resource agencies in cooperation with the Gulf States Marine Fisheries Commission (GSMFC) (Steele and Perry 1990). State regulations for Gulf of Mexico commercial blue crab fisheries have been summarized by the GSMFC (1993), but these regulations are subject to annual revision. A five inch minimum carapace width generally applies Gulf-wide, and there are additional regulations for fishing season, location, gear type and quantity, mandatory release of gravid females, etc.

Recreational: The blue crab supports a considerably large recreational fishery. Estimates for recreational landings vary widely, ranging from 4% of the commercial landings in Mississippi in 1971 (Herring and Christmas 1974) to 400% of the commercial landings in Louisiana in 1968 (Lindall and Hall 1970, Adkins 1972b). They are taken in the estuaries and nearshore Gulf waters by dip nets, baited lift nets, baited strings, "fold-up" traps, crab pots, and recreational shrimp trawls. No reliable estimates are available for Alabama or the west coast of Florida because reports for recreational landings do not exist (Lindall and Hall 1970, Killam et al. 1992). Regulations similar to the commercial fishery apply to recreational fishing, with marked traps being labeled with name, address, saltwater stamp number, and date set out (TPWD 1987b, GSMFC 1993). In Mississippi crabs can be taken by handline, drop net, dip net, hook and line, and crab pots/traps (MDWC 1988). The smaller crabs are considered to be excellent bait for game fishes such as red drum.

Indicator of Environmental Stress: This species is well known to be susceptible to low dissolved oxygen (DO) in estuarine waters during the summer (May 1973, Lowery and Tate 1986). The blue crab is sensitive to chemical pollution, and is commonly used in pollution studies due to its widespread distribution in the nation's estuaries, and its commercial, recreational, and ecological importance. Cadmium, mercury, and several chlorinated hydrocarbons have been found to be acutely toxic to megalopal blue crabs in low concentrations (Millikin and Williams 1984). Toxicity for several pesticides has been determined for juvenile stages as well as adults. Kepone released into the James River, Virginia from 1950 to 1975 may have affected juvenile crab abundance and fishery landings (Van Engel 1982). In a laboratory study, Kepone concentrations of 0.5 and 0.75 parts per billion (ppb) were sublethal to blue crab zoeae, whereas 1.0 ppb caused a survival rate of

5% to the first crab stage, compared with 22% in the control group (Bookout et al. 1980). Juvenile blue crabs exposed to Kepone were shown to have a 96 hour LC50 at concentrations greater than 210 ppb (Schimmel and Wilson 1977). Mirex has been reported to be toxic to blue crab zoeae at concentrations of 1.0 and 10 ppb, whereas 0.01 and 0.1 ppb were sublethal (Lowe et al. 1971, Bookout and Costlow 1975). DDT and its derivatives tend to accumulate in the hepatopancreas of adult crabs (Sheridan 1975) and have been demonstrated to cause high mortalities when combined with low temperatures in natural habitats (Koenig et al. 1976). Juvenile blue crabs (27 mm CW) died within a few days exposure to DDT concentrations greater than 0.5 ppb (Lowe 1965). Mass mortalities of blue crab occurred in South Carolina, North Carolina, and Georgia in 1966, and it was speculated that pesticides were responsible (Newman and Ward 1973). Lipid-rich blue crab eggs may serve as a route for exporting lipophilic compounds such as kepone (Roberts and Leggett 1980).

Ecological: The blue crab performs a variety of functions in the estuarine ecosystem, and plays an important role in trophic dynamics (Van Den Avyle and Fowler 1984). At different stages in its life cycle, it serves as predator and prey to plankton, small invertebrates, fish, and other crabs. It has been characterized as an opportunistic benthic omnivore whose food habits are governed by availability of food items (Darnell 1959).

**Range**

Overall: The blue crab is a cosmopolitan species found in coastal waters, primarily in bays and brackish estuaries. It occurs occasionally from Nova Scotia, Maine, and northern Massachusetts to northern Argentina, and also Bermuda and the Antilles (Millikin and Williams 1984, Williams 1974, Williams 1984). It is found north of Cape Cod only during favorable warm periods that allow it to move into these waters. This species has also been introduced into coastal waters of Europe and Japan.

Within the Study Area: This species is abundant throughout the nearshore and estuarine areas of the Gulf of Mexico (Table 5.11) (Millikin and Williams 1984, Williams 1974, Williams 1984). For the purposes of Table 5.11, all zoeal and megalopal stages are considered together as "Larvae".

**Life Mode**

The blue crab spends most of its life in estuaries and nearshore Gulf waters. Eggs are carried externally by the female for approximately two weeks. Egg-bearing females are commonly known as sponge or berry crabs. Eggs hatch near the mouths of estuaries, and the zoeal larvae are carried offshore. Zoeae are planktonic, and remain in offshore waters for up to one month. Metamorphosis to the megalopal stage follows the seventh zoeal molt. Re-entry to estuarine waters occurs during the megalopal stage. Juveniles and adults tend to be demersal and estuarine. Adult males spend most of their time in low salinity waters; females move into these lower salinities as they approach their terminal molt to mate. After mating, females move to higher salinity areas of estuaries and nearshore environments for spawning (Dudley and Judy 1971, Millikin and Williams 1984, Van Den Avyle and Fowler 1984, Williams 1984).

**Habitat**

Type: The blue crab is dependent on estuaries during portions of its life. Depending on the life stage, individuals can be neritic, estuarine and/or riverine. Zoeae are found in oceanic habitats (Williams 1984), and they are positively phototropic (Costlow et al. 1959). The megalopae swim freely and may be found in the surf area near the bottom in nearshore or lower estuarine high-salinity areas. In Tampa Bay, the primary habitat that megalopae use for settlement appears to be seagrass or vegetated bottom (Killam et al. 1992). In the northern Gulf of Mexico, megalopae move into nearshore marshes where molt to the first crab stage occurs (Perry pers. comm.). Within an estuarine system, habitat is partitioned for use by blue crabs based on size class, and may be related to food availability, predator avoidance, nutritional requirements, reproductive success, and growth (Steele and Bert 1994). Juveniles have been found in greatest numbers in low to intermediate salinities characteristic of upper and middle estuarine waters (Steele and Perry 1990). They prefer seagrass as nursery habitat but also utilize salt marsh habitat (Thomas et al. 1990, Killam et al. 1992). Juveniles and adults tend to be demersal and estuarine. Adult males spend most of their time in low salinity water and females move from higher to lower salinities as they approach their terminal molt in order to mate (Dudley and Judy 1971, Millikin and Williams 1984, Van Den Avyle and Williams 1984, Williams 1984). Although juvenile and adult blue crab distributions are affected by salinity (Killam et al. 1992, Steele and Bert 1994), other factors such as substrate type and food availability also play a major role (Steele and Perry 1990).

Substrate: Juveniles and adults are found on muddy and sandy bottoms. Juveniles have been found in greatest abundances in association with soft mud bottoms (Van Engel 1958, Perry 1975, Perry and McIlwain 1986).

Physical/Chemical Characteristics: Environmental requirements affecting the growth, survival, and distribution of the blue crab vary with the life stage and sex of the individual (Killam et al. 1992). The eggs of the blue crab are the most sensitive to change in environmental conditions such as temperature and salinity, while juveniles and adults have greater tolerances to flucutations. Juveniles and adults are also more mobile, and can avoid degraded areas if possible.

Temperature - Eggs: Eggs have been successfully hatched under laboratory conditions in temperatures ranging from 19° to 29°C (Sandoz and Rogers 1944).

Temperature - Larvae: Megalopal survival is highest at temperatures between 21.5° and 34.5°C, but larval development is fastest between 24° to 31°C (Costlow 1967, Copeland and Bechtel 1974).

Temperature - Juveniles and Adults: Blue crabs have been collected at temperatures from 3° to 35°C (Copeland and Bechtel 1974). Adults cease feeding at temperatures below 10.8°C, and burrow in mud at 5°C. Mortalities of blue crabs have been related to extreme cold and sudden drops in water temperature (Van Engel 1982, Couch and Martin 1982). Tagatz (1969) evaluated maximum and minimum median thermal tolerance limits (48 hours) of juvenile and adult blue crab from St. Johns River, Florida, and found them to be 3°C and 37°C. However, thermal limits are highly dependent on acclimation temperature and salinity. Adult males are more tolerant of temperature extremes than females and juveniles. Temperature apparently plays a key role in molting (Copeland and Bechtel 1974).

Salinity: This species is euryhaline and has been found from freshwater to hypersaline lagoons (0-50‰). Upper and lower lethal limits (LC-50s) determined for two different Gulf of Mexico populations were 56‰ and 67‰ for the upper limits, and 0‰ and 1‰ for the lower limits (Guerin and Stickle 1990).

Salinity - Eggs: Eggs have been observed to hatch under laboratory conditions in salinities ranging from 10.3 to 32.6‰, but the optimum salinities ranged from 23‰ to 28‰ (Sandoz and Rogers 1944).

Salinity - Larvae: Early zoeae are found at high salinities, usually 20‰ or greater (Dittel and Epifanio 1982). Megalopae may be transported to lower salinities, and have been found in waters as low as 5‰ (Costlow 1967, Benson 1982). Highest survival occurs between 16 and 43‰, but larval development is fastest from 11.5 to 35.5‰ at 24° to 31°C (Costlow 1967, Copeland and Bechtel 1974).

Salinity - Juveniles: Juvenile crabs are found in lower salinity waters, typically 2-21‰. Reported salinity values for juveniles vary, and specific salinities are not critical to postlarval crabs.

Salinity - Adults: Adult males are usually found at less than 10‰. Egg-bearing females (sponge) are found in 23-33‰ and 19-29°C waters (Millikin and Williams 1984, Van Den Avyle and Fowler 1984, Williams 1984). The interaction of salinity and temperature reveals the blue crab to be less tolerant of low salinities at high temperatures and high salinities at low temperatures (McKenzie 1970).

Dissolved Oxygen (DO): The blue crab is very sensitive to low DO conditions. Survival times of 2 hours at 0 parts per million (ppm) DO (32°C and 15‰ salinity) and 4.3 hours at 0 ppm DO (25°C and 15‰ salinity) were reported by Lowery and Tate (1986). The occurrence of dead crabs in traps is fairly common during warm water conditions. The fishermen usually remedy the problem by moving their traps into shallower water to avoid any low DO water layers. Often the presence or boundary of a low DO water mass can be inferred by the placement of crab traps in any given area. Mass mortalities have been reported to be associated with low DO conditions (May 1973).

Migration and Movements: Migrations within estuarine systems are related to phases of life cycle, season, and, to a lesser extent, the search for favorable environmental conditions. Most crabs move to relatively deeper, warmer waters during winter, but some juveniles will burrow in shallow water substrate for protection. Blue crab return to rivers, tidal creeks, salt marshes and sounds when conditions become more favorable. They also move out of waters with low DO levels, and in some cases will actually leave the water to escape anoxic conditions (Lowery 1987, Killam et al. 1992). In Mobile Bay, large masses of migrating blue crabs and other animals occasionally occur while attempting to avoid low DO conditions, and such events are referred to as "jubilees" (Lowery pers. comm.). Blue crabs are recruited to Gulf estuaries as megalopae, with molt to the first crab stage occurring in nearshore waters (Thomas et al. 1990, Perry et al. 1995). Oesterling and Evink (1977) proposed a larval dispersal mechanism for the northeastern Gulf in which larvae could be transported 300 km or more. If such mechanisms do exist, larvae produced by spawning females in one estuary could be responsible for recruitment in others. In the Gulf of Mexico, immature females approaching their final molt during the spring, move to lower salinities to mate, and then, typically, migrate back to higher salinity waters within the estuary during June and July (Adkins 1972b, Millikin and Williams 1984). In Florida, females may leave estuaries after mating and move along the coast to specific spawning areas near Apalachicola Bay (Oesterling and Evink 1977). Adult males appear to remain in lower salinity waters, and rarely move to higher salinities. Adults are known to migrate between estuaries along the Florida Gulf coast (Adkins 1972b, Oesterling 1976). Movement of mated females from Lakes Pontchartrain and Borgne into Mississippi waters occurs in the fall and early winter months (Perry 1975).

**Reproduction**

Mode: Sexes are separate (gonochoristic), fertilization is internal, and eggs develop oviparously (Williams 1965).

Mating and Spawning: Mating normally occurs in low salinity waters in the upper reaches of the estuary. Females mate while in the soft shell stage during their pubertal or terminal molt. The females are vulnerable to cannibalism and predation during these molts, and as a result, the recognition of amorous males interested in mating is important. Females approaching their pubertal or terminal molts initiate mating behavior upon recognition of a mature male via olfactory and visual stimuli (Teytaud 1971). Males recognize the females via a pheromone that triggers male mating behavior (Gleeson 1980). Males protect their mates during the females molt. The males accomplish this by grasping the females with their first pair of walking legs and "cradle-carry" her in an upright position underneath the male. The males transmit their spermatophores by tube-like pleopods into the females seminal receptacle (Cronin 1974). The sperm are stored in the seminal receptacle to be released later. Soon after mating, females move to the higher salinity waters near the mouths of estuaries or into the Gulf of Mexico in preparation for spawning.

Spawning may occur any time from 2 to 9 months after mating, but usually occurs during the spring by females that mated in August-September of the previous year (Van Engel 1958, Williams 1965). In the northern Gulf of Mexico, larvae have been found throughout the year except January and February, but their occurrence is low from December to April (Stuck and Perry 1981). Two spawning peaks typically occur in the Gulf, one in late spring and the other during late summer or early fall (More 1969, Jaworski 1972, Stuck and Perry 1981). In Florida's St. Johns River, spawning occurs from February through October, with peak occurrence from March through October (Tagatz 1968a). The primary spawning grounds along the Gulf coast of Florida are located off Apalachicola Bay (Oesterling 1976). Eggs are fertilized as they are passed from the ovaries to the seminal receptacle and are extruded out to the pleopods (Millikin and Williams 1984). Egg extrusion may be completed within 2 hours (Van Engel 1958). Females may ovulate more than once and sperm can survive for at least one year in their seminal receptacle.

Fecundity: Fecundity estimates range from 723,500 to 2,173,300 eggs per spawning (Truitt 1939), but generally between 1,750,000 and 2,000,000 eggs are produced per spawning (Millikin and Williams 1984). The egg mass (sponge) ranges from 24 to 98 g, with an average of 37 g (Tagatz 1965). Females may ovulate and spawn more than once (Millikin and Williams 1984). Second spawnings can occur for some females later in the summer after the first one, and it is possible for a third one to occur, possibly as late as the succeeding spring or at an age of three years (Williams 1965).

**Growth and Development**

Egg Size and Embryonic Development: Approximate ages (after fertilization and extrusion) of blue crab egg masses (sponges) can be estimated according to coloration. Yellow to orange egg masses are from 1 to 7 days old. Brown to black egg masses are from 8 to 15 days old (Bland and Amerson 1974). Hatching occurs from 14 to 17 days after egg extrusion at 26°C, and 12 to 15 days at 29°C (Churchill 1921). Freshly extruded eggs in the early stages of development are 273 x 263 µm, and enlarge to 320 x 278 µm before hatching (Davis 1965). Hatching occurs in high salinity waters in the lower estuary, and in adjacent Gulf waters. In laboratory experiments, successful hatching did not occur below 20‰ (Costlow and Bookout 1959).

Age and Size of Larvae: Newly hatched blue crab larvae are 0.25 mm in carapace width (CW) and usually develop through seven zoeal stages. Laboratory studies indicate that 31 to 43 days are required to complete the zoeal larval stages at 25°C and 26‰ salinity (Costlow and Bookout 1959). After the final zoeal stage when approximately 1 mm CW, larvae metamorphose into the megalopal larval stage (Costlow and Bookout 1959). The optimal salinity and temperature combination for zoeal and megalopal development is 30‰ and 25°C (Bookout et al. 1976, Costlow 1967). At 30‰ and 25°C, 6 to 12 days were required to develop through the megalopal larval stage into the first crab (juvenile) stage at 2.2-3.0 mm CW (Costlow 1967). In Mississippi Sound, settlement of blue crab megalopae is episodic, occurring primarily from late summer to early fall (Perry et al. 1995). Settlement in Mississippi Sound was associated with spring tides and onshore winds, rather than with salinity, temperature, or lunar period (Perry et al. 1995). Megalopal settlement in the northern Gulf of Mexico may be asynchronous among sites (Rabalais et al. 1995).

Juvenile Size Range: Juvenile blue crabs may reach maturity within one year along the Gulf coast (Perry 1975), while populations in more temperate climates may take up to 20 months (Millikin and Williams 1984). Salinities from 6 to 30‰ do not differentially affect growth of juveniles (Millikin and Williams 1984). Tagatz (1968b) observed that growth per molt remained similar regardless of temperature (summer vs. winter) in the St. Johns River, Florida, but that intermolt intervals were three to four times longer in the winter. Juvenile blue crabs may range in size from approximately 2 mm CW when the first crab stage is attained, to over 150 mm CW. Maturity in blue crabs is attained over a wide range of carapace widths (Perry pers. comm.). Guillory and Hein (in press) sampled 2,925 blue crabs in Louisiana estuarine waters, and reported that 50% of males were mature by 110-115 mm CW, and 50% of females were mature by 125-130 mm CW. The smallest mature male was 96 mm CW, and the smallest mature female 113 mm CW. One hundred percent of the males were mature by 130 mm CW, and 100% of the females by 160 mm CW.

Age and Size of Adults: Tagatz (1968b), sampling blue crabs from St. Johns River, Florida, reported mean carapace widths and ranges: adult males averaged 147 mm, ranging from 117 mm to 181 mm; adult females averaged 148 mm, ranging from 128 to 182 mm. Tagatz (1965) reported a maximum carapace width of 246 mm (male), and a heaviest weight of 550 g (male), from commercial catches in the St. Johns River, Florida. Adult males generally weigh more than females of a given size (excluding gravid females) (Millikin and Williams 1984). Females may vary in size from mature at 51 mm to immature at 177 mm. Females mate at their terminal molt, males continue to grow and molt after reaching sexual maturity. The blue crab has an estimated life span of 3-4 years (Tagatz 1968a). Growth equations for the blue crab have been calculated by Pullen and Trent (1970).

**Food and Feeding**

Trophic Mode: This crab is an omnivore, scavenger, detritivore, predator, and cannibal that feeds on a wide variety of plants and animals, selecting whatever is locally available at any time (Costlow and Sastry 1966, Laughlin 1982). Its feeding habits change with its ontogeny. Larval blue crabs are believed to feed on phytoplankton and zooplankton, while juveniles and adults are described as general scavengers, bottom carnivores, detritivores, and omnivores, that consume whatever is in the area (Costlow and Sastry 1966, Laughlin 1982).

Food Items: Food habits of the blue crab are variable, changing with season of the year, geographic location, and the developmental stages of its life cycle (Laughlin 1982, Steele and Perry 1990). Zoea consume phytoplankton and copepod nauplii. Aquaculture protocols recommend that zoeal stages be fed sea urchin embryos, *Artemia* nauplii, and/or rotifers (Millikin and Williams 1984, Schmidt 1993). The megalopal stage is omnivorous and consumes fish larvae, small shellfish and aquatic plants. The diet of juveniles and adults consists mainly of molluscs, crustaceans, and fish (Tagatz 1968a, Jaworski 1972, Alexander 1986). Laughlin (1982) evaluated stomach contents of blue crabs from Apalachicola Bay, Florida and observed the following: small juveniles (less than 31 mm carapace width) fed mainly on bivalves, plant matter, ostracods, and detritus; intermediate juveniles (31-60 mm) fed mostly on fishes, gastropods, and xanthid crabs; large juveniles and adults (greater than 60 mm) fed on bivalve molluscs, fishes, xanthid crabs, and smaller blue crabs. Molluscs known to be food items for blue crab include American oyster, hard clams, coot clam (*Mulina lateralis*), Atlantic ribbed mussel (*Geukensia demissa*), dark false mussel (*Mytilopsis leucophaeata*), scorched mussel (*Brachidontes exustus*), Atlantic rangia, and marsh periwinkle (*Littorina irrorata*) (Millikin and Williams 1984). The blue crab has been characterized as an opportunistic benthic omnivore, whose food habits are governed by availability of food items (Darnell 1959, Seed and Hughes 1997). Feeding generally decreases as temperature decreases, especially from 34° to 13°C (Leffler 1972).

**Biological Interactions**

Predation: Blue crab postlarvae can be 10 to 100 times more abundant in estuaries of the U.S. Gulf Coast (AL, MS, TX) than along the East Coast (DE, VA, NC, SC), but this does not necessarily result in elevated abundance of juveniles and higher fishery landings (Heck and Coen 1995). Abundances of blue crab juveniles are similar in estuaries of the two regions, suggesting that there is higher mortality of recently-metamorphosed juveniles in the Gulf region, possibly as a result of predation (Heck and Coen 1995). Numerous species of fish, mammals, and birds prey on the blue crab (Killam et al. 1992). Different species of shrimp, including *Palaemonetes pugio*, have been found to prey on blue crab megalopae (Olmi 1990). Fish that consume zooplankton, such as herring and menhaden species, are also probably important predators of blue crab larvae (Millikin and Williams 1984, Schmidt 1993). Major fish predators on juveniles are snook, black drum, juvenile and adult red drum, Atlantic croaker, spotted seatrout, and sheepshead (Fontenot and Rogillio 1970, Boothby and Avault 1971, Adkins 1972b, Fore and Schmidt 1973, Bass and Avault 1975, Overstreet and Heard 1978a, Overstreet and Heard 1978b). They have also been found in the stomach contents of the sandbar shark (*Carcharhinus plumbeus*) and spot (Levine 1980, Medved and Marshall 1981, Rozas and Hackney 1984). In addition, adult blue crabs will often cannibalize juveniles (Costlow and Sastry 1966, Martinez pers. comm.). Several freshwater fishes may prey on blue crab in oligohaline waters, including alligator gar (*Lepisosteus spatula*), spotted gar (*Lepisosteus oculatus*), and largemouth bass (*Micropterus salmoides*)(Lambou 1961). The primary mammalian predator (other than humans) is the raccoon (*Procyon lotor*) (Steele and Perry 1990, Killam et al. 1992). Avian predators include the clapper rail, great blue heron, American merganser, and hooded merganser. Other vertebrate predators include the Kemp's ridley sea turtle and the American alligator (Byles 1989, Platt et al. 1990).

Factors Influencing Populations: Natural mortality rates of juvenile (5-20mm CW) blue crab have been estimated at 70-91%/day in Alabama, 68-88%/day in Virginia, and 25-38%/day in New Jersey (Heck and Coen 1995). Estimated natural mortality rates were lower at sites with seagrass, and higher at sites with sand substrate. Estimation of fishery mortality is complicated by: (1) the lack of data on incidental harvest by non-directed fisheries, (2) inadequate recreational catch statistics, and (3) widespread under-reporting of soft and hard crab harvest (Adkins 1972b, Steele and Perry 1990). In addition to catches made by the recreational and commercial fisheries, large numbers of blue crabs are harvested incidentally by the shrimp trawl fishery (Adkins 1972b, Steele and Perry 1990). At present, increases in fishing effort have resulted in only slight declines in catch per fisherman, indicating that the fishery has remained fairly stable. Destruction of wetland habitat due to dredging, filling, impoundment, flow alteration, and pollution has been suggested to cause a decrease in fishery production, and, therefore, may be a significant factor in determining blue crab production (Steele and Perry 1990).

The blue crab can be infected by several diseases caused by viral, bacterial and fungal agents that result in mortality or morbidity (Steele and Perry 1990, Messick and Sinderman 1992). A variety of ecto-commensal symbionts and parasites are associated with blue crabs (Perry pers. comm.). Heavy infestations of symbionts may interfere with metabolic processes. Infested crabs are more vulnerable to predations, and less tolerant of unfavorable environmental conditions (Overstreet 1978). The cypris stage of the parasitic sacculinid barnacle, *Loxothylacus texanus*, infects soft juveniles retarding their growth (Overstreet 1978, Overstreet et al. 1983, Hochberg et al. 1992), and resulting in their loss to the fishery (Adkins 1972a). Predation and cannibalism may significantly affect abundance (Adkins 1972a, Heck and Coen 1995). Abiotic environmental variables may affect survival directly or indirectly. Mortality of blue crabs exposed to low dissolved oxygen coupled with high temperatures is common during the summer (May 1973, Tagatz 1969). Abiotic factors can influence blue crab populations indirectly through predator-prey relationships if they exert a greater influence on the distribution of food organisms than they do on the blue crab (Laughlin 1982).

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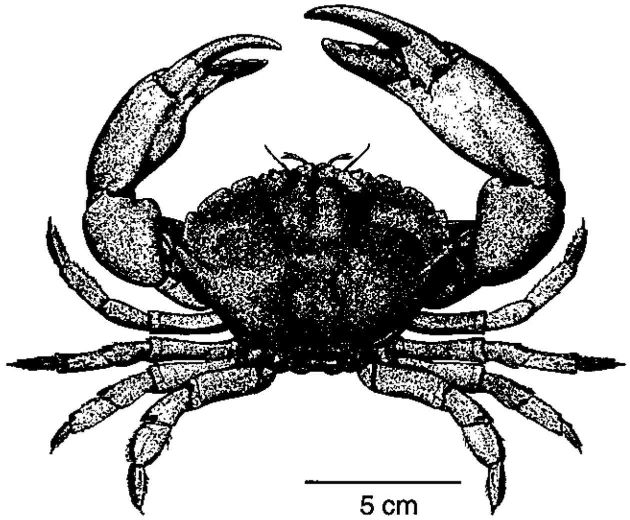
# Stone crab

**_Menippe_ species**
**Adult**




(from Goode 1884)

**Common Name**: stone crab
**Scientific Name**: *Menippe* species
**Other Common Names**: Florida stone crab, gulf stone crab (Williams et al. 1989); *cangrejo de piedra negro, cangrejo moro* (Spanish), *crabe caillou noir* (French) (Fischer 1978, NOAA 1985).
**Classification**
Phylum: Arthropoda
Class: Crustacea
Order: Decapoda
Family: Xanthidae

Stone crabs (genus *Menippe*) have recently undergone taxonomic revision, and two species are now recognized in U.S. waters of the Gulf of Mexico: *Menippe mercenaria*, the Florida stone crab; and *Menippe adina*, the gulf stone crab (Williams and Felder 1986, Williams et al. 1989). A third species, the Cuban stone crab (*M. nodifrans*), is smaller and occurs in the Caribbean but is not common in U.S. Gulf of Mexico estuaries (Fischer 1978, Williams et al. 1989). *M. mercenaria* occurs from North Carolina around peninsular Florida to the Big Bend region near Apalachicola Bay, and also in the Caribbean, the Yucatan, and Belize. *M. adina* occurs in the Gulf of Mexico from Florida's Big Bend region westward through Texas to northern Mexico (Williams and Felder 1986). The two species are sympatric in the Big Bend region of northwest Florida, and they often hybridize there. Their evolutionary divergence may have occurred as a result of geologic events and oceanic processes within the past 3 million years (Bert 1986). It has been hypothesized that the Miocene glaciation may have caused two populations of an ancestral *Menippe* species to become isolated, resulting in allopatric speciation (Brown and Bert 1993). Specific differences in coloration and morphometrics (Williams and Felder 1986, Bert et al. 1996), megalopal morphology (Martin et al. 1988, Guillory et al. 1995), habitat utilization (Wilber 1992), low salinity tolerance (Stuck and Perry 1992), low temperature tolerance (Brown and Bert 1993), and isozyme markers (Cline et al. 1992) have been described.

The life histories of these two species are summarized together here because their biology is very similar, and because much of the existing literature does not distinguish between them. They are referred to individually here as "Florida stone crab" and "gulf stone crab", and collectively as "stone crabs". It is presumed that life history characteristics of the two species are similar, but known differences are noted.

**Value**
Commercial: The commercial importance of stone crabs comes from the meat of their highly esteemed claws. The large claws contain much of the crab's muscle mass, can weigh over 300 g (Stuck 1989), and have a high market value. The claw is removed after capture, and the crab is released. This makes the stone crab fishery unique because the harvested animal does not necessarily die (Restrepo 1992). Crabs that survive de-clawing can then regenerate new claws, but regeneration to legal size (70 mm propodus length) may take a year or more. The major (crusher) claw is typically on the right and the minor (pincer) claw on the left, although crabs that have lost a right claw may regenerate a crusher on the left after one or more molts, indicating a reversal of handedness (Cheung 1976, Simonson and Steele 1981, Simonson 1985). Most of the legal-sized harvested claws are crushers, and most of the harvested crushers are right-handed (Sullivan 1979, Simonson and Hochberg 1992). Males

Table 5.12. Relative abundance of Florida stone crab (*M. mercenaria*) in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | M | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | O | O | √ | √ | O |
| Ten Thousand Islands | O | O | O | O | O |
| Caloosahatchee River | | | √ | √ | |
| Charlotte Harbor | O | O | O | O | O |
| Tampa Bay | O | O | O | O | O |
| Suwannee River | O | O | O | O | O |
| Apalachee Bay | O | O | O | O | O |
| Apalachicola Bay | √ | √ | √ | √ | √ |
| St. Andrew Bay | | | | | |
| Choctawhatchee Bay | | | | | |
| Pensacola Bay | | | | | |
| Perdido Bay | | | | | |
| Mobile Bay | | | | | |
| Mississippi Sound | | | | | |
| Lake Borgne | | | | | |
| Lake Pontchartrain | | | | | |
| Breton/Chandeleur Sounds | | | | | |
| Mississippi River | | | | | |
| Barataria Bay | | | | | |
| Terrebonne/Timbalier Bays | | | | | |
| Atchafalaya/Vermilion Bays | | | | | |
| Calcasieu Lake | | | | | |
| Sabine Lake | | | | | |
| Galveston Bay | | | | | |
| Brazos River | | | | | |
| Matagorda Bay | | | | | |
| San Antonio Bay | | | | | |
| Aransas Bay | | | | | |
| Corpus Christi Bay | | | | | |
| Laguna Madre | | | | | |
| Baffin Bay | | | | | |
| | A | M | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- O Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- M - Mating
- J - Juveniles
- L - Larvae
- E - Eggs

Table 5.13. Relative abundance of gulf stone crab (*M. adina*) in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | M | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | | | | | |
| Ten Thousand Islands | | | | | |
| Caloosahatchee River | | | | | |
| Charlotte Harbor | | | | | |
| Tampa Bay | | | | | |
| Suwannee River | √ | √ | √ | √ | √ |
| Apalachee Bay | O | O | O | O | O |
| Apalachicola Bay | O | O | O | O | O |
| St. Andrew Bay | √ | √ | √ | √ | √ |
| Choctawhatchee Bay | √ | √ | √ | √ | √ |
| Pensacola Bay | √ | √ | √ | √ | √ |
| Perdido Bay | √ | √ | √ | √ | √ |
| Mobile Bay | O | √ | O | √ | √ |
| Mississippi Sound | O | O | O | O | O |
| Lake Borgne | √ | | √ | | |
| Lake Pontchartrain | √ | | √ | | |
| Breton/Chandeleur Sounds | O | O | O | O | O |
| Mississippi River | O | | O | | |
| Barataria Bay | √ | | O | | |
| Terrebonne/Timbalier Bays | O | | O | | |
| Atchafalaya/Vermilion Bays | √ | | √ | | |
| Calcasieu Lake | √ | | O | | |
| Sabine Lake | √ | | √ | | |
| Galveston Bay | O | O | O | O | O |
| Brazos River | na | | na | | |
| Matagorda Bay | O | O | O | O | O |
| San Antonio Bay | O | O | O | O | O |
| Aransas Bay | O | O | O | O | O |
| Corpus Christi Bay | O | O | O | O | O |
| Laguna Madre | √ | √ | √ | √ | √ |
| Baffin Bay | O | O | O | O | O |
| | A | M | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- O Common
- √ Rare
- blank Not present
- na No data available

Life stage:
- A - Adults
- M - Mating
- J - Juveniles
- L - Larvae
- E - Eggs

tend to have larger claws and are therefore more likely to be harvested by the fishery. Male stone crabs are recruited into the fishery during their third year, and can live to at least 8 years (Restrepo 1989). Most crabs with legal-sized claws in Florida are 3 or 4 years old (Sullivan 1979). Both claws can be removed if they are legal size, but it is illegal to remove claws from a gravid female (Bert pers. comm.).

Southwest Florida is the major area of commercial harvest in the U.S. (NOAA 1985), although landings are also reported from South Carolina, Texas, Louisiana, Mississippi, and northwest Florida (Bert 1992). Stone crab fisheries also exist in the Caribbean, and landings have been reported from Cuba, Mexico, and the Dominican Republic (Fischer 1978). Florida has kept fishery statistics since 1962 (Williams and Felder 1986). In 1990, the Florida fishery reported landings of 1,225 metric tons, with a dockside value of over $15 million (Restrepo 1992). The stone crab fishery has been ranked as Florida's eighth most valuable (Adams and Prochaska 1992). Recent dockside prices have been near $4.75/lb for medium and $7.50/lb for jumbo claws (Newlin 1993), and consumer demand continues to be strong. Most of the claws harvested in Florida are marketed fresh or frozen and consumed locally. The same appears to be true of the Texas fishery, although some Texas claws are transported to meet increasing demand in Florida (Landry 1992, Tobb pers. comm.). Catches along the Texas coast are primarily incidental to the blue crab fishery (Stuck 1987, Landry 1992, Pattillo pers. obs.). Texas reported 39,000 kg of gulf stone crab claws landed in 1992, about one fourth of which came from the Galveston region (Newlin 1993). The prospect of a limited fishery in Barataria Bay, Louisiana, and the lower Mississippi Sound and adjacent nearshore waters has been studied and is considered feasible if regulations are enacted to prevent overharvest and minimize gear conflict (Horst and Bankston 1986, Stuck 1987, Stuck 1989, Baltz and Horst 1992). However, it has been suggested that only a fairly low percentage of the available stone crab claws in the northern Gulf of Mexico (Mississippi) would be of legal size, i.e. ≥70 mm propodus length (Perry et al. 1995).

In the south Florida stone crab fishery, stationary traps made of wood, plastic, or wire are baited with fish scraps, deployed on the bottom and marked with a buoy, and checked every few days for crabs (Overbey 1992). According to Florida regulations, claws must have a propodus length of ≥70 mm (2.75 in) to be legal for harvest, and commercial stone crabbers must have a Saltwater Products License (GSMFC 1993). Legal size is generally attained by males at approximately 80 mm carapace width (CW), and by females at 90 mm CW (Simonson 1985, GSMFC 1993). This minimum size is intended to allow crabs to reproduce at least once before being vulnerable to the fishery. Egg-bearing females are protected, and the fishery is open from mid-October to mid-May (Ehrhardt et al. 1990, GSMFC 1993, NOAA 1993). Similar regulations apply in offshore federal waters of the Gulf of Mexico as well (GMFMC 1996a). The Florida stone crab fishery is spatially separated from the pink shrimp trawl fishery to minimize gear conflict (Overbey 1992). In Texas, only right claws with propodus length ≥63 mm may be harvested, and the possession or sale of ovigerous (sponge) crabs and left claws is prohibited (GSMFC 1993).

<u>Recreational</u>: Many of the Florida permit holders can be considered recreational because their harvest is for home consumption, but the total recreational harvest is probably much smaller than the commercial (GMFMC 1978, Zuboy and Snell 1982, Lindberg and Marshall 1984, NOAA 1985). Some of the recreational harvest is with gear similar to the commercial fishery, i.e., crab traps, and a Saltwater Products License is required to use traps (GSMFC 1993). Stone crabs are also taken by hand or dipnet while wading or diving (GMFMC 1978, Williams 1984), or removed from their burrows with a hook attached to a long handle (Savage et al. 1975). In offshore federal waters of the Gulf of Mexico, recreational regulations include a 2.75 in (70 mm) minimum claw size, closed season from mid-May to mid-October, and prohibition of claw removal from egg-bearing females (GMFMC 1996b).

<u>Indicator of Environmental Stress</u>: Stone crabs are not typically used in studies of toxicity, bioaccumulation, and environmental stress.

<u>Ecological</u>: Stone crabs have a large claw adapted for crushing shells, and are formidable predators of molluscs. They are known to prey on juvenile oysters on reefs. The burrows of gulf stone crabs in mud flats remain filled with seawater at low tide, and can provide a unique intertidal refuge for small fishes and other organisms (Powell and Gunter 1968).

**Range**

<u>Overall</u>: The Florida stone crab occurs from North Carolina around peninsular Florida to the Big Bend region, and also in the Bahamas, Cuba, Jamaica, the Yucatan peninsula, and Belize. The gulf stone crab occurs in the Gulf of Mexico from Florida's Big Bend region westward through Texas to Tamaulipas in northern Mexico (Williams and Felder 1986). The two species co-occur and are known to hybridize in the Big Bend region of northwest Florida.

<u>Within Study Area</u>: Within U.S. estuaries of the Gulf of Mexico, the Florida stone crab occurs from Florida Bay

to Apalachicola Bay, Florida, and is especially abundant in the southwest Florida region (NOAA 1985) (Table 5.12). The gulf stone crab occurs from Suwannee River, Florida westward to Laguna Madre and Baffin Bay, Texas, and is relatively abundant in the south Texas estuaries (Table 5.13). The two species are sympatric in Suwannee River, Apalachee Bay, and Apalachicola Bay, and are known to hybridize in this region.

**Life Mode**

Eggs are maintained by the female beneath her abdomen until hatching. Zoeal larvae are planktonic. The megalopal stage is a transition from the planktonic larval life mode to the epibenthic life mode of juveniles (Stuck and Perry 1992). As megalopae transform into juveniles, they settle out and are found in areas providing cover such as rubble and seagrass beds. Adults and juveniles are demersal, with adults often forming deep burrows in mud sediments. Juveniles usually do not form burrows, but use readily available crevices or existing cavities in close proximity to food (Lindberg and Marshall 1984). Adult males may exhibit agonistic behavior and compete for burrows, but it is not known whether they establish and defend territories or whether their distribution changes between mating and non-mating seasons (Wilber 1986). Stone crabs have been suggested to be nocturnal; however, equal activity at mid-day and mid-night has been observed, suggesting a crepuscular activity cycle (Powell and Gunter 1968, Lindberg and Marshall 1984).

**Habitat**

Type: All life stages are marine to estuarine. Adult Florida stone crabs are generally found in deeper waters of estuaries or in nearshore waters of the Gulf of Mexico. Adults burrow under rock ledges, coral heads, dead shell, or grass clumps (Costello et al. 1979, Bert and Stevely 1989). In seagrass flats and along tidal channels they inhabit burrows and are rarely found on shallow flats during spring and early summer. Juveniles are found in estuaries around pilings, among shells and rocks, and in grass beds (NOAA 1985). They can change coloration patterns to blend with the background (Bert et al. 1978, Lindberg and Marshall 1984, Williams 1984). Maturing crabs move to deeper estuarine and nearshore waters. Adults have been collected at depths ranging from 5 to 54 m, but are not generally abundant in offshore waters (Bullis and Thompson 1965, Bert and Stevely 1989, Stuck 1989). The Florida stone crab occurs at greatest densities in seagrass, rocky outcrops, and hard bottom. It rarely occupies oyster bars, while the gulf stone crab commonly inhabits oyster bars, sandy or muddy bottoms, as well as seagrass or rocky habitats (Bert and Harrison 1988). Gulf stone crabs occur both sub- and intertidally, whereas the Florida stone crab is primarily subtidal (Wilber 1989a, Wilber 1992). In addition, males are more likely to be found in intertidal areas in the summer, and females in subtidal habitats (Wilber 1989a). Highest catches of gulf stone crab in Mississippi Sound are in the immediate vicinity of barrier island passes in depths less than 12 m, and they are not generally abundant in offshore waters (Stuck 1989).

Substrate: Florida stone crabs appear to require substrate suitable for refuge, using either available structure or excavated burrows. They are found in rock or shell substrates, seagrass meadows, and pilings (Costello et al. 1979), and are known to excavate burrows in emergent hard substrate or in seagrass (*Thalassia*) beds (Bert and Stevely 1989). In one study in Galveston Bay, gulf stone crabs were found to be more abundant on oyster reefs than in vegetated or non-vegetated habitat (Zimmerman et al. 1989).

Physical/Chemical Characteristics:

Temperature - Larvae: Florida stone crab larvae do not develop beyond the megalopal stage at temperatures below 20° C (Ong and Costlow 1970). Optimal conditions for zoeae appear to be 30°C at 30 to 36‰. Megalopae are sensitive to low salinities and extreme temperatures (Lindberg and Marshall 1984). In a factorial experiment of salinity and temperature, survival of Florida stone crab larvae (zoeae) was found to be highest at 30°C and 30‰, and diminished at salinities and temperatures above and below these values (Brown et al. 1992). The early zoeal stages (zoeae 1-3) were strongly affected by both temperature and salinity, whereas the later stages (zoeae 4-5) were less affected by salinity. Larval developmental rate and molting frequency were accelerated by increasing temperature, but not by salinity.

Temperature - Juveniles and Adults: Juvenile and adult stone crabs are eurythermal and, in general, can tolerate waters ranging from 8°-32°C. In cooler temperatures they become inactive and may seal their burrows with mud (Powell and Gunter 1968). Muscular movements of juvenile Florida stone crab virtually cease below 15°C (Brown et al. 1992). In Mississippi Sound, juvenile gulf stone crabs have been collected at temperatures from 7°-33°C, but mostly above 25°C (Stuck and Perry 1992). Molting and spawning are affected by temperature (Lindberg and Marshall 1984, Williams 1984), and low temperatures are known to inhibit molting (Brown et al. 1992). Ovigerous gulf stone crab females are not generally found at ≤18°C, and are most common at ≥22°C (Stuck and Perry 1992). In a factorial experiment of salinity and temperature, survival of juvenile Florida stone crab was found to be 100% at 15°, 20°, and 25°C (Brown et al. 1992).

Salinity - Larvae: Ong and Costlow (1970) reported that Florida stone crab zoeae have low survival rates at low salinities (20-25‰) at 20°C; and complete mortality occurs in a salinity of 10‰. At 23°-25°C, low survival of zoeae has been observed below 27‰ (Porter 1960). It has been suggested that gulf stone crab larvae may be more tolerant of low salinities than Florida stone crab larvae. In Mississippi Sound, gulf stone crab megalopae are commonly found in salinities of 15-25‰, and have been collected from salinities as low as 9‰ (Stuck and Perry 1992).

Salinity - Juveniles and Adults: Juveniles and adults of both species are considered euryhaline, although they are usually found in higher salinities. It has been suggested that *M. mercenaria* may be less tolerant of lower salinities and/or prefer higher salinities than *M. adina* (Williams and Felder 1986). Juvenile Florida stone crabs are generally found in salinities ≥24‰ (Bender 1971). In Mississippi Sound, gulf stone crab juveniles have been collected in salinities from <4 to 34‰, although they are most abundant in salinities from 20-29‰ (Stuck and Perry 1992). Gulf stone crab adults are found in salinities above 13‰ in Mississippi Sound (Stuck 1989, Stuck and Perry 1992), but they have been reported from salinities as low as 11.6‰ in Texas (Powell and Gunter 1968). In a factorial experiment of salinity and temperature, survival of juvenile Florida stone crab was found to be 100% at 25, 30, 35, and 40‰ (Brown et al. 1992). In a similar experiment comparing survival of juvenile gulf stone crab and Florida stone crab, it was found that gulf stone crab had greater tolerance for low salinity and low temperature than did Florida stone crab (Brown and Bert 1993). This may be due to species-specific differences, or to local adaptation of populations. These differences generally reflect the known biogeographic and inshore/offshore distribution of the two species (Brown and Bert 1993).

Dissolved Oxygen (DO): Adults are fairly tolerant of periods of low DO, although long-term effects are not well known (Lindberg and Marshall 1984).

Turbidity: Stone crabs may become more active in turbid waters, possibly as a result of waves and turbulence that agitate the bottom substrate (Savage et al. 1975).

<u>Migrations and Movements</u>: Movements by Florida stone crabs of up to 30 km/year have been recorded in Florida's Everglades National Park (Bert and Harrison 1988), but most movements appear to be short-range and along shore (1.6-8.0 km) (Ehrhardt 1990). Minor movements by the females from grass flats to deeper waters to avoid especially high or low temperatures have been noted (Lindberg and Marshall 1984, NOAA 1985, Wilber 1986). In northwest Florida's "hybrid zone", adult females may migrate into intertidal oyster habitats (Wilber and Herrnkind 1986). This is followed by the gradual emigration of nearly all crabs from the intertidal region in the late fall and early winter, probably in response to falling temperature.

**Reproduction**

<u>Mode</u>: Stone crabs have separate male and female sexes (gonochoristic), and exhibit sexual dimorphism (Savage 1971, Bert and Stevely 1989).

<u>Mating and Spawning</u>: Mating occurs from November to March, but primarily in January and February. It is sequenced with the spawning season, generally from March to November. In Florida Bay, peak mating periods have been noted in April and October (Bert and Stevely 1989). Mating takes place within a burrow or crevice (Savage 1971, Bert and Stevely 1989, Wilber 1989b). Males will guard the females after copulation, and for longer periods after females molt if another male stone crab is present. Sperm are transferred from the male to the female within spermatophores which are stored by the female in the seminal receptacle. Only a portion of the sperm is used at a spawning period, some being maintained for later spawns. A female can spawn up to six times before mating again. After hatching one batch of eggs, a female may deposit a new egg mass within a week. Fertilized eggs are released into a basket formed by the female's extended abdomen and the exopods of her abdominal appendages. The eggs are attached to hairs on the exopods by a secretion. Temperature and photoperiod are primary regulators of spawning frequency (Bert et al. 1978, Lindberg and Marshall 1984, Williams 1984, Bert et al. 1986). In south Florida, most spawning of Florida stone crabs is from March to October, with peaks in May and September (Sullivan 1979). However, spawning can also occur throughout the year in warm areas such as Florida Bay. Ovigerous gulf stone crabs occur in Mississippi Sound from March through October, with apparent spawning peaks in June and September (Stuck and Perry 1992). Evidence indicates that females molt and mate soon after spawning is terminated. The movement of adult females to oyster reefs in the fall suggests this may be an important mating habitat for first and second year adults (Wilber 1986).

<u>Fecundity</u>: A single female can produce between 4 and 6 egg masses (sponges) during a spawning season, averaging 4.5 spawnings per molt (Cheung 1969). Ten spawnings during an intermolt period have been reported from a single female held in the laboratory (Yang 1971). Each sponge may contain 0.5 to 1.0 million eggs. Wilber (1989a) observed a maximum number of five clutches carried by a single female in a

93 day period. Fecundity is higher in larger females (Sullivan 1979).

**Growth and Development**

Egg Size and Development: Fertilized eggs are maintained by the female until hatching, usually 9 to 14 days (Lindberg and Marshall 1984). The embryonic duration of eggs held in the laboratory at temperatures of 29 to 30°C was approximately 10 days (Yang 1971).

Age and Size of Larvae: Stone crabs typically pass through five (sometimes six) zoeal stages with one molt per stage, and then metamorphose into megalopae. Each zoeal stage lasts three to six days (Porter 1960), and total time from hatch to metamorphosis is 21 to 28 days (Brown et al. 1992). Fastest larval growth of Florida stone crabs was achieved in the laboratory at 30°C and 30-35‰, in which the megalopal stage was reached in 14 days and first crab stage in 21 days (Ong and Costlow 1970). At 25°C and 30‰, laboratory-reared gulf stone crab megalopae developed in 17 days (Martin et al. 1988). Development of planktonic larvae to first crab stage usually requires 27 to 30 days, but may be affected by diet. The megalopal stage of gulf stone crab is thought to last 4 to 7 days (Stuck and Perry 1992).

Juvenile Size Range: Megalopae metamorphose to juveniles and settle at 1.5 to 2.0 mm carapace width (CW) (Bert et al. 1986). Intermolt period for post-settlement juveniles ≤10 mm CW is approximately 36 days (Brown et al. 1992). Juveniles molt several times, and growth can vary from 10 to 40 mm CW in their first year. At a size of about 35 mm CW, the carapace shape transforms to the adult coloration. Size increases in increments of approximately 15% per molt.

Age and Size of Adults:
Female *M. mercenaria* begin to reach sexual maturity at about 40 mm CW and some mate during the winter at age 1, although most mature later at age 2 (60-70 mm CW) or age 3 (70-80 mm CW). Males are generally mature at 70 mm CW, at age 2. In laboratory studies, measured growth of adults has been approximately 15 to 20% of the carapace width per molt, which is comparable with field growth observations (Simonson 1985, Tweedale et al. 1993). After four years of age, crabs generally molt only once per year, typically in the fall. Terminal molts have been suggested to occur around 112 mm CW, but crabs can reach sizes of 130 to 145 mm CW (Bert et al. 1978, Sullivan 1979, Lindberg and Marshall 1984, Bert et al. 1986). Recruitment into the Florida stone crab fishery probably occurs at about age 2 (Ehrhardt and Restrepo 1989, Restrepo 1989). The maximum age of Florida stone crabs has been estimated as six to eight years or more (Bert et al. 1986, Restrepo 1989). Gulf stone crabs are morphometrically similar to Florida stone crabs, and their carapace widths at 50% sexual maturity have been estimated at 71 mm for males, and 73 mm for females (Perry et al. 1995).

**Food and Feeding**

Trophic Mode: Stone crabs are high trophic level predators and are primarily carnivorous at all life stages (Bert and Stevely 1989). After feeding to satiation, these crabs can live for two weeks without feeding again (Bert et al. 1986).

Food Items: It has been suggested that larvae have specific dietary requirements, apparently met by only certain types of planktonic animals (Guillory et al. 1995). Juveniles feed on small molluscs, polychaete worms and crustaceans. Juveniles in captivity are known to consume small bivalves, oyster drills, beef liver and chicken parts, polychaetes, and each other. Adults use their heavy chelae to crush all types of molluscs, and are known to prey on oysters (Williams 1984, NOAA 1985, Bert et al. 1986) and mussels (*Brachidontes* spp.) (Powell and Gunter 1968). Stone crabs are also known to consume carrion and vegetable matter such as seagrass (NOAA 1985).

**Biological Interactions**

Predation: Larvae are preyed on by other planktivores, while the larger juveniles are prey for black sea bass, groupers, common octopus (*Octopus vulgaris*), and other large predators (Lindberg and Marshall 1984, Lindberg et al. 1992). Adults can usually defend against predators, but may be vulnerable to attack when caught in crab traps.

Factors Influencing Populations: Although "harvested" crabs are released alive, subsequent mortality of declawed crabs has been estimated at 50% and has a significant impact on stone crab populations. After removal from traps, crabs are sometimes held onboard and declawed while enroute to port; mortality of these crabs is higher if they are held too long and not kept moist, and if the claws are not severed along the natural fracture plane (Simonson and Hochberg 1986). The Florida stone crab fishery is considered to be fully exploited. Recent annual harvests have been over 1,000 metric tons per year (mt/y), although long-term potential yield has been estimated as 976 mt/y (NOAA 1993), and Zuboy and Snell (1982) estimated a maximum sustainable yield (MSY) of 853 mt/y. Declines in catch per unit effort (CPUE) have been observed in recent years, further suggesting that the fishery is fully utilized (Phares 1992). Mariculture methods have been developed to produce stone crab megalopae (McConnaughey and Krantz 1992), although commercial-scale mariculture of stone crab claws is not yet feasible.

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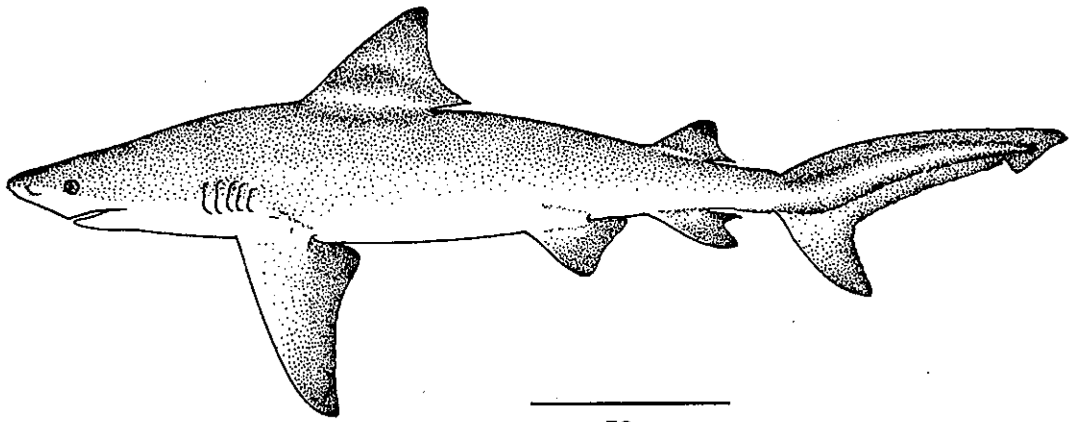
# Bull shark

*Carcharhinus leucas*
**Adult**




(from Fischer 1978)

**Common Name**: bull shark
**Scientific Name**: *Carcharhinus leucas*
**Other Common Names**: cub shark, *réquiem taureau* (French), *tiburón sarda* (Spanish) (Fischer 1978).
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Chondrichthyes |
| Order: | Lamniformes |
| Family: | Carcharhinidae |

## Value

Commercial: The bull shark is becoming more important in the commercial shark fishery of the Gulf of Mexico as the market demand for sharks increases (Branstetter pers. comm., NOAA 1992, NMFS 1993). The flesh is edible, but it is primarily used for fish meal. The hide is processed into leather and has good quality (Castro 1983, NOAA 1992). This species was once sought for its liver which contains large amounts of vitamin A; however, synthetic substitutes have reduced the demand for this product (Fischer 1978, NOAA 1992, NMFS 1993). Bull sharks will take almost any bait, but may prefer shark or ray. Recently, many Gulf of Mexico shrimp fishermen have changed to longline rigs to catch sharks because of the high export demand for shark fins. A Fishery Management Plan (FMP) has been developed for sharks in the western Atlantic, Caribbean Sea, and Gulf of Mexico (NMFS 1993). Some of the features of this plan include an annual permit required for commercial shark fishing vessels in the U.S. exclusive economic zone, and an annual quota of 2,436 mt dressed weight for large coastal species during the 1993 fishing year. Future quotas will be based on the shark fishery rebuilding program (NMFS 1993).

Recreational: In general, shark populations in the Gulf of Mexico and Atlantic waters of the southeast U.S. are suffering from overfishing to which they are especially vulnerable (NOAA 1992). Most sharks caught by recreational anglers are released or discarded, but some are used as mounted trophies or for home consumption. In the Gulf of Mexico, the bull shark comprises 7% by number and 11% by weight of the sharks caught by recreational fishermen (Casey and Hoey 1985). The recreational bag limit is four sharks per boat per trip (NMFS 1993).

Indicator of Environmental Stress: This species is not typically used in studies of environmental stress, but monitoring by the Florida Department of Health and Rehabilitative Services has shown high concentrations of mercury present in shark flesh sold in the retail market (NMFS 1993).

Ecological: Sharks are often studied as top trophic level predators (Casey and Hoey 1985). The bull shark is a top trophic level carnivore in many estuarine systems, and is one of the most common species of inshore sharks in the Gulf of Mexico (Casey and Hoey 1985, Shipp 1986).

## Range

Overall: This is a cosmopolitan species in both tropical and subtropical areas with range extensions into some temperate regions. In the western Atlantic, it extends from Cape Cod, Massachusetts to southern Brazil, including Bermuda, Gulf of Mexico, and Caribbean islands (Fischer 1978, Lee et al. 1980, Garrick 1982). It is most abundant in Gulf of Mexico and Caribbean Sea (Garrick 1982, Castro 1983). In the Pacific, it is known from Anacapa Island off the California coast to

Table 5.14. Relative abundance of bull shark in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | M | J | P |
|---|---|---|---|---|
| Florida Bay | √ | √ | ○ | √ |
| Ten Thousand Islands | ○ | √ | ○ | ○ |
| Caloosahatchee River | ○ | | ○ | ○ |
| Charlotte Harbor | ○ | √ | ○ | ○ |
| Tampa Bay | ○ | √ | ○ | ○ |
| Suwannee River | ○ | √ | ○ | ○ |
| Apalachee Bay | ○ | √ | ○ | ○ |
| Apalachicola Bay | ○ | √ | ○ | ○ |
| St. Andrew Bay | ○ | √ | ○ | ○ |
| Choctawhatchee Bay | ○ | √ | ○ | ○ |
| Pensacola Bay | ○ | √ | ○ | ○ |
| Perdido Bay | √ | √ | √ | √ |
| Mobile Bay | ○ | √ | ○ | ○ |
| Mississippi Sound | ○ | ○ | ○ | |
| Lake Borgne | ○ | | ○ | |
| Lake Pontchartrain | ○ | | ○ | |
| Breton/Chandeleur Sounds | ◉ | | ○ | ○ |
| Mississippi River | √ | | √ | |
| Barataria Bay | ○ | | √ | √ |
| Terrebonne/Timbalier Bays | ○ | | ○ | √ |
| Atchafalaya/Vermilion Bays | | | ○ | |
| Calcasieu Lake | √ | | √ | √ |
| Sabine Lake | | | √ | |
| Galveston Bay | √ | | ○ | |
| Brazos River | | | na | |
| Matagorda Bay | | | ○ | |
| San Antonio Bay | | | ○ | |
| Aransas Bay | | | ○ | |
| Corpus Christi Bay | | | ○ | |
| Laguna Madre | | | √ | |
| Baffin Bay | | | √ | |
| | A | M | J | P |

Relative abundance:

- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present
- na No data available

Life stage:

- A - Adults
- M - Mating
- J - Juveniles
- P - Parturition

Ecuador and possibly to northern Peru (Lee et al. 1980).

Within Study Area: This species is common in inshore waters and estuaries from Texas to Florida, and is fairly abundant in Louisiana and Florida estuaries (Table 5.14). It is generally the most common shark species in brackish water areas of the Gulf of Mexico, and is known to enter fresh water (Shipp 1986).

**Life Mode**

Bull sharks are demersal predators. They are euryhaline and occur from the nearshore marine zone to freshwater rivers (Fischer 1978, Lee et al. 1980, Shipp 1986).

**Habitat**

Type: This species is predominantly a coastal species that is frequently found in shallow waters, especially in bays and river estuaries (Fischer 1978, Lee et al. 1980, NMFS 1993).

Substrate: No particular substrate preference by this species has been noted, but it is considered a bottom dweller (Fischer 1978).

Physical/Chemical Characteristics:

Temperature: Thomerson and Thorson (1977) suggested water temperatures to be the limiting factor for the advancement of bull shark up the Mississippi River. Only when temperatures are above 24°C, particularly during the summer and fall, do the sharks ascend the Mississippi River. Snelson and Williams (1981) collected juvenile bull shark in temperatures from 20 to 32°C, and reported that two individuals had succumbed to hypothermal stress around a temperature of 8°C, during January. Branstetter (pers. comm.) suggests that 18°C is the minimum temperature necessary before bull sharks advance into estuaries.

Salinity: The bull shark occurs in brackish or freshwater, mainly as pups and juveniles but also as adult females. This occurrence may be related to inshore migrations of the females for parturition (Garrick 1982, Snelson et al. 1984). As a result, juveniles often spend considerable time in these brackish waters (Garrick 1982). Branstetter (1986) noted that the fishery for these is located primarily near freshwater inflows. One study reported the collection of juveniles from a salinity range of 1.6 to 2.3‰ (Kelley 1965). Thomerson and Thorson (1977) report that the bull shark is the only shark known to withstand the osmotic demands of either fresh water or sea water for periods of at least months and probably years. Other sharks may be capable of withstanding these osmotic conditions, but do not typically enter freshwater (Branstetter pers. comm.).

Movements and Migrations: Movements of sharks to estuarine nursery areas appears to be mainly for parturition (Lineaweaver and Backus 1970). Females move towards whelping grounds in the spring, but do not actually enter them until parturition is eminent. Other movements are probably associated with changing temperatures. Springer (1940) suggested a north and south migration coinciding with spring and fall on the northern Gulf coast.

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic). The male inseminates the female with the assistance of modified pelvic fins known as clasper organs. Fertilization is internal, and development is viviparous (Castro 1983).

Mating and Parturition: Descriptions of mating are unavailable due to a lack of detailed observations and reports (Castro 1983). Mating takes place in coastal waters during June and July in the Gulf of Mexico, with pups being born the following year in April, May, and June (Clark and Schmidt 1965). Gestation probably lasts 10 to 11 months (Clark and Schmidt 1965, Branstetter 1981). In warmer waters, mating and parturition can occur year-round (Castro 1983).

Fecundity: Snelson et al. (1986) took a 249 cm total length (TL) female with 12 near term embryos. Most other investigators report litters of six to eight.

**Growth and Development**

Embryonic Development: Development is viviparous with embryos initially dependent on stored yolk, but later nourished by the mother through a placental connection. Dodrill (1977) proposed that during uterine development one or more pups may develop to extraordinary size at the expense of other litter mates.

Juvenile Size Range: Pups measure around 75 cm at birth (Castro 1983). Size at birth is highly variable ranging from 60 to greater than 75 cm (Branstetter 1986, Branstetter and Stiles 1987). Caillouet et al. (1969) showed no significant differences between lengths or weights for male and female neonates shortly after birth. Juvenile weights increased rapidly as maturity approached (Branstetter 1981). Branstetter and Stiles (1987) estimated growth rates were 15 to 20 cm/year for the first five years, 10 cm/year for 6 to 10 year old sharks, 5 to 7 cm/year for 11 to 16 year old sharks and less than 4 to 5 cm/year for sharks older than 16 years.

Age and Size of Adults: The smallest reported mature male and female are 212 cm TL and 228 cm TL respectively (Branstetter 1981). Males mature at 210-220 cm TL or 14 to 15 years of age, and females mature at >225 cm TL or over 18 years of age (Branstetter and Stiles 1987). Females grow larger than males (Clark and Von Schmidt 1965, Branstetter 1986). The bull shark is thought to live to 20 years and possibly longer, and may reach lengths of 2.7 m and weights near 270 kg (Shipp 1986).

**Food and Feeding**

Trophic Mode: Larvae development is *in uterine* and nutrients are derived from the mother. At parturition the bull shark is considered a juvenile. Both juveniles and adults are carnivorous predators, but they will also scavenge (Shipp 1986). The bull shark typically feeds during the evening around bridges, passes, and channels. Although usually a sluggish moving fish, it is capable of great speed when pursuing prey (Fischer 1978, Shipp 1986).

Food Items: The bull shark is an opportunistic predator (Lee et al. 1980). Reported stomach contents have included species of loliginid squid and several fishes (longspine porgy, sand perch, striped anchovy, menhaden). Jaws commonly contained spines from rays (Branstetter 1981). Other bony fishes reported from the stomachs of bull sharks are sheepshead, various jacks, common snook, little tunny, hardhead catfish, trunkfish, tarpon, mullets (Clark and Von Schmidt 1965); American eel, white perch, Atlantic croaker (Schwartz 1960), mackerels, tunas, and carrion (Fischer 1978). Bull sharks are also known to feed on other sharks, preying heavily on small sandbar sharks, as well as rays, molluscs, sea urchins, crabs, shrimp, porpoises, and sea turtles (Fischer 1978, Lee et al. 1980, Castro 1983). Snelson et al. (1984) suggest that saltwater catfishes (hardhead and gafftopsail) and stingrays are very important food items in the diet of bull sharks. This shark is considered to be potentially dangerous to humans. Its habits frequently place it in the vicinity of swimmers and fishermen, and it has been reponsible for several documented attacks (Lee et al. 1980, Shipp 1986).

**Biological Interactions**

Predation: The bull shark is not known to be a prey item for other species.

Factors Influencing Populations: The bull shark is a top trophic level carnivore with slow growth and relatively low reproductive capacity. It is therefore vulnerable to overfishing, and probably should be managed conservatively (Casey and Hoey 1985, NMFS 1993). A major commercial fishery for these sharks is not recommended, and if sport fishing pressures increase there may be need to further regulate the fishery (Casey and Hoey 1985, NOAA 1992). Shark mortality also occurs in the form of bycatch from the commercial swordfish, tuna, and shrimp fisheries (NMFS 1993). The loss and degradation of habitat, especially nursery areas, is another factor that may affect shark abundance.

**Personal communications**

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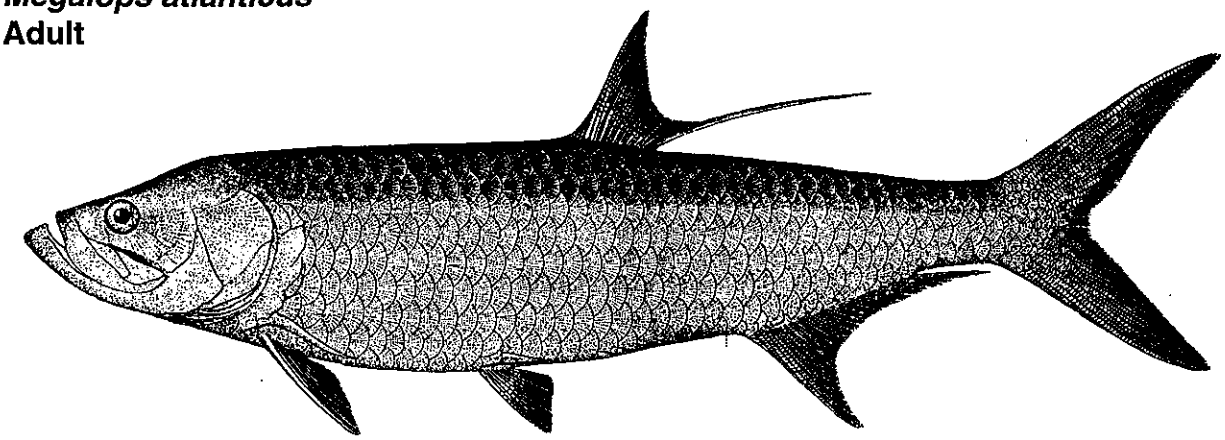
# Tarpon

***Megalops atlanticus***
**Adult**



20 cm (from Goode 1884)

**Common Name:** tarpon
**Scientific Name:** *Megalops atlanticus*
**Other Common Names:** Tarpum, caffum, silverfish, silver king, jewfish, big scale; *grande ecaille, grand ecoy, palika* (French); *sábalo, sábalo real, tarpón* (Spanish) (Gunter 1945, Wade 1962, Hildebrand 1963, Hoese and Moore 1977, Fischer 1978, NOAA 1985).
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Elopiformes |
| Family: | Elopidae |

### Value

Commercial: There is no commercial fishery for tarpon in the United States. Its flesh is generally considered to be fatty and of second rate quality, but in Central America and West Africa, it is marketed locally and consumed fresh or salted (Breder 1944, Wade 1962, Hildebrand 1963). Historically, there was a substantial fishery for tarpon in Ceara, Brazil in the 1960's (de Menezes and Paiva 1966, Cyr pers. comm.). Their large scales are sometimes used for ornamental purposes (artificial pearls, wind chimes, etc.) (Manooch 1984).

Recreational: The tarpon is considered a superb inshore game fish, and it is valuable to the economies of areas where it is fished (Hoese and Moore 1977, Killam et al. 1992). Its fighting ability and aerial acrobatics are famous, and it is sought for sport throughout most of its range. Fishing occurs primarily from March through June and from October to November from bridges, piers, and anchored boats (Manooch 1984, NOAA 1985). Tarpon fishing in the state of Florida is regulated, with anglers required to purchase a permit before they can harvest a fish (Crabtree et al. 1992). In Texas, fishing is currently allowed on a catch and release basis only (TPWD 1993). Proposed regulations would allow the harvest of a single tarpon over 80 inches (203.2 cm) with the purchase of tag from Texas Parks and Wildlife Department (TPWD) (Hegen pers. comm.).

Indicator of Environmental Stress: Because of its high trophic level, the tarpon was chosen as a test species in a study of the effects of chlorinated hydrocarbon insecticides (Wade 1969). The tarpon is also considered a natural monitor of toxic pollutants in inshore areas because of its freedom from reliance on dissolved oxygen for survival. Oxygen depletion could result in an immediate kill of other fish species, masking the ultimate cause of death that would occur when toxicants are present (Harrington 1966).

Ecological: The tarpon is a high trophic level carnivore, preying mainly on fish (Wade 1969).

### Range

Overall: The tarpon occurs in the eastern Atlantic Ocean along the coast of west Africa, and in the western Atlantic along the coasts of North, Central, and South America (Wade 1969). Its range in the western Atlantic is from Nova Scotia to central Brazil, and throughout the West Indies. However, it is only rarely found north of the Carolinas. It has also been reported at the Pacific terminus of the Panama Canal (Wade 1962, Hildebrand 1963, Harrington 1966, Wade 1969, Hoese and Moore 1977). Centers of abundance are the Gulf of Mexico, coastal Florida, Central America, and Brazil (Hildebrand 1963, de Menezes and Paiva 1966, Wade 1969, Fahay 1973, Smith 1980, Cyr pers. comm.). Its range in the eastern Atlantic is from Ireland

Table 5.15. Relative abundance of tarpon in 31 Gulf of Mexico estuaries (Nelson et al. 1992, Crabtree pers. comm., Cyr pers. comm.).

| *Estuary* | *Life stage* A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | O | | O | | |
| Ten Thousand Islands | O | | O | | |
| Caloosahatchee River | ◉ | | ◉ | √ | |
| Charlotte Harbor | ◉ | | ◉ | O | |
| Tampa Bay | ◉ | | O | √ | |
| Suwannee River | O | | O | O | |
| Apalachee Bay | O | | O | O | |
| Apalachicola Bay | O | | O | O | |
| St. Andrew Bay | O | | √ | O | |
| Choctawhatchee Bay | O | | O | O | |
| Pensacola Bay | O | | O | O | |
| Perdido Bay | √ | | √ | | |
| Mobile Bay | O | | O | O | |
| Mississippi Sound | O | | O | O | |
| Lake Borgne | O | | O | √ | |
| Lake Pontchartrain | O | | O | | |
| Breton/Chandeleur Sounds | | | | | |
| Mississippi River | O | | | | |
| Barataria Bay | √ | | √ | | |
| Terrebonne/Timbalier Bays | √ | | | | |
| Atchafalaya/Vermilion Bays | √ | | | | |
| Calcasieu Lake | | | | | |
| Sabine Lake | | | √ | | |
| Galveston Bay | √ | | √ | | |
| Brazos River | | | na | | |
| Matagorda Bay | O | | O | | |
| San Antonio Bay | O | | O | | |
| Aransas Bay | √ | | √ | √ | |
| Corpus Christi Bay | √ | | √ | √ | |
| Laguna Madre | √ | | √ | | |
| Baffin Bay | | | √ | | |
| | A | S | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- O Common
- √ Rare
- blank Not present
- na No data available

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

to the Congo, with reports of occurrence from Bermuda, the Azores, and the Formigas (Wade 1962, Wade 1969, Twomey and Byrne 1985), but it is most common from Senegal to the Congo (Wade 1969).

Within Study Area: The tarpon occurs from the Rio Grande to Florida Keys with high numbers noted in: south Texas; Calcasieu Lake, Louisiana; Grand Isle, Louisiana; western Florida; the waterways and rivers among the Ten Thousand Islands and the interior waterways of the Florida Keys (Hildebrand 1963, Wade 1969). Greatest densities in the in the U.S. Gulf of Mexico probably occur along the coast of southwestern Florida (Shipp 1986) (Table 5.15).

**Life Mode**

Tarpon are known to form schools while feeding (Hildebrand 1963, Harrington 1966). Little information is available on eggs. Early larval forms are pelagic and planktonic, while later larval stages, juveniles, and adults are pelagic and nektonic (Gehringer 1959, Smith 1980). Adults are known to actively feed both day and night (Wade 1962).

**Habitat**

Type:

Larvae: Stage I (leptocephali) are found in warm, western Atlantic epipelagic waters north of the equator. They occur in the upper 100 m of water (Wade 1962) in euhaline salinities offshore as far as 250 km in depths ranging from 90 to 1400 m (Gehringer 1959, Wade 1962, Smith 1980, Crabtree et al. 1992). Stage II (shrinking) larvae have been recorded from depths of <1 to 12 m in inshore waters (Erdman 1960, Tagatz 1973, Tucker and Hodson 1976). They have been collected in salt marshes, rivers, mangrove swamps, estuaries, and upper reaches of bays as far north as Cape Fear River, North Carolina (Erdman 1960, Harrington and Harrington 1960, Harrington 1966, Tagatz 1973, Tucker and Hodson 1976) in mesohaline to euhaline salinities (Wade 1962, Tagatz 1973, Tucker and Hodson 1976). The stage III (growing) larvae are found along beaches in lagoons, salt marshes, tidal ponds and potholes, and tidal rivers and canals (Harrington 1958, Harrington 1960, Wade 1962, Hildebrand 1963, Jones et al. 1978). They occur rarely as far north as North Carolina (Tucker and Hodson 1976). Juveniles are recovered from salinities ranging from freshwater to hypersaline (Breder 1944, Gunter 1945, Simpson 1954, Tabb and Manning 1961, Rickards 1968, Randall 1959, Wade 1969, Franks 1970, Kushlan and Lodge 1974, Marwitz 1986). Smaller juveniles occur in shallow streams, lakes, marshes, lagoons, ponds, ditches, canals, rivers, estuaries, mangrove swamps, pools, and drainage ditches nearly or completely landlocked except for periods of extreme high water, also in headwaters of small freshwater streams

(Henshall 1895, Breder 1944, Randall 1959, Harrington and Harrington 1960, Tabb et al. 1962, Wade 1962, Hildebrand 1963, Rickards 1968, Wade 1969, Odum 1971, Hoese and Moore 1977, Howells 1985, Marwitz 1986). They are usually found in organic-stained brackish waters that can be either stagnant or flowing (Randall 1959, Wade 1962, Rickards 1968) in depths of 1.5 to 15 m (Simpson 1954, Randall 1959, Rickards 1968, Wade 1969, Franks 1970). Tarpon 305 to 487 mm are common in headwaters of brackish and freshwater streams. Movement to deeper rivers, canals, pools, lakes, and eventually to the ocean occurs as they grow larger (Hildebrand 1963, Wade 1969) At this time, they are found in waters 0.9 to 2.5 m deep (Gunter 1945, Tabb and Manning 1961, Rickards 1968, Wade 1969, Franks 1970). Adults are primarily found in coastal inshore waters, inlets, estuaries, and passes between islands, but they also occur in deeper rivers, canals, streams, and lakes (Breder 1944, Hildebrand 1963, Wade 1969, Kushlan and Lodge 1974, Hoese and Moore 1977, Loftus and Kushlan 1987) in fresh to euhaline salinities (Breder 1944, Randall 1959, Tabb et al. 1962, Kushlan and Lodge 1974, Loftus and Kushlan 1987). Adults are found over a wide variety of water depths that range from shallow waters to deep (90-1400 m) offshore spawning sites (Killam et al. 1992). In summer, they have been reported in offshore areas such as coral reefs as far as 70 miles west of Key West, Florida, in the Dry Tortugas National Park (Schmidt pers. comm.).

Substrate: Juveniles and adults are generally found over soft mud bottoms that sometimes contain hydrogen sulfide; but, they also occur over sand, firm mud, sandy mud with no vegetation, and peat (Gunter 1945, Simpson 1954, Randall 1959, Tabb and Manning 1961, Tabb et al. 1962, Rickards 1968, Wade 1969, Franks 1970).

Physical/Chemical Characteristics:
Temperature - Eggs and Larvae: The physical and chemical requirements of tarpon are not completely known. Stage I larval specimens have been collected from waters at 22.2° to 30.0°C (Wade 1962, Smith 1980, Zale and Merrifield 1989, Crabtree et al. 1992), and it is assumed that eggs require similar conditions for proper development (Zale and Merrifield 1989). They appear to prefer warmer waters (Jones et al. 1978). Stage II larvae have been recorded in temperatures ranging 19.8° to 30.8°C (Tagatz 1973, Tucker and Hodson 1976). Stage III larvae have been collected in waters 25° to 27°C (Harrington 1966).

Temperature - Juveniles and Adults: The known temperature ranges are similar for both juveniles and adults (Wade 1962). They have been recorded from 16° to 40°C (Gunter 1945, Simpson 1954, Odum and Caldwell 1955, Randall 1959, Tabb and Manning 1961, Wade 1962, Rickards 1968, Franks 1970, Marwitz 1986). Loss of equilibrium or death has been observed from 9.5° to 18.2°C in vitro with the greatest occurrence at 14.0°C (Howells 1985). Other studies report mortalities occurring between 12° to 14°C and 12° to 16°C for sudden cold snaps, but resistance to cold might be greater during slow temperature falls (Tabb and Manning 1961, Rickards 1968).

Salinity - Eggs and Larvae: Stage I larval specimens have been collected from waters at 28.5 to 39‰ (Wade 1962, Smith 1980, Zale and Merrifield 1989, Crabtree et al. 1992), and it is assumed that eggs require similar conditions for proper development (Zale and Merrifield 1989). Early larvae (Stage I) are possibly stenohaline, seeming to prefer high salinities as they are generally not found in low or fluctuating salinities, and probably stay well offshore until the approach of metamorphosis (Smith 1980).

Salinity - Juveniles and Adults: All developmental forms except Stage I larvae are euryhaline. They have been recorded from 0.0 to 47‰, but seem to prefer salinities between 5.1 and 22.3‰ (Gunter 1945, Simpson 1954, Odum and Caldwell 1955, Gunter 1956, Simmons 1957, Randall 1959, Tabb and Manning 1961, Harrington 1966, Rickards 1968, Wade 1969, Franks 1970, Tagatz 1973, Tucker and Hodson 1976, Marwitz 1986).

Turbidity: Stage I larvae only occur in clear offshore waters (Zale and Merrifield 1989). In subsequent life history stages, the tarpon appears to be tolerant of high turbidities.

Dissolved Oxygen: Tarpon have been considered to be obligate air breathers (Wade 1962), able to breathe by means of rolling and gulping air which is held in a highly vascularized air bladder (Odum and Caldwell 1955, Wade 1969). However, more recent evidence suggests that they are not obligate air breathers and can survive at least two weeks without air breathing in well oxygenated water (Killam et al. 1992). Larvae have been observed to die if prevented from surfacing as larger fish do (Harrington 1966). Their air breathing capability allows them to survive in waters with a dissolved oxygen content as low as 0.00 to 0.81 parts per million (Odum and Caldwell 1955).

Movements and Migrations: Leptocephalus larvae are probably transported into estuaries by tidal currents (Killam et al. 1992). In the Everglades, tarpon are able to move between bodies of water during high water periods, resulting in their occurrence in isolated ponds (Loftus and Kushlan 1987). As juvenile tarpon grow, they move from nursery grounds to deeper inshore waters and finally to the ocean (Wade 1969). This move typically occurs when juveniles reach approximately 400 mm SL, after nearly one year of growth (Killam et al. 1992). It could be speculated that this shift in habitat occurs after tarpon reach a sufficient size to avoid most predators, or it may be related to the the increasing food requirements of juveniles. Adult and large juvenile tarpon are capable of extensive movements, but patterns of coastal migration other than inshore-offshore movements in response to the seasonal temperature changes are not evident (Randall 1959, Hildebrand 1963, Moe 1972). Adult tarpon are reported to be most abundant in inshore waters from April to November (Breuer 1949, Hoese 1958, Springer and Pirson 1958). Assemblages of sexually maturing tarpon during spring and summer may be preparatory to an offshore spawning migration from the inshore feeding areas (Moe 1972, Crabtree et al. 1992, Killam et al. 1992). They have been observed in large schools 2-5 km offshore, swimming together in a circular motion referred to as a "daisy chain" (Crabtree et al. 1992). These schools can range from 25 to more than 200 individuals. Based on collections of larvae (Crabtree et al. 1992, Crabtree 1995), it has been inferred that adult tarpon migrate from inshore feeding areas to offshore (up to 250 km) spawning areas from May through July.

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic), and fertilization is external through the release of milt and roe into the water column.

Spawning: The exact locations of spawning areas are not well known. They are apparently restricted to offshore waters such as the east coast of Florida to Cape Hatteras, Florida Straits, west central Florida, southwestern Gulf of Mexico, outer continental shelf and slope of the eastern Gulf of Mexico, Gulf Stream, and Caribbean Sea. Spawning activity has not been documented, but adult tarpon have been observed in large schools or aggregations known as "daisy chains" off of the Florida Gulf Coast (Crabtree et al. 1992). Larvae with estimated ages of 2 to 25 days have been collected over the continental shelf and slope of the Florida Gulf coast, indicating spawning in the immediate vicinity (Crabtree et al. 1992). Similar exhaustive larval sampling efforts have not yet occurred in the northwest Gulf of Mexico, the Yucatan Peninsula, or elsewhere, so other spawning locations remain unknown (Cyr pers. comm.). The estimated spawning season of Florida tarpon is from April to July, with near ripe females and milt producing males occurring in March and April respectively, and spent females occurring in July and August (Breder 1944, Hildebrand 1963, Eldred 1967, Jones et al. 1978, Randall 1969, Wade 1969, Smith 1980, Crabtree et al. 1992, Killam et al. 1992, Cyr pers. comm.). Crabtree et al. (in press) reported that spawning of tarpon in the tropical waters of Costa Rica is not seasonal, and that reproductively active females were caught during all months.

Fecundity: One female tarpon, 2,032 mm, was reported to contain approximately 12,202,000 eggs (Babcock 1936, Wade 1962). Crabtree et al. (in press) examined the gonads of 737 Florida tarpon, and reported that fecundity ranged from 4.5 to 20.7 million oocytes per female, and that fecundity is positively correlated with fish weight.

**Growth and Development**

Egg Size and Embryonic Development: No information is available on ripe eggs, but ovarian eggs in spent females were non-adhesive, opaque, and ranged 0.6 to 1.7 mm in diameter (Randall 1959, Wade 1962). Fertilized eggs have not been successfully collected and identified (Crabtree 1995).

Age and Size of Larvae: Larval development is often described in three stages: Stage I, a fully formed leptocephalus; Stage II, a period of marked shrinking during which the larva gradually loses its leptocephalus form; Stage III, begins with a second period of length increase and ends with the onset of the juvenile stage (Wade 1962). Larvae are reported to occur in the Gulf of Mexico from June through August (Ditty et al. 1988). Crabtree et al. (1992) described the age, size, and growth of tarpon leptocephalus larvae collected off of the Florida Gulf Coast. These collections occurred over depths ranging from 90 to 1,400 m, at sea surface temperatures of 27 to 30°C, and salinities of 35 to 36‰. In June 1981 a total of 54 larvae were collected, ranging from 7.3 to 23.8 SL. In 1989, a total of 275 larvae were collected, ranging from 5.5 to 24.4 mm SL, and with an estimated age of two to 25 days. Based on the collected specimens, standard length (in mm) and age (in days) can be described by the equation SL = 2.78 + 0.92(age). Estimated size at hatching was 2.78 ± .63 mm, and estimated hatching dates were from May 12 to July 10. Based on back-calculation of hatching dates, it can be inferred that peak hatching activity occurs approximately one week after a full moon, and one week after a new moon (Crabtree 1995). Alternately, it is possible that larval survival, not spawning activity, is associated with lunar phase (Crabtree 1995).

Juvenile Size Range: The minimum size described for juveniles is 25.2 mm SL (Wade 1962). Juvenile growth is seasonal, averaging about 30 mm per month during the summer and early fall (Rickards 1968, Killam et al. 1992). Cyr (1991) examined length-frequencies of juvenile tarpon from the east coast of Florida, and found that average first year growth (October to October) was 230 mm, corresponding to a size-specific growth rate of 0.5% SL/day April to September, and 0.11 SL/day September to February. The body is opaque at 25.2 mm SL with pigment mostly above the lateral line. Scale formation begins along the lateral line at about 29.7 mm SL (Harrington 1966), and the lateral pores are visible at 51.0 mm SL (Wade 1962). By at least 140 mm SL two specialized ray scales cover the uppermost and lowest caudal rays (Jones et al. 1978). At 194.1 mm SL, the filamentous ray of the dorsal becomes grooved on the underside, the anal ray has a scaly sheath and the last ray is produced. The caudal fin is scaly (Wade 1962, Jones et al. 1978). Juveniles become darker dorsally with age (Harrington 1958).

Age and Size of Adults: From 1988 through 1993, Crabtree et al. (1995) examined 1,469 juvenile and adult tarpon from south Florida, ranging from 102 to 2,045 mm fork length (FL), and estimated their ages based on otoliths. All fish older than ten years were sexually mature. All males were sexually mature by 1,175 mm FL, but the smallest mature female was 1,285 mm FL (Cyr pers. comm.). Tarpon are long-lived, with ages of males estimated at 0 to 43 years, and females at 0 to 55 years. Growth is rapid until age 12, after sexual maturity is attained, then slows considerably. For any given age greater than four years, females tend to be larger than males. It has been suggested that tarpon scales are not appropriate for age estimation, as they would indicate a maximum age of only 15 years. A VonBertalanffy growth equation based on otolith age estimates more accurately predicts the known maximum size of tarpon. Ages exceeding 50 years have been reported in captive fish (Killam et al. 1992). Crabtree et al. (1995) examined eighteen captive tarpon with oxytetracycline-marked otoliths, and found growth rates that varied from 95 mm in 20 months, to 235 mm in 21 months. Crabtree et al. (in press) estimated the ages of 87 tarpon from tropical Costa Rican waters, and reported that most were 15 to 30 years old, with a maximum age of 48 years. The Costa Rican tarpon sampled were significantly smaller than Florida tarpon, and apparently reached maturity at a smaller size.

**Food and Feeding**

Trophic Mode: The tarpon is strictly carnivorous, preying on a wide variety of animal species (Wade 1962, de Menezes and Paiva 1966, Odum 1971). Feeding begins in Stage II larvae (Mercado and Ciardelli 1972).

Food Items: Metamorphic larvae and small juveniles are primarily plankton feeders, preying on copepods (cyclopoid and harpacticoid), mosquito larvae, and detritus (Randall 1959, Harrington and Harrington 1960, Harrington and Harrington 1961, Wade 1962, Odum 1971). Large juveniles (>45 mm SL) begin gradually switching from copepods to small fish such as killifishes (*Fundulus* sp.), mosquitofish (*Gambusia affinis*), silversides (*Membras martinica* and *Menidia* sp.), and mullet (*Mugil* sp.), and to caridean shrimp, ostracods, and insects (Simpson 1954, Harrington and Harrington 1960, Harrington and Harrington 1961, Tabb and Manning 1961, Hildebrand 1963, Rickards 1968, Odum 1971). Adults are strictly carnivorous and feed primarily on mid-water prey (Killam et al. 1992). They are predominately piscivorous with fish composing up to 95% of their total food volume (Harrington and Harrington 1961). Fish prey includes such species as mullet, marine catfishes (hardhead and gafftopsail), pinfish, sunfish (*Lepomis* species), sardines, needlefish, silversides, cutlassfish (*Trichiurus lepturus*), and anchovies. Shrimp are also an important diet component. Other food items include insects, blue crabs, and ctenophores (Gunter 1945, Miles 1949, Harrington and Harrington 1961, Wade 1962, Hildebrand 1963, Rickards 1968, Odum 1971).

**Biological Interactions**

Predation: Predation of adults is limited to other large predators such as sharks, porpoises, and alligators, while the young fall victim to a variety of fish, including ladyfish (*Elops saurus*), spotted seatrout, other tarpon, and to piscivorous birds that include kingfishers, pelicans, and herons (Randall 1959, Wade 1962, Hildebrand 1963, Rickards 1968, Killam et al. 1992).

Factors Influencing Populations: Although juvenile and adult tarpon are able to penetrate coastal freshwater habitats, they are sensitive to low temperatures and may be susceptible to fish kills during winter months (Loftus and Kushlan 1987). The development of wetland areas utilized as nursery habitat by tarpon to provide marketable real estate, highway and bridge construction, etc. may be impacting juvenile survival and recruitment (Randall 1959, Robins 1978). The impoundment of estuarine areas for mosquito control has reduced available habitat for juveniles and may also be affecting recruitment (Cyr 1991, Killam et al. 1992). The tarpon is very sensitive to chemicals, and the wide-spread use of pesticides may have a negative impact on this species (Robins 1978). Possible competition may exist between tarpon and such frequently associated species as common snook, spotted seatrout, and ladyfish (Wade 1962, Rickards 1968). Recorded parasites include: isopods (*Cymothoa destrum, Nercilia acuminata*), remoras (*Echeneis naucrates*), copepods (*Paralebion pearsei*), trematodes (*Bivescula tarponis*), and parasites of the family Hemiuridae (Wade 1962).

**Personal communications**

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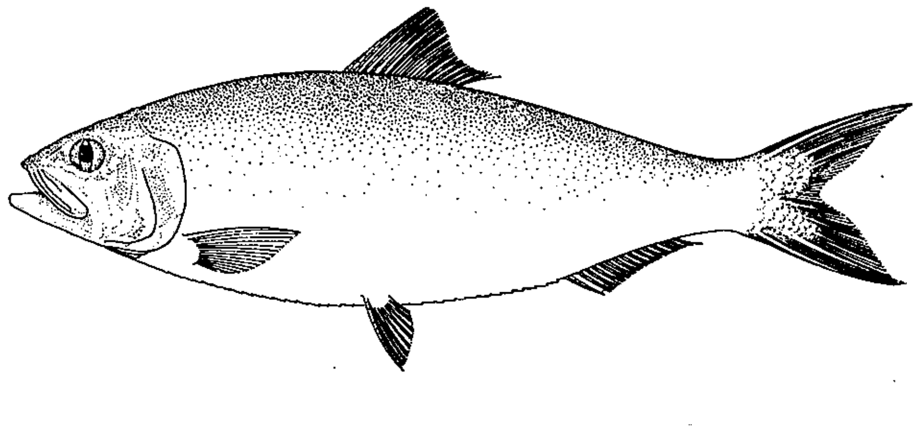
## Alabama shad

***Alosa alabamae***
**Adult**




(from Fischer 1978)

**Common Name:** Alabama shad
**Scientific Name:** *Alosa alabamae*
**Other Common Names:** white shad, gulf shad, Ohio shad (Daniell 1872, Hildebrand 1963); *alose de l'Alabama* (French), *sabalo de Alabama* (Spanish) (Fischer 1978).
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Clupeiformes |
| Family: | Clupeidae |

### Value

Commercial: The Alabama shad is not an important food fish, and no commercial landings have been recorded since 1902 (Hildebrand 1963, Mills 1972). However, it was historically seined from rivers and marketed fresh in some local areas in the 1800's (Fischer 1978, Mettee pers. comm.).

Recreational: The Alabama shad has potential as a recreational fish, and its taste compares favorably with the more sought-after shad species. Despite this, it is generally considered to be undesirable and too bony for eating, thus receiving little attention from anglers (Laurence and Yerger 1967, Mills 1972). Fish caught are not usually kept, although some anglers fish for this species to use as bait, or as recreation while waiting for more desirable game fish to bite (Hildebrand 1963, Laurence and Yerger 1967, Mills 1972).

Indicator of Environmental Stress: The Alabama shad is not typically used in studies of environmental stress, but its decline in numbers throughout its range may be at least a partial result of river impoundment, channelization, and siltation (Lee et al. 1980).

Ecological: All shad species are important forage fish for predators (Eddy and Underhill 1982). Diminished numbers of Alabama shad have led to its listing under state endangered species laws in Kentucky, Missouri, and Tennessee (Johnson 1987). It is being considered as a candidate species under the federal Endangered Species Act (NMFS 1997).

### Range

Overall: The Alabama shad originally inhabited most principal stream tributaries and major river drainages of the Gulf coast from the Suwanee River in Florida to Grand Isle, Louisiana (Behre 1950, Bailey et al. 1954, Hildebrand 1963, Laurence and Yerger 1967, Moore 1968, Mills 1972, Walls 1976). It formerly ascended the Mississippi River and many of its major tributaries, including the Red, Ouachita, Arkansas, Missouri, Ohio, and Tennessee Rivers, but has become rare or extirpated this far inland (Hildebrand 1963, Laurence and Yerger 1967, Mills 1972, Lee et al. 1980).

Within Study Area: This fish is indigenous to the coastal waters of the northeastern Gulf of Mexico and its drainages. It is found from Grand Isle, Louisiana to the Suwanee River in Florida (Table 5.16) (Behre 1950, Hildebrand 1963, Laurence and Yerger 1967, Moore 1968, Swingle 1971, Mills 1972, Millican et al. 1984). Within its current range it is probably most common in the Apalachicola River system (Laurence and Yerger 1967, Mills 1972, Mettee pers. comm.).

### Life Mode

Eggs and larvae are pelagic and planktonic, and have been collected only at night (Mills 1972). Juveniles are pelagic, nektonic, and schooling (Laurence and Yerger 1967, Mills 1972). Adults are pelagic, schooling, and

Table 5.16. Relative abundance of Alabama shad in 31 Gulf of Mexico estuaries (Nelson et al. 1992, Mettee pers. comm.).

| Estuary | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | | | | | |
| Ten Thousand Islands | | | | | |
| Caloosahatchee River | | | | | |
| Charlotte Harbor | | | | | |
| Tampa Bay | | | | | |
| Suwannee River | √ | √ | √ | √ | √ |
| Apalachee Bay | | | | | |
| Apalachicola Bay | O | O | O | O | O |
| St. Andrew Bay | √ | | √ | | |
| Choctawhatchee Bay | √ | | √ | | |
| Pensacola Bay | | | | | |
| Perdido Bay | | | | | |
| Mobile Bay | √ | | √ | | |
| Mississippi Sound | √ | √ | √ | √ | √ |
| Lake Borgne | √ | | √ | | |
| Lake Pontchartrain | | | √ | | |
| Breton/Chandeleur Sounds | √ | | | | |
| Mississippi River | | | | | |
| Barataria Bay | | | | | |
| Terrebonne/Timbalier Bays | | | | | |
| Atchafalaya/Vermilion Bays | | | | | |
| Calcasieu Lake | | | | | |
| Sabine Lake | | | | | |
| Galveston Bay | | | | | |
| Brazos River | | | | | |
| Matagorda Bay | | | | | |
| San Antonio Bay | | | | | |
| Aransas Bay | | | | | |
| Corpus Christi Bay | | | | | |
| Laguna Madre | | | | | |
| Baffin Bay | | | | | |
| | A | S | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- O Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

anadromous (Laurence and Yerger 1967, Turner 1969.

**Habitat**

Type: Eggs and larvae are riverine and have been collected only at night in areas with appreciable current (Mills 1972). Young juveniles are freshwater riverine and nektonic. Older juveniles descend rivers and move into estuarine and Gulf waters (Mills 1972). Adults are anadromous, inhabiting neritic waters of the Gulf and migrating into estuaries and then up major river systems to spawn. They occur in fresh to euhaline waters in both rivers and bays (Hildebrand 1963, Laurence and Yerger 1967, Moore 1968, Swingle 1971, Mills 1972, Douglas 1974, Swift et al. 1977).

Substrate: Eggs and larvae have been collected over coarse sand and gravel (Mills 1972). Juveniles and adults are found over a wide variety of substrates due to their anadromous nektonic life history.

Physical/Chemical Characteristics: Eggs and larvae have been collected from freshwater at 19-23°C (Mills 1972). Juveniles have been found in a water temperature range of 13.3 to 28.1°C and are considered euryhaline along with adults (Mills 1972, Douglas 1974, Walls 1976) because they occur in both freshwater and seawater at different times in their life cycle (Laurence and Yerger 1967, Mills 1972). Adults occur in water temperatures of 12.1 to 23°C. Below 17°C, males are reported to outnumber females, but at 19.5°C, females may occur in larger numbers than males (Laurence and Yerger 1967, Mills 1972).

Migrations and Movements: The Alabama shad is an anadromous species, and could be considered the only anadromous clupeid along the Gulf coast (Mettee et al. 1996). Juveniles are present in freshwater rivers and streams from late May to early July. They leave these areas to enter saltwater at the end of their first summer when they reach a fork length (FL) of 120 mm, but they will migrate at smaller sizes in cold weather (Hildebrand 1963, Laurence and Yerger 1967, Mills 1972). Juvenile shad have been taken in the rivers as late as November (Mills 1972, Beecher and Hixson 1982). Adults leave salt water and ascend freshwater rivers and streams in the spring to spawn (Hildebrand 1963, Eddy and Underhill 1982). Adults first begin to arrive at freshwater spawning areas in Apalachicola River during late January and February when water temperatures are 15° (Laurence and Yerger 1967). In Alabama's Choctawhatchee and Conecuh Rivers, adult shad are reported to arrive in March, spawn in April, then migrate seaward (Mettee et al. 1995, Mettee et al. 1996). In the Mississippi River valley, arrival has been reported from May to July (Fischer 1980). Abundance in the Apalachicola River generally peaks during late March through late April when water temperatures are about 17°C, and then drops as water temperatures increase (Laurence and Yerger 1967, Mills 1972). Males, especially older ones, enter freshwater earlier and at lower temperatures than females, but when water temperatures reach 19.5°C, females begin to outnumber males at the spawning areas (Laurence and Yerger 1967, Mills 1972). After spawning the adults return downriver to estuarine and marine waters.

**Reproduction**

Mode: Species in the herring family (Clupeidae) have separate male and female sexes (gonochoristic), and fertilization is external through the broadcast of milt and roe.

Spawning: Eggs are partially developed when females arrive in spawning areas, then complete maturation (Mettee et al. 1995). Spawning occurs in the headwaters of the major drainages along the northern Gulf of Mexico during spring months (March-April) when water temperatures are 19° to 23°C. It takes place in freshwater rivers and streams over coarse sand and gravel with water currents of 0.5-1.0 m/sec (Laurence and Yerger 1967, Mills 1972). Alabama shad are repeat spawners, but some spawning mortality occurs. The spawning population is dominated by two year old fish. This group produces the most viable offspring and its dominance has been interpreted as an adaptation to increase populations (Laurence and Yerger 1967, Mills 1972).

Fecundity: Reported fecundity estimates range from 46,400 to 257,655 eggs produced by female shad (Laurence and Yerger 1967, Mills 1972). Fecundity will vary considerably with total length, weight, and age. A decrease in the number of repeat spawners present in the population results in an increase in overall fecundity (Laurence and Yerger 1967, Leggett 1969, Mills 1972).

**Growth and Development**

Egg Size and Embryonic Development: Embryonic development is oviparous. Well developed uterine eggs averaged 1.159 mm in diameter (Mills 1972). Eggs are released in the spring with partially and completely spent females being collected December through April (Laurence and Yerger 1967, Turner 1969).

Age and Size of Larvae: Little information is available on the age and size of larval Alabama shad.

Juvenile Size Range: This stage ranges in size from 25 to 142 mm FL. Modal growth of most juveniles varies from 10 to 30 mm/month. Maturity in males is reached during their first year or shortly after. One fish measuring 128 mm FL was collected with mature gonads, but was considered atypical (Laurence and Yerger 1967, Mills 1972).

Age and Size of Adults: Alabama shad are reported to live up to 4 years, based on scale aging studies (Laurence and Yerger 1967, Leggett 1969). Average sizes for these age classes are: 269 mm total length (TL) for Class I males; 340.4 mm TL for Class II males and 368.3 mm for Class II females; 365.8 mm TL for Class III males and 388.6 mm TL for Class III females; and average measurements for Class IV fish were 383.5 and 408.9 mm TL for males and females respectively (Laurence and Yerger 1967). This information corresponds well with Mills (1972) who reported average size for males as Class I - 219 and 155 mm FL, Class II - 316 and 326 mm FL, Class III - 334 mm FL; and for females as Class I - unknown, Class II - 340 mm FL, Class III - 356 and 370 mm FL. Females are larger than males in every year class (Laurence and Yerger 1967, Mills 1972). Average sizes and weights for this shad are 312 mm FL and 474 g for males, and 347 mm FL and 737 g for females. The largest reported fish measured 450 mm TL (Douglas 1974). A length/weight equation has been derived by Laurence and Yerger (1967). Recent otolith aging studies of Alabama shad in the Choctawhatchee River suggest that fish may live up to six years (Mettee et al. 1995).

**Food and Feeding**

Trophic Mode: The feeding habits of the Alabama shad are not well known. Stomach contents of adults and juveniles suggest that they are opportunistic carnivores (Hildebrand 1963, Laurence and Yerger 1967, Mills 1972). Adults generally do not feed during their spawning migration (Hildebrand 1963, Laurence and Yerger 1967, Mills 1972).

Food Items: Stomach contents of some migrating adults show insects, plant material, and detritus (Hildebrand 1963, Laurence and Yerger 1967). Juveniles are opportunists and will feed on whatever is available, especially fish and larval, pupal, and adult insects (Laurence and Yerger 1967). They also feed on copepods, Cladocera (water fleas), worms, spiders, detritus, and plant material. Food habits of shad in marine and estuarine environments are not well known.

**Biological Interactions**

Predation: All shad species are important forage fish for piscivorous fish and birds.

Factors Influencing Populations: Declines in populations may be at least partially due to dams barring this species from its historical spawning grounds, and possibly also to channelization of rivers and siltation of spawning areas (Hildebrand 1963, Lee et al. 1980).

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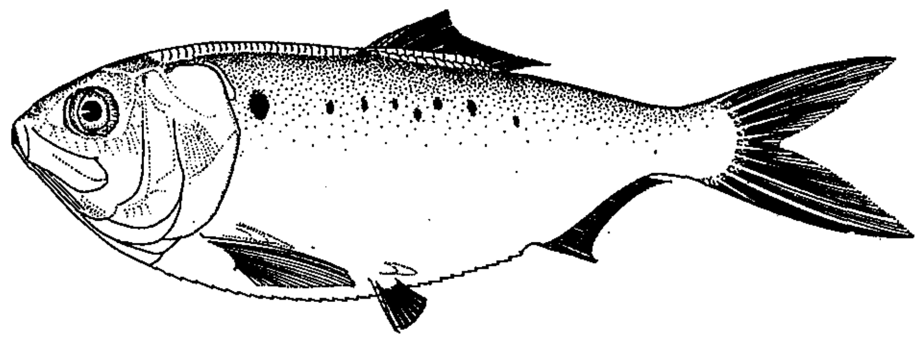
## Gulf menhaden

***Brevoortia patronus***
**Adult**



5 cm (from Fischer 1978)

**Common Name**: gulf menhaden
**Scientific Name**: *Brevoortia patronus*
**Other Common Names**: Pogy, shad, large-scale menhaden, sardine, *menhaden écailleux* (French), *lacha escamuda* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Clupeiformes |
| Family: | Clupeidae |

### Value

Commercial: The Gulf menhaden fishery dates back to the turn of the century, and developed into a major industry after World War II (Lassuy 1983, Smith 1991). This is a unique American fishery that is vertically integrated, that is, menhaden processing companies generally own the vessels, the gear, the processing facilities, and often the spotter aircraft used to find the fish schools (Newlin 1993, Smith pers. comm.). Crews are hired to fish for the length of the fishing season. Although schools of Atlantic thread herring are occasionally harvested by this fishery, vessels are designed to fish specifically for menhaden, and are not convertible to other fisheries (Smith pers. comm.). Except for a few small bait purse-seiners, vessels from other fisheries do not "free-lance" and sell their catch to the menhaden plants. The gulf and Atlantic menhaden fisheries combined supported the second largest commercial landings by weight in 1995 (O'Bannon 1996). Landings of gulf menhaden in that year were 463,900 mt valued at $51.9 million. Landings of gulf menhaden in 1996 have been estimated at 479,400 mt (Smith 1997). Traditionally the majority of the landings are taken in the north central Gulf of Mexico. Menhaden are harvested from April to October as they move into more shallow inshore areas from their wintering grounds on the middle part of the continental shelf (Lewis and Roithmayr 1981, Vaughan and Merriner 1991). Presently, the gulf menhaden purse-seine fishery for reduction extends for 28 weeks, from mid-April through late October (Smith pers. comm.). Up to 90% of the catch is made within ten miles of the northern Gulf of Mexico shoreline (Leard et al. 1995). Fishing grounds in the Gulf extend from Apalachee Bay, Florida to Matagorda Bay, Texas, but the heaviest fishing is in Louisiana and Mississippi waters (Christmas and Etzold 1977, Nelson and Arenholz 1986). This fishery is currently considered to be fully exploited and appears reasonably stable under present conditions of age composition, life span, and effects of environmental factors (Vaughan and Merriner 1991). At present, long-term average annual yields of 544.3 thousand mt are considered realistic.

From 1990 to 1993, approximately 86% of the gulf menhaden catch for reduction came from the Louisiana coast, 6% from Texas, 5% from Mississippi, and 3% from Alabama (Leard et al. 1995, Smith pers. comm.). Five reduction plants operated in 1996, at Moss Pt. MS, Empire LA, Morgan City LA, Abbeville LA, and Cameron LA (Smith 1996). Menhaden schools are located by spotter planes who notify large, refrigerated carrier vessels, known locally as pogy boats. Two purse seine boats from the carrier vessel encircle the school with a net. The captured school is then pumped into the hold of the carrier vessel and taken to the reduction plant on shore for processing (Simmons and Breuer 1964, Nicholson 1978, Smith 1991). Menhaden are used primarily for the production of fish meal, fish oil, and fish solubles. The fish meal and oil are in high demand for use in poultry and other

Table 5.17. Relative abundance of gulf menhaden in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | | | √ | | |
| Ten Thousand Islands | | | √ | | |
| Caloosahatchee River | | | √ | | |
| Charlotte Harbor | | | √ | | |
| Tampa Bay | ● | | ● | √ | |
| Suwannee River | √ | | ○ | ○ | |
| Apalachee Bay | ◉ | | ◉ | ◉ | |
| Apalachicola Bay | ◉ | | ◉ | ◉ | |
| St. Andrew Bay | ◉ | | ● | ○ | |
| Choctawhatchee Bay | ◉ | | ● | ● | |
| Pensacola Bay | ◉ | | ● | ○ | |
| Perdido Bay | ○ | | ◉ | ○ | √ |
| Mobile Bay | ● | | ● | ● | ● |
| Mississippi Sound | ● | ◉ | ● | ● | ◉ |
| Lake Borgne | ● | | ● | ● | |
| Lake Pontchartrain | | | ● | ◉ | |
| Breton/Chandeleur Sounds | | | ● | | |
| Mississippi River | | | ◉ | | |
| Barataria Bay | | | ● | ○ | |
| Terrebonne/Timbalier Bays | ◉ | | ◉ | | |
| Atchafalaya/Vermilion Bays | | | ● | ○ | |
| Calcasieu Lake | | | ● | ◉ | |
| Sabine Lake | ○ | | ● | | |
| Galveston Bay | | | ● | | |
| Brazos River | | | ◉ | | |
| Matagorda Bay | ● | | ● | | |
| San Antonio Bay | ○ | | ◉ | | |
| Aransas Bay | | | ◉ | ◉ | |
| Corpus Christi Bay | ○ | | ◉ | ○ | |
| Laguna Madre | ○ | | ◉ | | |
| Baffin Bay | √ | | ● | √ | |
| | A | S | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

domestic animal feeds, aquaculture feeds, cosmetics, and margarine. Most fish meal is used domestically, but a portion is exported. In the past most fish oil was exported, but it is now being used domestically in a greater variety of products and markets (Smith pers. comm.). There has been an increasing use of whole menhaden in the past few years as bait for crabs and crayfish (Christmas et al. 1988, O'Bannon 1993). Small quantities of menhaden are also used for canned pet food (O'Bannon 1993).

Recreational: The gulf menhaden has little sport fish value since it is a filter feeder and has a poor tasting meat (Simmons and Breuer 1964). It is an important forage fish for many sport and food fish and is also used for fishing bait. Gulf menhaden are considered to be excellent bait for crevalle jack, tarpon, king mackerel (*Scomberomorus cavalla*), and other large game fish.

Indicator of Environmental Stress: Gulf menhaden larvae have been used to study uptake and effects of heavy metals on the early life stages of fishes (Hanson and Hoss 1986). Juveniles have been used to assess the effects of the uptake of aldrin and dieldrin from agricultural applications (Ginn and Fisher 1974). Stout et al. (1981) reviewed chlorinated hydrocarbon levels in the products of gulf menhaden and reported that levels have decreased with restriction of their use. The chlorinated hydrocarbon levels present are generally safely below U.S. FDA tolerance limits.

Ecological: Gulf menhaden are an important link in the food chain between primary producers, phytoplankton and detritus, and top predators. It is an extremely important forage fish for a variety of piscivorous birds and fish (Gunter and Christmas 1960, Palmer 1962, Christmas et al. 1988). It is also important in the translocation of energy between estuarine and offshore ecosystems (Deegan 1985). Larval gulf menhaden are one of the dominant species of ichthyoplankton in the Gulf of Mexico during the winter months (Raynie and Shaw 1994).

**Range**

Overall: This species is restricted to the Gulf of Mexico, ranging from southwestern Florida near Cape Sable to Vera Cruz, Mexico on the Yucatan Peninsula. It occurs in estuarine and nearshore marine waters in depths up to 111 m, and is most abundant from Apalachicola, Florida to Galveston, Texas (Reintjes and Pacheco 1966, Lewis and Roithmayr 1981, Nelson and Arenholz 1986, Powell and Phonlor 1986, Christmas et al. 1988, Ahrenholz 1991).

Within Study Area: Within U.S. Gulf of Mexico estuaries, the gulf menhaden occurs from Florida to Texas, but the principal area of abundance in this region is from Calcasieu Lake, Louisiana to between Mobile Bay and Perdido Bay, Alabama (Table 5.17) (Reintjes and Pacheco 1966, Dugas 1970, Lewis and Roithmayr 1981, Powell and Phonlor 1986, Christmas et al. 1988, Nelson et al. 1992).

**Life Mode**
This is an estuary dependent, marine migratory species (Ahrenholz 1991). Eggs and larvae spend 3-5 weeks in offshore waters as currents carry them into estuaries. Juveniles are nektonic and adults are pelagic (Tagatz and Wilkens 1973, Wagner 1973, Perry and Boyes 1978, Deegan 1985). Schooling behavior first appears during late larval development, and continues throughout the gulf menhaden's life span (Christmas et al. 1983).

**Habitat**
Type: Food availability is probably the most important requirement for determining habitat suitability (Christmas et al. 1982, Deegan 1990). The gulf menhaden is estuarine dependent, spending most of its life in estuaries and nearshore waters of the Gulf of Mexico (Lewis and Roithmayr 1981, Christmas et al. 1982). It spawns in coastal and offshore waters in the winter. Larvae are found in greatest densities near the surface (Govoni et al. 1989), and over the inner to middle continental shelf. Larvae are known to occur from September through April (Ditty et al. 1988), with peak densities in January and February (Ditty 1986, Shaw et al. 1985b). They spend 3-5 weeks in offshore waters before moving into the quiet, low salinity shallows of marshes and estuaries and their tributaries, where they transform into juveniles. Juveniles move to deeper, open estuarine waters, and individuals greater than 50 mm SL are found primarily in this area. They remain in open water habitats until the following fall. Adults live in estuaries and nearshore waters during the spring and summer, and occur in depths of 1.8 to 14.6 m (Fore and Baxter 1972, Christmas and Waller 1975, Lewis and Roithmayr 1978, Simoneaux 1979, Christmas et al. 1982, Deegan 1985, Nelson and Ahrenholz 1986, Deegan 1990, Ahrenholz 1991). During the fall and winter months they are found offshore at depths of 7.3 to 87.8 m.

Substrate: This fish inhabits the water column, and no direct use of the substrate is apparent. It is generally caught over soft mud bottoms, and it is assumed soft mud substrates are preferred because of the abundance of benthic organisms and the richer organic content (Christmas et al. 1982, Lassuy 1983).

Physical/Chemical Characteristics:
Temperature: Eggs have been collected in the wild from 17 to 20°C (Christmas et al. 1988). Water temperature preference for juveniles and adults is between 12° and 30°, but they have been taken in waters over a range extending from 2.5 to 35.5°C. Temperature tolerances have also been observed to be quite wide at lower salinities. Active avoidance of temperatures above 30°C has been reported, as well as a kill occurring at 39°C (Miller 1965, Holcomb 1970, Copeland and Bechtel 1971, Wagner 1973, Gallaway and Strawn 1974, Christmas and Waller 1975, Pineda 1975). Gunter and Christmas (1960) reported that fishery activities in Mississippi Sound begin in the spring as water temperatures reached 23°C, and slow in the fall at approximately the same temperature.

Salinity: This species has been collected in salinities ranging from fresh to hypersaline. Gravid adults, fertilized eggs, and early larvae are typically associated with the higher salinities of the open Gulf of Mexico, generally 29‰ and higher. Post-larvae and juveniles occupy a wider range of tolerance, generally occurring from 5 to about 30‰. However, they may also enter freshwater tributaries (Mettee et al. 1996). Non-gravid and developing adults occupy mid-range salinities in the deeper part of estuaries, with high abundances at 20-25‰ reported (Wagner 1973, Pineda 1975, Perry and Boyes 1978, Marotz et al. 1990), but are capable of tolerating ranges from 0 to 67‰ (Etzold and Christmas 1979). Mass mortalities have been reported under hypersaline conditions of 80‰ or greater (Springer and Woodburn 1960, Holcomb 1970, Tagatz and Wilkens 1973, Wagner 1973, Gallaway and Strawn 1974, Shaw et al. 1985a, Christmas et al. 1988).

Dissolved Oxygen: Christmas (1981) suggests a minimum dissolved oxygen (DO) concentration of 3 parts per million (ppm); however, the empirical basis for this minimum was not given. Marotz et al. (1990) found that in estuarine waters with DO concentrations below 2 ppm, seaward movements of gulf menhaden increased.

Movements and Migrations: Gulf menhaden migration patterns coincide with productivity peaks occurring in different areas of an estuarine system (Deegan 1985, Deegan 1990). Larvae are carried shoreward from the central breeding grounds offshore for 3 to 5 weeks by currents, and then are distributed along nearshore areas throughout the range, predominantly by longshore current (Shaw et al. 1985b). Larvae can begin migrating into estuaries in October, and continue through late May. Peak influxes of larvae moving into Texas and Louisiana tidal passes occur during November-December and February-April. During flood tides, larval gulf menhaden may be dense in the the mid-stream of tidal passes, to maximize transport into estuarine areas (Raynie and Shaw 1994). They are then carried through open bays and into shallow estuarine areas (tidal creeks and ponds) by tidal flow when about 15-25 mm. They may then enter brackish and/or freshwater areas and utilize such areas as nursery grounds (Simoneaux 1979). As juveniles grow, they begin to move into deeper, higher salinity areas of the estuary (Suttkus 1956, Dugas 1970, Fore 1970, Holcomb 1970, Fore and Baxter 1972, Tagatz and Wilkens 1973, Dunham 1975, Hinchee 1977, Perry and Boyes 1978, Allshouse 1983, Guillory et al. 1983, Marotz 1984, Deegan 1985, Shaw et al. 1985a, Shaw et al. 1985b, Deegan 1990). This migration appears to be size related, but may also be influenced by environmental parameters (Marotz 1984, Deegan 1985, Deegan 1990). Larvae show a diel pattern in vertical distribution, in which they concentrate at the water surface by day, but are more vertically dispersed at night (Sogard et al. 1987). This is thought to be due to a slow sinking in the water column as a result of passive depth maintenance during the night time nonfeeding period. During daylight hours, larvae are actively swimming, and maintain their position close to the surface.

The gulf menhaden does not exhibit an extensive migratory pattern (Ahrenholz 1991). Adults and maturing juveniles (80-105 mm SL) migrate from estuaries to open Gulf waters to overwinter or spawn from late summer to winter, with peak movement occurring from October to January (Roithmayr and Waller 1963, Dugas 1970, Holcomb 1970, Tagatz and Wilkens 1973, Deegan 1985, Ahrenholz 1991). Some emigration of larger individuals occurs throughout the year (Marotz 1984, Marotz et al. 1990). In Louisiana, most movement of older fish is inshore/offshore with little east-west movement noted (Shaw et al. 1985a, Shaw et al. 1985b). Tagging studies by Kroger and Pristas (1974) indicate localized populations with little movement occurring between fishing grounds east and west of the Mississippi River Delta. However, there is evidence from other tagging studies that gulf menhaden which leave estuaries and enter the Gulf of Mexico in the edges of their range (e.g. Florida) tend to disperse or "drift" towards the center of the range (e.g. Louisiana) as they age (Ahrenholz 1981, Ahrenholz pers. comm.).

The gulf menhaden has been reported to begin migration from Tampa Bay, Florida in June and July (Springer and Woodburn 1960). Migration from Pensacola Bay, Florida has been reported to occur by September (Tagatz and Wilkens 1973). One study reports large schools in Louisiana migrating offshore in June (Wagner 1973). Adults in the Gulf begin an apparent offshore movement in October from the shallow waters inshore. Movement back into estuaries after overwintering and/or spawning in the open Gulf occurs from March to April (Christmas 1981, Lewis and Roithmayr 1981). Christmas (1981) speculates that this inshore movement is "by random movement, probably in search of high food concentrations." This leads the menhaden back into the food rich estuarine waters. Some studies indicate that the lipid content of the menhaden is related to the time of movement. Lipid and energy content increase as fish metamorphose from larvae to subadults. Fish with high lipid content are the first to migrate offshore in response to small changes in temperature; and those with lower lipid content migrate later or not at all (Wagner 1973, Deegan 1985, Deegan 1986).

**Reproduction**

Mode: Reproduction is sexual, with separate male and female sexes (gonochoristic). Milt and roe are broadcast, and fertilization is external.

Spawning: Actual spawning in the wild has not been observed (Guillory et al. 1983). Information is based on capture of eggs, larvae, spent adults, and laboratory fertilizations. Most spawning probably occurs off the Mississippi and Atchafalaya River deltas from nearshore to about 97 km offshore, in waters from 2 to 128 m deep (Roithmayr and Waller 1963, Etzold and Christmas 1979, Lewis and Roithmayr 1981, Shaw et al. 1985a, Shaw et al. 1985b, Sogard et al. 1987), with most spawning in waters less than 18 m deep (Christmas and Waller 1975, Christmas et al 1988). Adults are intermittent spawners, having as many as five peaks during a season in different parts of the Gulf. A spawning season usually runs from October through March, but can begin as early as August and last as late as May. Separate peaks can be observed during the season from November to April (Miller 1965, Tagatz and Wilkens 1973, Sabins and Truesdale 1974, Etzold and Christmas 1979, Lewis and Roithmayr 1981, Allshouse 1983, Guillory et al. 1983, Marotz 1984, Shaw et al. 1985a, Christmas 1988, Warlen 1988, Marotz et al. 1990).

Fecundity: Actual fecundity for menhaden is difficult to determine as they are intermittent, fractional spawners (Lewis and Roithmayr 1981). Studies have shown that fecundity increases significantly with age and length (Suttkus and Sundararaj 1961, Lewis and Roithmayr 1981). Mean number of eggs per fish are: 21,960 in age classes I; 68,655 in age class II; and 122,062 in age class III (Suttkus and Sundararaj 1961). Lewis and Roithmayr (1981) have developed equations to describe fecundity based on age, length, and weight.

**Growth and Development**

Egg Size and Embryonic Development: Eggs are planktonic and pelagic. They are spherical with unsculptured chorion, a faintly segmented yolk, and a single oil droplet. Observed mean total diameters of eggs have ranged from $1.22 \pm 0.04$ to $1.30$ mm $\pm 0.05$. Hatch rate can vary from 1 to 3 days depending on the ambient water temperature. In one study, eggs incubated at 19° to 20°C and 30‰ salinity hatched in 40 to 42 hours.

Hatching of menhaden eggs occurs mostly from October to March (Hettler 1984, Shaw et al. 1985a, Christmas et al. 1988, Powell 1993).

Age and Size of Larvae: Larvae are 2.6 to 3.1 mm SL immediately after hatching. Growth rate at 20° ± 2°C averaged 0.30 ± 0.03 mm/day through 90 days of rearing, but growth rate can vary with age and temperature (Chen et al. 1992, Powell 1993). Transformation from the larval to juvenile form began at approximately 19 mm and was completed at approximately 25 mm SL (Hettler 1984). One field study of larvae showed metamorphosis beginning at 20-21 mm SL and being completed at 30-35 mm SL. Other studies have reported metamorphosis taking place when larvae reach a total length (TL) of 30-40 mm TL and 30-33 mm TL (Tagatz and Wilkens 1973, Guillory et al. 1983, Deegan 1985, 1986). By May, most larvae have metamorphosed into juveniles (Tagatz and Wilkens 1973). Size-selective mortality may be significant for larval gulf menhaden, with the smaller larvae more vulnerable to predation (Grimes and Isely 1996). This may result in overestimation of larval growth, as smaller larvae are removed from the population. Growth of larval fish proceeds through a series of ontogenetic intervals, with periods of rapid growth followed by periods in which structures form (Raynie and Shaw 1994). Raynie and Shaw (1994) reported that the growth rate of larval gulf menhaden was lower in estuaries than in coastal waters, as they approached metamorphosis to the juvenile stage.

Juvenile Size Range: Juveniles may grow as much as 20-30 mm/month and become sub-adults at SL's greater than 85 mm.

Age and Size of Adults: Menhaden mature after two seasons of growth and have a maximum life span of five years (Nelson and Ahrenholz 1981). Nicholson (1978) developed the following year class size information based on fork length (FL) data from ports throughout the Gulf of Mexico:
Age-0: 102-123 mm FL range with 115 mm mean FL, 22-47 g range with 32 g mean weight (W).
Age-I: 147-165 mm FL range with 155 mm mean FL, 65-101 g range with 78 g mean W.
Age II: 181-188 mm FL range with 184 mm mean FL, 122-148 g range with 133 g mean W.
Age III: 201-214 mm FL range with 207 mm mean FL, 170-217 g range with 190 g mean W.
Nicholson (1978) also presents a length-weight equation for gulf menhaden based on these data.

Aging of gulf menhaden based on scale analysis is problematic, and length-frequency data are not reliable for assigning age classes. However, otolith analysis suggests that age IV fish do exist in the population (Vaughan et al. 1996). The bulk of the population is composed of fish from age classes I and II, with few class III and even fewer class IV fish present (Christmas et al. 1988, NOAA 1992). Sizes at maturity range from 147-165 mm FL (Nicholson 1978). Lewis and Roithmayr (1981) found no maturing ova in fish less than 100 mm FL. Growth information has been compared from Florida and Louisiana by Springer and Woodburn (1960); they found that Florida's menhaden seemed to grow at a slower rate that those in Louisiana, and that both groups experienced "a sudden burst of growth after May." Maximum lengths up to 250 mm, and weights up to 300 g have been recorded. Slight sexual dimorphism has been reported for menhaden, but it is insufficient to readily distinguish the sexes (McHugh et al. 1959, Turner 1969, Hoese and Moore 1977, NOAA 1992).

**Food and Feeding**

Trophic Mode: Larvae are selective carnivores feeding on zooplankters. Metamorphosis of larvae into juveniles is accompanied by loss of teeth. Juveniles and adults then become omnivorous filter feeders at the first and second trophic level of the food web utilizing phytoplankton, zooplankton, and detritus (Guillory et al. 1983, Govoni et al. 1983, Deegan 1985, Deegan 1986, Deegan et al. 1990, Ahrenholz 1991). Food availability affects swimming speeds, with increased swimming speeds associated with increased food availability in the water column (Durbin et al. 1981). Gulf menhaden are unique in that much of their stored energy is lipid which results in the highest energy content per gram weight found among estuarine species. As predators, gulf menhaden ingest large numbers of planktonic larvae of other species, but the effects of this predation have not been quantified. Its role as an important forage species is also in need of more research (Christmas et al. 1988).

Food Items: Small larvae feed on larger phytoplankton and some zooplankton (Ahrenholz 1991). As larvae grow, phytoplankton is replaced in importance by larger zooplankton, such as copepods, tintinnids, pteropods, and invertebrate eggs (Ahrenholz 1991, Chen et al. 1992). The diet of the remaining developmental stages of this species consists of phytoplankton, zooplankton, and detritus (Deegan 1985, Deegan 1986).

**Biological Interactions**

Predation: Gulf menhaden are potential prey for a large variety of predators throughout their life cycle (Ahrenholz 1991). Many invertebrate predators (e.g. chaetognaths), especially in oceanic waters, probably prey on this species (Ahrenholz 1991). Other potential invertebrate predators include squids, ctenophores, and jellyfishes. Predation of larval gulf menhaden may be size-selective, with predation highest for smaller larvae after hatching, reaching a plateau at five to eight days, then declining after 14 days (Grimes and Isely 1996). In estuarine and marine waters, juvenile and adult gulf menhaden are prey items for several fish species. Piscine predators include spotted seatrout, silver perch, silver sea trout (*Cynoscion nothus*), red drum, Spanish mackerel, king mackerel (*Scomberomorus cavalla*), bluefish, and sharks (Simmons and Breuer 1964, Fontenot and Rogillio 1970, Reintjes 1970, Swift et al. 1977, Etzold and Christmas 1979, Levine 1980). Menhaden are also thought to be an important forage species for piscivorous birds such as brown pelicans, and are known prey of the osprey and common loon (Ahrenholz 1991). Marine mammals are also reported to prey on menhaden.

Factors Influencing Populations: Gulf menhaden are frequently involved in "fish kills" along the Gulf coast. They are extremely sensitive to hypoxia, which is common in Gulf estuaries during the summer months. Dead-end sloughs, bayous, and harbors are particularly dangerous to menhaden during the summer. Postlarvae and juveniles are highly susceptible to such kills, as their mobility and ability to avoid hypoxia is limited (Lassuy 1983, Shipp 1986). Decaying menhaden remove still more oxygen from the water which can cause a fish kill to spread over a larger area. Gulf menhaden are susceptible to parasitic copepods and two major diseases, "spinning disease" and ulcerative mycosis (UM). Ulcerative mycosis was previously thought to be associated with infection by oomycete fungi (Noga et al. 1988), but it is now suspected to be a condition resulting from the destruction of epidermal tissue by the toxins released by the dinoflagellate *Pfiesteria piscicida* (Burkholder et al. 1995, Ahrenholz pers. comm.).

The timing of migrations from nursery areas to open bay habitats varies between different estuarine systems. This may be a response to differences in timing of primary productivity and thus food availability (Deegan 1990). Larvae occur in high concentrations at the Mississippi River plume front (Govoni et al. 1989). This may provide larvae with an enhanced feeding environment, but may also make them more susceptible to predation. The construction of water control structures in wetlands may seriously affect the recruitment of young gulf menhaden into nursery areas (Marotz et al. 1990). Some gulf menhaden are landed as bycatch on commercial shrimping vessels, but the impact of these landings on the menhaden population has not been studied, and remains largely unknown (Vaughan pers. comm.).

Gulf menhaden are generally shorter-lived and have higher natural mortality than Atlantic menhaden (*B. tyrannus*), resulting in high interannual variation in fishable stock (Vaughan et al. 1996). The gulf menhaden population is considered stable and capable of supporting an annual harvest, although declines in landings have been noted since the peak landings of the 1980's (Christmas et al. 1988, NOAA 1992, Vaughan et al. 1996). To maintain this valuable resource, the Menhaden Advisory Committee and the Gulf States Marine Fisheries Commission impose fishing limits to regulate the fishery and monitor development activities that impact the population (Christmas et al. 1988, NOAA 1992).

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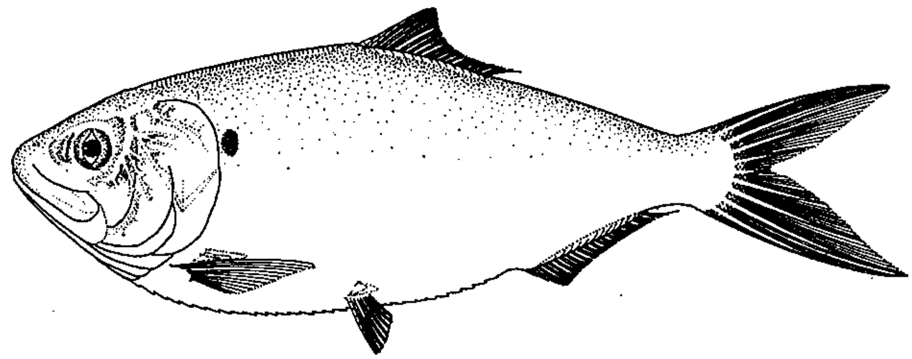
## Yellowfin menhaden

**_Brevoortia smithi_**
**Adult**



5 cm (from Fischer 1978)

**Common Name**: yellowfin menhaden
**Scientific Name**: *Brevoortia smithi*
**Other Common Names**: yellowfin shad (Hildebrand 1963), yellowtail (Reintjes 1969), Atlantic finescale (Gunter and Hall 1963), *menhaden jaune* (French), *lacha amarilla* (Spanish) (Fischer 1978).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Clupeiformes
Family: Clupeidae

### Value

Commercial: Separate commercial harvest statistics are not reported for this species (Fishcher 1978). It co-occurs with gulf menhaden, but is not abundant enough to contribute appreciably to the commercial menhaden catch (Dahlberg 1970, Hettler 1984). In some areas it was historically separated from the rest of the catch because it was considered to have superior flavor compared to other menhaden, and marketed fresh in some local markets (Hildebrand 1963, Fischer 1978). It is not specifically sought by any commercial fishery; however, it is harvested as crab bait on both coasts of Florida (Ahrenholz 1991, Hettler pers. comm.).

Recreational: Menhaden are not sought by sport fishermen as they are filter-feeders and are not caught by hook and line. However, they are important forage fish for many game species, and are often used as bait (Hildebrand 1963, Simmons and Breuer 1964).

Indicator of Environmental Stress: The yellowfin menhaden is not well studied due to its low abundance and lack of importance as a commercial species (Ahrenholz 1991).

Ecological: Menhaden serve as an important link in the food chain between primary producers, phytoplankton and detritus, and top predators. They are extremely important forage fish for a variety of piscivorous birds and fish (Gunter and Christmas 1960, Palmer 1962, Christmas et al. 1988). They are also important in the translocation of energy between estuarine and offshore ecosystems (Deegan 1985).

### Range

Overall: The yellowfin menhaden is found from Chandeleur Sound, Louisiana eastward and southward to Caloosahatchee River, Florida with distribution continuous around Florida to as far north as Cape Lookout, North Carolina (Dahlberg 1970, Christmas et al. 1983, Hettler 1984, Vaughan 1991). Yellowfin menhaden on each side of the Florida peninsula are probably members of genetically separate populations (Ahrenholz 1991). Levi (1973) reported the collection of this species off Grand Bahama Island.

Within Study Area: Within U.S. Gulf of Mexico estuaries, this species has been reported from Chandeleur Sound, Louisiana to Florida Bay, Florida (Dahlberg 1970) (Table 5.18).

### Life Mode

Yellowfin menhaden are a euryhaline species, inhabiting coastal and tidal waters (Vaughan 1991). They are an estuarine dependent, marine migratory species (Ahrenholz 1991). Eggs and larvae of yellowfin menhaden are planktonic (Hettler 1968). Juvenile and adults are pelagic (Dahlberg 1970) and aggregate in loosely scattered schools (Reintjes 1960). These schools are typically much smaller in size than those of other menhaden species (Dahlberg 1970).

Table 5.18. Relative abundance of yellowfin menhaden in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | | | ◉ | ◉ | |
| Ten Thousand Islands | | | ● | ◉ | |
| Caloosahatchee River | | | O | √ | |
| Charlotte Harbor | O | | O | O | |
| Tampa Bay | ◉ | | ◉ | | |
| Suwannee River | | | | | |
| Apalachee Bay | √ | | √ | √ | |
| Apalachicola Bay | | | | | |
| St. Andrew Bay | | | | | |
| Choctawhatchee Bay | | | | | |
| Pensacola Bay | | | | | |
| Perdido Bay | | | | | |
| Mobile Bay | | | | | |
| Mississippi Sound | √ | | | | |
| Lake Borgne | √ | | √ | | |
| Lake Pontchartrain | √ | | √ | | |
| Breton/Chandeleur Sounds | | | | | |
| Mississippi River | | | | | |
| Barataria Bay | | | | | |
| Terrebonne/Timbalier Bays | | | | | |
| Atchafalaya/Vermilion Bays | | | | | |
| Calcasieu Lake | | | | | |
| Sabine Lake | | | | | |
| Galveston Bay | | | | | |
| Brazos River | | | | | |
| Matagorda Bay | | | | | |
| San Antonio Bay | | | | | |
| Aransas Bay | | | | | |
| Corpus Christi Bay | | | | | |
| Laguna Madre | | | | | |
| Baffin Bay | | | | | |

*Life stage*

Relative abundance:

- ● Highly abundant
- ◉ Abundant
- O Common
- √ Rare
- blank Not present

Life stage:

- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

**Habitat**

Type: The yellowfin menhaden is a neritic species (Dahlberg 1970, Hettler pers. comm.). Larvae and juveniles probably occur in all tidal waters of the spawning area (Gunter and Hall 1963, Reintjes 1969, Ahrenholz 1991). Adults frequent estuaries and tidal embayments during a portion of the year, and are typically found in depths less than 18 m (Reintjes 1960, Turner 1969, Dahlberg 1970).

Substrate: This species inhabits the water column, and no substrate preference is apparent.

Physical/Chemical Characteristics: Eggs have been collected in waters with surface temperatures ranging from as low as 16.4° (Reintjes 1962) to 25.4°C (Houde and Swanson 1975) and salinities as low as 20.1‰ (Reintjes 1962) to 33‰ (Houde and Swanson 1975). Juveniles have been reported from a temperature range of 17.0° to 26.1°C and in salinities of 0.19 to 27.2‰ (Gunter and Hall 1963, Wang and Raney 1971).

Migrations and Movements: This species has no apparent systematic, annual migratory behavior. There is some evidence, however, for an increased northward distribution in late summer, and a southward movement of the species during the spawning season (Reintjes 1969, Turner 1969, Dahlberg 1970, Ahrenholz 1991).

**Reproduction**

Mode: Reproduction is sexual, with separate male and female sexes (gonochoristic). Milt and roe are broadcast, and fertilization is external.

Spawning: The yellowfin menhaden is a winter spawner. The spawning season appears to be relatively short, and occurs nearshore, apparently in tidal waters (Reintjes 1960, Dahlberg 1970, Ahrenholz 1991). Spawning may occur as early as November, but is probably most common from February to March (Ahrenholz 1991). Yellowfin menhaden reportedly spawn later than gulf menhaden (Hettler 1968, Reintjes 1969). Larvae are known to occur in Gulf of Mexico waters from December through March (Ditty et al. 1988).

Fecundity: Determinate fecundity is likely for menhaden, but this condition has not been demonstrated, nor has batch fecundity been estimated for any menhaden species (Ahrenholz 1991).

**Growth and Development**

Embryonic Development: Embryos develop oviparously. Egg diameters range from 1.21 to 1.48 mm (Houde and Swanson 1975, Ditty et al. 1994). The time of hatching varies with temperature. Hatching occurs in less than 24 hours above 22°C (Houde and Swanson 1975), 34 hours at 21°C, 26 hours at 26°C, and within 46 hours at 19°C (Reintjes 1962, Hettler 1968).

Age and Size of Larvae: The standard length (SL) of larvae at hatching is about 3.0 mm (Houde and Swanson 1975). Larvae begin transforming at about 14.0 mm, with transformation being complete between 20 and 23 mm (Houde and Swanson 1975). Larval growth is rapid, and is probably dependent on temperature and food availability (Reintjes 1969, Ahrenholz 1991). Larval growth at 20°C averaged 0.36 mm/day over a 32 day period, and 0.45 mm/day at over 20 days at 26°C (Hettler 1984).

Juvenile Size Range: Juveniles reach a fork length (FL) of 160 mm by the end of their first summer and approximately 220 mm by the end of their second summer. Sexual maturity is attained during the second winter for most individuals (Reintjes 1969). In one study, the smallest ripe adults reported were a 186 mm FL female and a 215 mm FL male (Hettler 1968).

Age and Size of Adults: Adults differ from juveniles and young adults in that their scales are more strongly serrated and their bodies are not as deep. The largest recorded total length (TL) for a specimen is 330 mm (Hildebrand 1963), and the maximum life span is thought to be somewhere between 5 and 12 years (Ahrenholz 1991).

**Food and Feeding**

Trophic Mode: Menhaden selectively sight-feed on individual planktonic organisms from the larval stage into the prejuvenile stage. After metamorphosis, juvenile yellowfin menhaden become filter-feeding planktivores (Ahrenholz 1991).

Food Items: The diet of this species consists of phytoplankton, small zooplankton, and detritus strained from the water column (Ahrenholz 1991, Hettler pers. comm.).

**Biological Interactions**

Predation: Menhaden are potential prey throughout their life cycle (Ahrenholz 1991). Larval and juvenile piscivorous fish and some invertebrates (e.g., chaetognaths) can prey on menhaden larvae. Other potential invertebrate predators may include squids, ctenophores, and jellyfish. Many piscivorous fishes (sciaenids, bluefish, bonito, etc.) prey opportunistically on juvenile and adult menhaden. Menhaden are also an important forage item for piscivorous birds such as the brown pelican and the common loon. Marine mammals are also reported to prey on menhaden. A potential also exists for menhaden to feed on their own eggs.

Factors Influencing Populations: There is little published information on yellowfin menhaden due to its low abundance and lack of commercial importance (Ahrenholz 1991). This species is known to hybridize with Atlantic menhaden (*B. tyrannus*) and gulf menhaden (*B. patronus*) (Dahlberg 1970, Ahrenholz 1991). Parasitic copepods have been found on yellowfin menhaden, and parasitic isopods have been found on yellowfin x gulf menhaden hybrids (Ahrenholz 1991).

**Personal communications**

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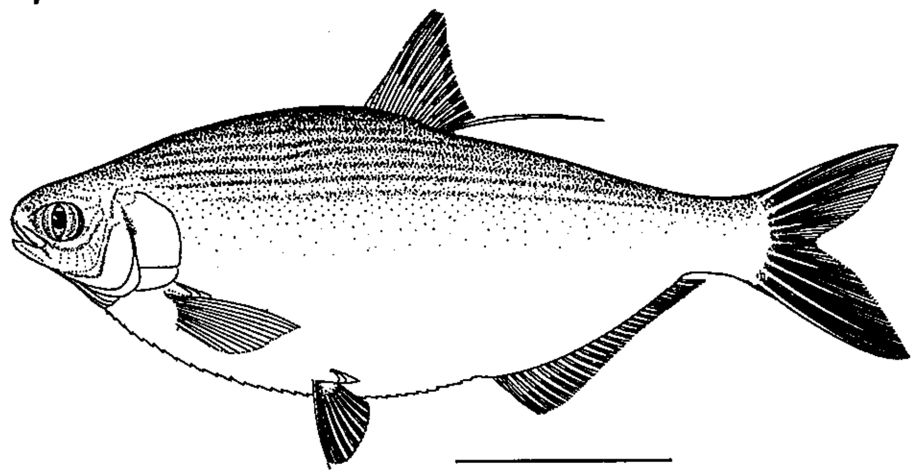
## Gizzard shad

***Dorosoma cepedianum***
**Adult**



5 cm (from Fischer 1978)

**Common Name**: gizzard shad
**Scientific Name**: *Dorosoma cepedianum*
**Other Common Names**: eastern gizzard shad, skipjack, hickory shad, mud shad, sawbelly, jackshad, *aucun* (French Canadian), *alose noyer* (French), *sábalo molleja* (Spanish) (Fischer 1978). Occasionally referred to as threadfin shad, the accepted common name for *Dorosoma petenense* (Miller 1960, Robins et al. 1991).
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Clupeiformes |
| Family: | Clupeidae |

### Value

Commercial: This species has little commercial value, although it is sometimes reportedly harvested by net from freshwater lakes and reservoirs, and processed for animal feed or fertilizer. It is occasionally eaten, but is not popular because of poor flavor, undesirable texture, and being too bony. Gizzard shad are sold as live bait for striped bass in Alabama (Mettee pers. comm.).

Recreational: The gizzard shad is generally considered a "trash" and/or nuisance fish by anglers, but small sport fisheries have developed around dams and other congregation points (Manooch 1984). It is sometimes used as live bait, especially for striped bass (Mettee pers. comm.). Its greatest value is as forage for commercial and recreational fish species, and it has been introduced into reservoirs as a prey species (Manooch 1984, Guest et al. 1990).

Indicator of Environmental Stress: Gizzard shad are not typically used in studies of environmental stress, but their populations have been used to assess the management needs of fresh water lakes and reservoirs (Jenkins 1970).

Ecological: The gizzard shad is an important forage fish (Lee 1980), and is often the primary prey of game fish in some reservoirs (Guest et al. 1990). In estuaries, this species is important in converting detritus, algae, and benthic invertebrates into forage fish biomass available to predatory fish (Lippson et al. 1979).

### Range

Overall: The gizzard shad occurs from the Great Lakes (except Lake Superior) and St. Lawrence River to southeastern South Dakota and central Minnesota, south across New Mexico, east to the Gulf of Mexico and throughout Mississippi and the Great Lakes drainages to about 40° N latitude on the Atlantic coast (Fischer 1978, Lee 1980). The populations that exist in the interior of the United States are generally landlocked from the coastal populations which occur from the St. Lawrence River southward along the Atlantic coast to central Florida and the Gulf of Mexico, and south to northeastern Mexico (Fischer 1978). In southern Florida it is found occasionally in freshwater canals, and rarely in the Tampa Bay area (Springer and Woodburn 1960, Springer 1961, Loftus and Kushlan 1987).

Within Study Area: The gizzard shad occurs in estuarine and coastal fresh waters from the Rio Grande, Texas, to southern Florida. It is abundant in some estuaries, especially those with high freshwater inflow (Table 5.19) (Fischer 1978, Loftus and Kushlan 1987).

Table 5.19. Relative abundance of gizzard shad in 31 Gulf of Mexico estuaries (Nelson et al. 1992, Mettee pers. comm.).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | | | | | |
| Ten Thousand Islands | | | | | |
| Caloosahatchee River | | | | | |
| Charlotte Harbor | | | | | |
| Tampa Bay | | | | | |
| Suwannee River | ○ | ○ | ○ | ○ | ○ |
| Apalachee Bay | ○ | ○ | ○ | ○ | ○ |
| Apalachicola Bay | ○ | ○ | ○ | ○ | ○ |
| St. Andrew Bay | | | | | |
| Choctawhatchee Bay | ○ | ○ | ○ | ○ | ○ |
| Pensacola Bay | ○ | ○ | ○ | ○ | ○ |
| Perdido Bay | √ | √ | √ | √ | √ |
| Mobile Bay | ◉ | ◉ | ◉ | ○ | ○ |
| Mississippi Sound | ◉ | ◉ | ○ | ○ | ○ |
| Lake Borgne | ● | ○ | ● | ○ | ○ |
| Lake Pontchartrain | ○ | | ○ | | |
| Breton/Chandeleur Sounds | ○ | | | | |
| Mississippi River | ○ | | ◉ | ○ | |
| Barataria Bay | ○ | | ○ | | |
| Terrebonne/Timbalier Bays | ○ | | ○ | | |
| Atchafalaya/Vermilion Bays | ○ | | ○ | | |
| Calcasieu Lake | ○ | | ○ | | |
| Sabine Lake | ○ | | | | |
| Galveston Bay | ○ | | | | |
| Brazos River | ○ | | na | | |
| Matagorda Bay | ◉ | | ◉ | | |
| San Antonio Bay | ○ | | ○ | | |
| Aransas Bay | √ | | √ | | |
| Corpus Christi Bay | ○ | | ○ | | |
| Laguna Madre | √ | | | | |
| Baffin Bay | ◉ | | ◉ | | |
| | A | S | J | L | E |

*Life stage*

Relative abundance:

- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present
- na No data available

Life stage:

- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

**Life Mode**
This is generally a pelagic fish occurring at or near the surface of shallow, quiet waters for all life stages (Miller 1960). Young-of-the-year gizzard shad form compact schools, but in subsequent years aggregations occur with no true schooling. An upstream spring "run" occurs in rivers prior to the spawning season (Swift et al. 1977).

**Habitat**
Type: The gizzard shad is nektonic in fresh to polyhaline waters. It prefers areas with warm water and high phytoplankton production, and occurs in the littoral and limnetic regions of lakes and reservoirs, and in rivers, canals and coastal bays. This species commonly enters brackish and occasionally marine waters (Lee et al. 1980).

Substrate: This species is widely distributed over mud bottoms, but also occurs over hard bottom lake shores. It is taken over mud, vegetation, rubble, sand, gravel, boulders, and bedrock (Nash 1950).

Physical/Chemical Characteristics:
Temperature: This species is not considered hardy, and is susceptible to changes in temperature and low dissolved oxygen (Manooch 1984). Juveniles and adults have been collected from 5.0° to 34.9°C and suffer high mortality rates when temperatures fall to 2.2°C. Northern populations are susceptible to cold-induced winter kills (Bodola 1966, Perret 1971, Jester and Jensen 1972, Juneau 1975, Pineda 1975, Tarver and Savoie 1976).

Salinity: Eggs, larvae and small juveniles are limited to freshwater. Juveniles less than 40 mm are found in 1.1‰ or less (Renfro 1960, Swingle 1971). Larger juveniles, usually greater than 70 mm TL, begin to enter brackish and more saline waters with one being collected at 41.3‰ (Renfro 1960, Dunham 1972). Although adults are euryhaline (2-33.7‰), they are rare in "pure saltwater" (Gunter 1942, Gunter 1945, Perret 1971, Pineda 1975). They prefer oligohaline to mesohaline salinities with the greater abundance occurring below 15‰. One study reported captures from 4 to 20‰ (Wagner 1973).

Dissolved Oxygen: The lowest reported dissolved oxygen (DO) concentration where this species has been collected is 4.6 parts per million (ppm) (Chambers and Sparks 1959).

Movements and Migrations: As larvae, there is a general movement from surface to midwater as size increases. Juveniles slowly make their way to more saline waters with age, but do not enter until about 70 mm TL. Adults are concentrated in deeper water during the fall and winter. Adults in salt water migrate upstream to spawn during spring months (Gunter 1938, Gunter 1945, Pineda 1975, Jones et al. 1978). The increased abundance in inshore waters during winter months (November-February) may be due to this upstream spawning movement (Chambers and Sparks 1959).

**Reproduction**

Mode: Reproduction is sexual, with separate male and female sexes (gonochoristic). Milt and roe are broadcast, and fertilization is external.

Spawning: Spawning takes place in freshwater sloughs, ponds, lakes, and rivers, from mid-March to late August, with a peak from April to June in temperate waters. A second spawn may occur in late summer in some areas. This spawning period is generally later and more prolonged than that of Alabama shad (*Alosa alabamae*) or American shad (*Alosa sapidissima*) (Swift et al. 1977, Lippson et al. 1979). Eggs are scattered in open water or along the shoreline. Several individuals of each sex are often involved at the time of gamete release, which usually takes place at midday with rising temperatures that range from 10 to 28.9°C. They are reported to be most active around 18°C (Miller 1960, Bodola 1966, Kelley 1965, Jones et al. 1978, Manooch 1984).

Fecundity: Reported fecundity ranges from 3,000 to 543,900, but can change with age, averaging 59,480 at Age I, 378,990 at Age II and declining to 215,330 at Age VI (Bodola 1966, Manooch 1984).

**Growth and Development**

Egg Size and Embryonic Development: Eggs are demersal and adhesive, sticking to the substrate (rocks, sticks, roots, etc.) if it is not covered with sediment. Fertilized eggs are creamy yellow, nearly transparent, and 0.75 mm in size. When eggs are first extruded they are hard and irregularly shaped, but become spherical after contact with water. The incubation period is temperature dependent and lasts from 36 hours to 1 week. Egg hatching occurs after 95 hours at 17°C and 36 hours at 27°C (Lippson and Moran 1974, Jones et al. 1978).

Age and Size of Larvae: At hatching larvae are around 3.25 mm TL. This stage lasts for a few weeks, during which the alimentary canal develops into the form necessary for omnivorous filter-feeding (Miller 1960).

Juvenile Size Range: The juvenile stage is reached at about 20 mm TL. Juveniles mature in about 2 or 3 years, with some females maturing as soon as 1 year. Average length at maturity is 178-279 mm TL.

Age and Size of Adults: In Florida, gizzard shad averaged about 254 mm after the first year, 317.5 mm after the second and 345.4 mm after the third with none surviving to the fourth year. In other areas, particularly temperate freshwater locations, growth is much slower with a life span extending to almost 10 years (Miller 1960), but most fish die before they are 7 years old (Manooch 1984). This species has attained lengths up to 520.7 mm TL, but does not commonly grow larger than 254 to 355.6 mm TL (Miller 1960).

**Food and Feeding**

Trophic Mode: Gizzard shad are primarily filter-feeders (Miller 1963). For a short period after hatching, larvae are carnivorous. Juveniles and adults become filter-feeders. They may feed both on the bottom and in the water column, and may or may not be selective (Baker and Schmitz 1971).

Food Items: During the first few weeks as larvae, the primary food items are small animals, such as protozoa, water fleas (Cladocera), copepods and ostracods (Miller 1960). After this initial phase when the intestine has had a chance to develop, there is a switch to algae, zooplankton, detritus, and bottom sediments containing benthic infauna (Miller 1963, Baker and Schmitz 1971, Lippson et al. 1979).

**Biological Interactions**

Predation: Although this species provides a forage base for predator fish, the rapid first year growth of the gizzard shad often makes it nearly invulnerable to predation by the fall of its first year (Jenkins 1970, Lee et al. 1980). Known estuarine predators of this species include spotted gar and longnose gar (Bonham 1940, Darnell 1958), and freshwater predators include largemouth bass (*Micropterus salmoides*) (Houser and Netsch 1971) and white bass (*Morone chrysops*) (Netsch et al. 1971).

Factors Influencing Populations: Gizzard shad populations usually grow rapidly when introduced into new systems (e.g., reservoirs), possibly due to abundant detritus and other food sources. Where gizzard shad are abundant, they affect the populations, growth and habitat of game fish such as largemouth bass (*Micropterus salmoides*) and crappie (*Pomoxis* species) (Jenkins 1970, Guest et al. 1990). Where they co-occur with threadfin shad (*Dorosoma petenense*), it is possible that the two species compete for available food sources (Baker and Schmitz 1971). Winter kills occasionally occur in the lower Great Lakes, and when they do, gizzard shad provide a source of food for birds (Miller 1960). Extensive die-offs may also occur in late summer (Mettee et al. 1996).

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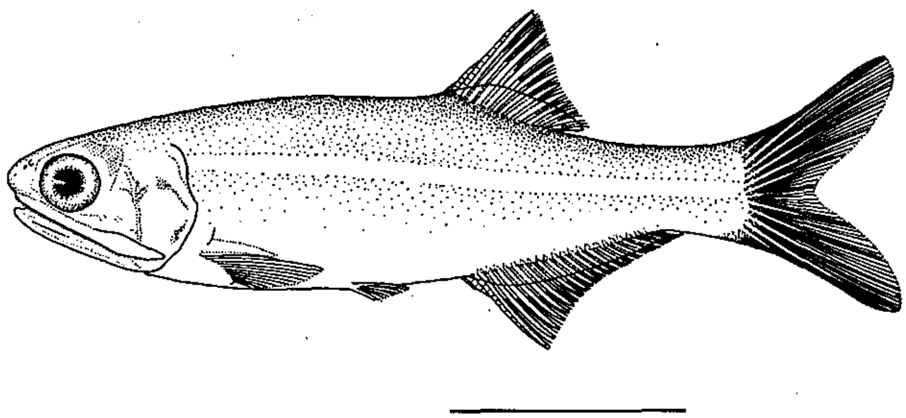
## Bay anchovy

***Anchoa mitchilli***
**Adult**




(from Fischer 1978)

**Common Name**: bay anchovy
**Scientific Name**: *Anchoa mitchilli*
**Other Common Names**: anchovy, *anchois bai* (French), *anchoa de caleta* (Spanish) (Fischer 1978)
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Clupeiformes |
| Family: | Engraulidae |

### Value

Commercial: The bay anchovy is not currently harvested in the United States due to its small size, but is of some use as bait and in the preparation of anchovy paste (Hildebrand 1943, Hildebrand 1963, Daly 1970, Christmas and Waller 1973). It can be caught with beach seines and trawls (Fischer 1978). This species and other "coastal herrings" represent a large underutilized fishery resource with a potential yield of 1 to 2 million mt (SEFSC 1992). Anchovies are seldom taken as bycatch by trawl or purse seine fisheries due to their small size (Christmas et al. 1960).

Recreational: The bay anchovy is indirectly important to recreational fisheries as a major forage item for many game fish (Hildebrand 1943, Christmas and Waller 1973).

Indicator of Environmental Stress: Because of its importance as a forage species, this species can be considered an indicator of the health of an estuary (Shipp 1986). Studies supported by the Texas Water Quality Board show that the bay anchovy can be used to indicate poor water quality. This species can quickly adapt to pollution stress due to its small size and short food chain and become the dominant species of the polluted area. Its dominance in a particular area for two or more consecutive seasons can be indicative of deteriorating water quality (Bechtel and Copeland 1970, Livingston 1975).

Ecological: Bay anchovies probably constitute the greatest biomass of any fish in the estuarine waters of both the southeastern U.S. and the U.S. Gulf of Mexico (Reid 1955, Perret 1971, Christmas and Waller 1973, Perry and Boyes 1977, Perry 1979, Shipp 1986). This species is a staple item in the diet of many predatory bird and fish species, and is a crucial link in the estuarine food web between zooplankton and higher trophic level predators (Hildebrand 1943, Reid 1955, Christmas and Waller 1973, Robinette 1983, Shipp 1986). Distributions of predators indicate that the bay anchovy is an important prey species in the weedy shallows as well as surface and bottom waters (Darnell 1961). Larval bay anchovy are one of the dominant species of ichthyoplankton in the Gulf of Mexico during the summer months (Raynie and Shaw 1994).

### Range

Overall: This species occurs from Casco Bay, Maine to near Tampico, Mexico (Hildebrand 1943, Hildebrand 1963, Daly 1970, Houde 1974, Hoese and Moore 1977). It is taken only rarely in the Yucatan, Gulf of Maine, and Florida Keys, and never in the West Indies (Hildebrand 1943, Daly 1970, Hoese and Moore 1977). It has also been shown by morphometric methods that virtually every section of the coast within the range of the bay anchovy has a distinctive population, and that clinal variation over this species' range may account for differences in form (Hildebrand 1943, Hildebrand 1963, Lee et al. 1980).

Table 5.20. Relative abundance of bay anchovy in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ● | ● | ● | ● | ● |
| Ten Thousand Islands | ● | ● | ● | ● | ● |
| Caloosahatchee River | ● | ● | ● | ● | ● |
| Charlotte Harbor | ● | ● | ● | ● | ● |
| Tampa Bay | ● | ● | ● | ● | ● |
| Suwannee River | ● | ● | ● | ● | ● |
| Apalachee Bay | ● | ● | ● | ● | ● |
| Apalachicola Bay | ● | ● | ● | ● | ● |
| St. Andrew Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Choctawhatchee Bay | ● | ● | ● | ● | ● |
| Pensacola Bay | ● | ● | ● | ● | ○ |
| Perdido Bay | ◉ | ○ | ◉ | ○ | ○ |
| Mobile Bay | ● | ● | ● | ● | ● |
| Mississippi Sound | ● | ● | ● | ● | ● |
| Lake Borgne | ● | ● | ● | ● | ● |
| Lake Pontchartrain | ● | ● | ● | ● | ● |
| Breton/Chandeleur Sounds | ◉ | ◉ | ◉ | ◉ | ◉ |
| Mississippi River | ● | ◉ | ● | ◉ | ◉ |
| Barataria Bay | ● | ● | ● | ● | ● |
| Terrebonne/Timbalier Bays | ● | ● | ● | ● | ● |
| Atchafalaya/Vermilion Bays | ● | ● | ● | ● | ● |
| Calcasieu Lake | ● | ● | ● | ● | ● |
| Sabine Lake | ◉ | ○ | ◉ | ○ | ○ |
| Galveston Bay | ● | ● | ● | ● | ● |
| Brazos River | ● | ● | ● | ● | ● |
| Matagorda Bay | ● | ● | ◉ | ◉ | ○ |
| San Antonio Bay | ● | ● | ◉ | ● | ● |
| Aransas Bay | ● | ● | ● | ● | ● |
| Corpus Christi Bay | ● | ● | ● | ● | ● |
| Laguna Madre | ● | ● | ● | ● | ● |
| Baffin Bay | ● | ● | ● | ● | ● |
| | A | S | J | L | E |

*Life stage* (column heading)

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning adults
- J - Juveniles
- L - Larvae
- E - Eggs

Within Study Area: Within U.S. Gulf of Mexico estuaries, the bay anchovy occurs from the Rio Grande, Texas to the Florida Keys, primarily in open bays (Springer and Woodburn 1960, Hoese and Moore 1977) (Table 5.20).

**Life Mode**

All life stages are pelagic, and occur throughout the water column (Kuntz 1913, Reid 1955, Hoese 1965, Houde 1974, Hoese and Moore 1977, Ward and Armstrong 1980). Eggs are most abundant at the surface; however, they are found throughout the water column, while larvae, juveniles, and adults are primarily nektonic (Kuntz 1913, Hildebrand 1943, Reid 1955, Darnell 1958, Darnell 1961, Jones et al. 1978). Larvae primarily occupy the upper portion of the water column, while juveniles are more closely associated with deeper waters. Adults are pelagic and are found primarily in inshore waters, but they occur in offshore waters as well (Hildebrand 1963, Jones et al. 1978). Large schools form during the day in protected areas, usually close to shore. The bay anchovy has been observed to form small schools at night while feeding in the presence of predators (Hildebrand 1943, Arnold et al. 1960, Daly 1970, Hoese and Moore 1977, Ward and Armstrong 1980). Activity is primarily nocturnal and is probably associated with feeding (Zimmerman 1969, Daly 1970).

**Habitat**

Type: This is primarily a shallow estuarine and inshore coastal water species (Gunter 1945, Kilby 1955, Arnold et al. 1960, Springer and Woodburn 1960, Swingle and Bland 1974, Jones et al. 1978, Sheridan 1978, Ward and Armstrong 1980, Sheridan 1983). The bay anchovy is able to exploit a wide variety of habitats, including bays and bayous, sandy beaches, muddy coves, grassy areas along beaches, rivers and their mouths, and both shallow and deeper waters offshore (Reid 1955, Swingle and Bland 1974, Swift et al. 1977, Jones et al. 1978, Sheridan 1978), but prefers bays and estuaries to shallow waters of the Gulf of Mexico (Gunter 1945, Kilby 1955, Springer and Woodburn 1960, Christmas and Waller 1973). It is particularly abundant in primary and secondary bays, around shallow bay margins, islands, spoil banks, and sheltered coves, and is less common in tertiary bays (Kilby 1955, Simmons 1957, Swingle 1971, Ward and Armstrong 1980). It has been reported to occur from fresh to hypersaline waters (Simmons 1957, Perret 1971, Swingle and Bland 1974) and from depths of 0.5 to 20.0 m, appearing to prefer 2 to 3 m (Reid 1954, Renfro 1960, Miller 1965, Bechtel and Copeland 1970, Franks 1970, Perret 1971, Swingle 1971, Dunham 1972, Dokken et al. 1984). This species has been collected in water with turbidities of 0.5 m to 0.7 m secchi depth (Reid 1955), and it has been suggested that the bay anchovy is attracted to areas of high turbidity (Livingston 1975).

Substrate: The bay anchovy is known to occur over unvegetated mud substrates (Cornelius 1984), but also occurs in grassy areas (Hildebrand and Cable 1930, Reid 1954, Kilby 1955, Hildebrand 1963, Gallaway and Strawn 1974). It has also been collected over bottoms of clay, hard sand, silty clay, clayey silt, silt and sand, sandy mud, and muddy sand (Reid 1954, Reid 1955, Miller 1965, Franks 1970, Swingle 1971, Dunham 1972, Tarver and Savoie 1976, Dokken et al. 1984).

Physical/Chemical Characteristics:
Temperature and salinity: Eggs are commonly found between 8 and 15‰ with spawning and development having been observed at 30.9 to 37‰ and from 22° to 32°C (Kuntz 1913, Hoese 1965, Detwyler and Houde 1970, Dunham 1972, Houde 1974, Tarver and Savoie 1976). Preferred temperatures range from 27.2° to 27.8°C (Ward and Armstrong 1980). The larvae, juvenile and adult stages are considered both euryhaline and eurythermal. They have been collected from waters ranging from 0.0 to 80‰ and from water temperatures ranging from 4.5° to 39.8°C (Gunter 1945, Reid 1954, Kilby 1955, Simmons 1957, Renfro 1960, Springer and Woodburn 1960, Miller 1965, Edwards 1967, Franks 1970, Perret 1971, Swingle 1971, Wang and Raney 1971, Dunham 1972, Wagner 1973, Gallaway and Strawn 1974, Swingle and Bland 1974, Juneau 1975, Pineda 1975, Tarver and Savoie 1976, Swift et al. 1977, Barrett et al. 1978, Chung and Strawn 1982, Cornelius 1984). Although they can occur in warmer temperatures, bay anchovies in Galveston Bay are not abundant above 33°C (Gallaway and Strawn 1974). Larvae are generally collected in greatest abundance between 3 and 7‰ (Perry and Boyes 1977, Ward and Armstrong 1980). Adults prefer temperatures ranging from 8.1° to 32.2°C with one Mississippi study reporting greatest abundances between 20° to 30°C (Perry and Boyes 1977, Ward and Armstrong 1980). A possible upper lethal limit of 40°C was reported in one temperature study (Chung and Strawn 1982).

Salinity: Salinity generally appears to have little relationship with juvenile and adult distribution and abundance (Hoese 1965, Christmas and Waller 1973, Krull 1976, Perry and Boyes 1977, Ward and Armstrong 1980, Cornelius 1984). Reported salinity ranges vary among the different life stages and among different locations. In Texas, larvae have been collected at 0.5 to 1‰ in Matagorda Bay while juveniles and adults have been collected at 1 to 32‰ (Ward and Armstrong 1980). The reported salinity range in Alazan Bay is 11 to 30‰ for adults, and 11 to 20‰ and 31 to 40‰ for juveniles (Cornelius 1984). Gunter (1945) reports an overall occurrence at ≤5‰ in Copano and Aransas Bays, while Simmons (1957) reported it to be <50‰ in the upper Laguna Madre. In Alabama, it has been reported from 20 to 29.9‰ in Mobile and Baldwin counties (Swingle 1971), and 0.0 to 14.9‰ in Lake Pontchartrain, LA (Tarver and Savoie 1976). Along the Mississippi coastline, occurrence was reported at 20.0 to 25.0‰ for larvae, 15 to 20‰ for small juveniles, 0-5‰ and 25-30‰ for larger juveniles (Christmas and Waller 1973, Perry and Boyes 1977). Bay anchovies have been collected in freshwater rivers of Alabama, many miles upstream of Mobile Bay (Mettee et al. 1996).

Turbidity: The bay anchovy may be attracted to areas of high turbidity, and has been collected in water with a turbidities of 0.5 m to 0.7 m secchi depth (Robinette 1983).

Dissolved oxygen (DO): In Louisiana, the bay anchovy was collected in waters with a dissolved oxygen range of 1.5 to 11.9 ppm (Barrett 1978). In the Chesapeake Bay, DO concentrations below 3 mg/l probably limit the viability and productivity of this species (Killam et al. 1992).

Movements and Migrations: Migrations are probably limited to seasonal inshore-offshore movements. Bay anchovies move into deeper waters of bays and estuaries during winter, and back inshore during summer (Hildebrand 1943, Hildebrand 1963, Christmas and Waller 1973, Swingle and Bland 1974, Perry and Boyes 1977, Robinette 1983). Larvae appear to migrate into lower salinity nursery areas to mature, and then, as juveniles and adults, move to deeper, more saline areas (Gunter 1945, Hoese 1965, Edwards 1967, Swingle and Bland 1974, Killam et al. 1992). Larvae appear on inshore nursery grounds in Mississippi waters during April and May (Perry and Boyes 1977). Peak larval movement into a Texas tidal pass occurred during June in one study (Allshouse 1983). Immigration into nursery areas continues through October and November (Perry and Boyles 1977). During flood tides, larval bay anchovy may move to the middle of tidal passes to maximize transport into estuarine areas (Raynie and Shaw 1994).

**Reproduction**
Mode: This species has separate male and female sexes (gonochoristic). Milt and roe are broadcast, and fertilization is external.

Spawning: Spawning occurs in waters less than 20 m deep near barrier islands, in bays and estuaries, tidal passes, harbors, sounds, and in the Gulf of Mexico where it is limited to the shallow inshore areas in bay water masses (Hoese 1965, Bechtel and Copeland 1970, Sabins and Truesdale 1974, Perry and Boyes 1977, Jones et al. 1978, Ward and Armstrong 1980). Spawning has been observed in higher salinity portions of estuaries with ranges of 30 to 37‰ and <45‰ (Bechtel and Copeland 1970, Swingle and Bland 1974, Dokken et al., 1984). Spawning by large schools usually occurs in the early evening, between 6 and 9 pm, during warm water (>19°C) periods (Kuntz 1913, Hoese 1965, Jones et al. 1978, Ward and Armstrong 1980). Egg densities peak at different times depending on location. Based on studies of gonads and collection of juveniles and larvae, reported spawning seasons are: February to March, and June to August in the Gulf near Port Aransas, Texas and the latter part of March in Copano and Aransas Bays (Gunter 1945, Hoese 1965, Allshouse 1983); summer months (June and July) in East Bay, Texas; February to October in Galveston Bay, Texas (Bechtel and Copeland 1970); spring and summer with peak spawning from March through October in Louisiana (Dugas 1970, Wagner 1973, Sabins and Truesdale 1974); and February through October with a July peak along the Mississippi coastline (Edwards 1967, Christmas and Waller 1973, Perry and Boyes 1977). Based on collection of larvae, the spawning season in the north-central Gulf of Mexico is March through September/October (Ditty pers. comm.). In Tampa Bay, spawning begins after water temperatures have reached 20°C and stops by November (Phillips 1981). Some additional spawning is reported to occur throughout the year in some areas (Miller 1965, Perret 1971, Swingle 1971, Wagner 1973, Ward and Armstrong 1980, Dokken et al. 1984). This may be attributable to the Gulf's usually short and mild winters that sometimes allow shallow water winter temperatures to approach and exceed 20°C (Hoese 1965, Dokken et al. 1984). In Biscayne Bay, Florida, it is suggested that spawning occurs all year, but is uncommon in December and January (Jones et al. 1978).

Fecundity: Data using fish from Chesapeake Bay indicate that during the peak spawning period females spawn a batch of 400 to 2000 eggs every four days (Luo and Musick 1991), with the actual number directly related to the weight of the female (approximately 400 eggs per gram of wet weight female). This can conceivably result in a female producing 30,000 to 50,000 eggs during the four month season in Chesapeake Bay (Houde pers. comm.).

**Growth and Development**

Egg Size and Embryonic Development: Eggs have a barely elliptical shape, and are 0.84 to 1.11 mm in diameter (Farooqi et al. 1995). Average egg size tends to decrease with increasing salinity (Jones et al. 1978). Eggs are transparent with no oil globule and the yolk is composed of separate masses appearing as large cells with an overall volume of 0.15 $mm^3$ (Kuntz 1913, Hildebrand 1943, Houde 1974, Farooqi et al. 1995). Eggs float at or near water surface until near hatching and then gradually sink (Kuntz 1913, Hildebrand 1943). Incubation takes approximately 24 hours at 27.8°C (Kuntz 1913, Farooqi et al. 1995)

Age and Size of Larvae: Larvae are 1.8 to 2.7 mm total length (TL) at hatching and weigh 17.6 µg (Kuntz 1913, Detwyler and Houde 1970, Houde 1978, Ward and Armstrong 1980, Farooqi et al. 1995). The yolk sac is comparatively large and greatly elongated tapering to a point posteriorly. It is completely absorbed 15 to 18 hours after hatching (AH). The body is elongate, slender, and nearly transparent with little pigmentation. Larvae are 2.6 to 2.8 mm TL at 12 hours AH. Development of mouth and gut, pigmentation of eyes, and yolk exhaustion are completed simultaneously at 36 hours after hatching at 26.2°C and 30.9‰ (Kuntz 1913, Hildebrand 1943, Detwyler and Houde 1970). The critical period in which the larvae must begin to feed is 2.5 days after hatching (Houde 1974). Size when feeding was initiated was 2.9 mm SL (Houde 1978). A growth rate of 0.70 mm/day was reported for the fourth day (AH) (Detwyler and Houde 1970) reaching a weight of 236.0 µg after 16 days (Houde 1978). Larval survival in the laboratory is highest from 24 to 28°C, with faster growth at the higher temperatures (Houde 1974).

Juvenile Size Range: Metamorphosis into juvenile form begins at 15.5 mm SL, and is essentially complete by 22.5 mm SL (Jones et al. 1978, Ward and Armstrong 1980). A length of 18 mm TL is attained during the first month (AH) and a growth rate of 10 mm/month occurs over the following 2 months (Edwards 1967, Christmas and Waller 1973). Juveniles mature rapidly, becoming sexually mature within their first year.

Age and Size of Adults: The bay anchovy matures in approximately 2.5 months (Hildebrand 1963, Jones et al. 1978) at 34 to 45 mm TL (Gunter 1945, Edwards 1967, Ward and Armstrong 1980). Reported sizes for adults in the study area range from 34 to 93 mm TL (Gunter 1945, Renfro 1960, Franks 1970, Perret 1971, Dunham 1972, Wagner 1973, Pineda 1975, Tarver and Savoie 1976) with a recorded mean of 56.3 mm TL for males and 60.0 mm TL for females (Ward and Armstrong 1980). Two and possibly three size classes have been observed in populations, but they are virtually indistinguishable due to the occurrence of spawning throughout the year (Gunter 1945, Miller 1965, Perret 1971, Cornelius 1984).

**Food and Feeding**

Trophic mode: Bay anchovies are primary consumers, feeding primarily on zooplankton in currents at night

(Reid 1955, Bechtel and Copeland 1970, Daly 1970).

Food Items: Young anchovies are plankton strainers. They consume zooplankton such as copepod nauplii and rotifers until a body length of approximately 7 mm is reached, at which time they switch to copepodites and copepods (Darnell 1958, Detwyler and Houde 1970). Some detritus is also consumed, but phytoplankton generally is not, which suggests that food straining occurs near the bottom (Darnell 1958). As anchovies grow in size their diet becomes increasingly selective, shifting from copepods to small shrimp, larval and juvenile fish, mysids, insect larvae, crab zoeae, clam larvae, cladocerans, schizopods, gastropods, copepods, isopods, malacostracans, oligochaetes, polychaetes, and supplemented by detritus from occasional bottom feeding (Hildebrand 1943, Reid 1954, Reid 1955, Darnell 1958, Arnold et al. 1960, Darnell 1961, Bechtel and Copeland 1970, Detwyler and Houde 1970, Carr and Adams 1973, Weaver and Halloway 1974, Sheridan 1978, Levine 1980). Gut analysis of anchovies 30 to 49 mm long showed the following diet proportions: 9% microinvertebrates; 58% zooplankton, and 33% organic detritus (Darnell 1961). Benthic animals and sand are most frequently encountered during the winter, suggesting more intensive benthic feeding at this time (Darnell 1958).

**Biological Interactions**

Predation: The small size and high abundance of this species makes it one of the most important forage species in the Gulf of Mexico (Robinette 1983). Many species are known to consume bay anchovies, including snook, gar (*Lepisosteus* species), red drum, sand seatrout, spotted seatrout, silver perch, Atlantic needlefish (*Strongylura marina*), inshore lizardfish (*Synodus foetens*), ladyfish (*Elops saurus*), blue catfish (*Ictalurus furcatus*), Atlantic croaker, southern flounder, crevalle jack, and cobia (*Rachycentron canadum*) (Gunter 1945, Reid 1955, Darnell 1958, Darnell 1961, Carr and Adams 1973, Sheridan 1978, Rozas and Hackney 1984, Killam et al. 1992, Franks et al. 1996).

Factors Influencing Populations: Population density appears to be primarily influenced by food supply (i.e., zooplankton) present in the water column (Reid 1955). This probably accounts for their preference for bay habitats and, when found in the Gulf, bay water masses (Hoese 1965).

**Personal communications**

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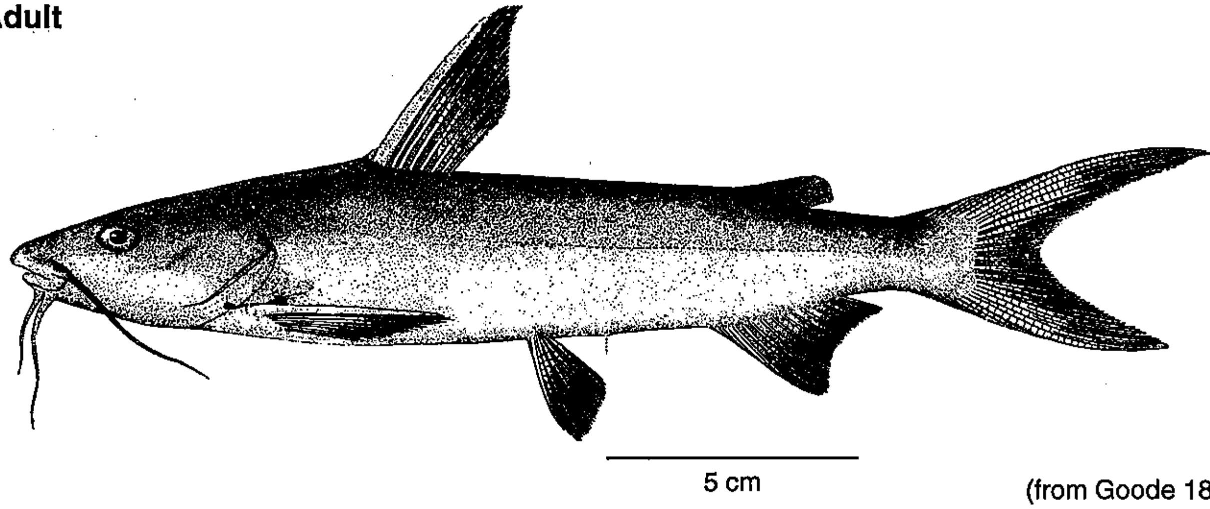
***Arius felis***
**Adult**




(from Goode 1884)

**Common Name**: hardhead catfish
**Scientific name**: *Arius felis*
**Other Common Names:** sea catfish, hardhead, silver cat, tourist trout (Arnold et al. 1960, Benson 1982, Breuer 1957, Bryan 1971, Christmas and Waller 1973); *mâchoiron chat* (French), *bagre gato* (Spanish) (Fischer 1978).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Cypriniformes
Family: Ariidae

**Value**
Commercial: The hardhead catfish is not sought by the commercial fishery because it has a low market value and becomes entangled in nets and pump hoses. It contributes a small portion (2-3%) to the industrial bottom fish fishery of Louisiana and Mississippi, which uses low value fish to produce pet food, fish meal, fish oil, and protein supplements for animal feeds. However, it is frequently discarded due to the possibility of animals ingesting its spines (Haskell 1961, Roithmayr 1965, Dunham 1972, Swingle 1977, Benson 1982). It was used briefly as a food fish during World Wars I and II (Gunter 1945). Its nutritive value compares favorably with croaker, spot, and spotted seatrout, but attempts to market it as human food have failed because the meat is dark and often has a strong odor (Benson 1982).

Recreational: Hardhead catfish are frequently caught, but are usually discarded by anglers. They are held in low esteem because of their sharp venomous spines, undesirable flesh, and difficulty in handling and removing them from the hook (Gunter 1945, Arnold et al. 1960, Harris and Rose 1968, Fontenot and Rogillio 1970, Hoese and Moore 1977, Swingle 1977). Fishery statistics for the Gulf of Mexico showed a combined total recreational catch of 18,474,000 saltwater catfishes (hardhead catfish and gafftopsail catfish (*Bagre marinus*)) in 1988 (NMFS 1989). Although edible, this fish is not often consumed due to its reputation of feeding on any available organic matter (Gallaway and Strawn 1974).

Indicator of Environmental Stress: This species has been used in research on the effects of sublethal copper exposure on marine fish (Scarfe et al. 1982, Steele 1989). It has been used to study prevalence of pathological abnormalities as an indicator of environmental stress (Fournie et al. 1996). Bioaccumulation of contaminants and liver lesions in hardhead catfish have been found to be correlated with substrate contaminant levels in Tampa Bay (McCain et al. 1996).

Ecological: The hardhead catfish is highly abundant in shallow coastal waters of southeastern U.S., but is occasionally found in deep water (Chittenden and McEachron 1976). It is an opportunistic feeder, and can utilize diverse food sources. This may account for its successful adaptation to different habitats (Darnell 1958, Hildebrand 1958, Hellier 1962, Diener et al. 1974, Dugas 1975, Hoese and Moore 1977, Benson 1982). It is not a major forage species, but is important in estuarine ecosystems as a scavenger (Fontenot and Rogillio 1970, Wagner 1973). This fish is very abundant in estuarine habitats, and can compete with game fishes for space and food (Fontenot and Rogillio 1970, Muncy and Wingo 1983).

Table 5.21. Relative abundance of hardhead catfish in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Ten Thousand Islands | ○ | ○ | ○ | ○ | ○ |
| Caloosahatchee River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Charlotte Harbor | ◉ | ◉ | ● | ◉ | ◉ |
| Tampa Bay | ○ | ○ | ○ | ○ | ○ |
| Suwannee River | ● | ○ | ◉ | ○ | ○ |
| Apalachee Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Apalachicola Bay | ● | ● | ● | ● | ● |
| St. Andrew Bay | ● | ● | ● | ● | ● |
| Choctawhatchee Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Pensacola Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Perdido Bay | ◉ | ○ | ◉ | ○ | ○ |
| Mobile Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Mississippi Sound | ● | ◉ | ◉ | ○ | ○ |
| Lake Borgne | ● | ○ | ◉ | ○ | ○ |
| Lake Pontchartrain | ◉ | ○ | ◉ | ○ | ○ |
| Breton/Chandeleur Sounds | ○ | ○ | ◉ | ○ | ○ |
| Mississippi River | ● | ◉ | ◉ | ◉ | ◉ |
| Barataria Bay | ● | ◉ | ● | ◉ | ◉ |
| Terrebonne/Timbalier Bays | ◉ | ◉ | ◉ | ◉ | ◉ |
| Atchafalaya/Vermilion Bays | ◉ | ○ | ○ | ○ | ○ |
| Calcasieu Lake | ◉ | ○ | ◉ | ○ | ○ |
| Sabine Lake | ○ | ○ | ○ | ○ | ○ |
| Galveston Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Brazos River | ○ | na | ○ | na | na |
| Matagorda Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| San Antonio Bay | ● | ● | ● | ● | ● |
| Aransas Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Corpus Christi Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Laguna Madre | ◉ | ◉ | ● | ◉ | ◉ |
| Baffin Bay | ● | ● | ● | ● | ● |
| | A | S | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present
- na No data available

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

**Range**

Overall: The range is along the Atlantic coast from Cape Cod, Massachusetts to Yucatan, Mexico (Jones et al. 1978, Lee et al. 1980). This species is extremely abundant in the shallow coastal waters of North Carolina, around Florida, and throughout the Gulf of Mexico, but is absent from the Caribbean (Shipp 1986).

Within Study Area: Within U.S. Gulf of Mexico estuaries, hardhead catfish are found from the Rio Grande, Texas, to Florida Bay, Florida. This is one of the most ubiquitous fishes present in the brackish and salt waters of the bays and shallow waters of the northern Gulf of Mexico (Table 5.21) (Gunter 1945, Harris and Rose 1968, Cornelius 1984).

**Life Mode**

Eggs and yolk sac larvae are carried in mouths of males, but are demersal if dropped (Gunter 1947). Juveniles and adults are demersal and predominantly nocturnal (Darnell 1958, Harris and Rose 1968, Hoese et al. 1968, Zimmerman 1969, Diener et al. 1974, Dugas 1975, Steele 1984, Steele 1985, DeLancey 1989, Sogard et al. 1989) with some diurnal activity, which can possibly be attributed to differences in life cycle stages or seasonal variation (Hoese et al. 1968, Moore et al. 1970). In areas of the Gulf of Mexico with pronounced tidal fluctuations, activity associated with high tides has been noted (Sogard et al. 1989). It is often found in schools (Gunter 1938, Benson 1982) which may be formed and maintained by specific sounds it produces (Tavolga 1962).

**Habitat**

Type: Eggs and yolk sac larvae are carried in the mouths of adult males usually in shallow oligohaline to mesohaline waters of bays, lagoons, or Gulf inlets (Lee 1937, Gunter 1947, Ward 1957, Zimmerman 1969, Bechtel and Copeland 1970, Bryan 1971). Juveniles are collected from fresh to euhaline salinities in waters 0.6 to 3.0 m in depth (Miller 1965, Swingle 1971, Dunham 1972). They are apparently more numerous than adults in waters of low salinity (Gunter 1947). Adults are taken from fresh to hypersaline waters. They have been collected at depths from 0.6 to 91.4 m, but principally from 4 to 7 m (Lee 1937, Gunter 1947, Hildebrand 1954, Simmons 1957, Hoese 1960, Miller 1965, Perry 1970, Perret et al. 1971, Swingle 1971, Dunham 1972, Franks et al. 1972, Swift et al. 1977, Benson 1982, Cornelius 1984). They prefer warm waters in shallow grassy areas of bays and the Gulf (Lee 1937, Miles 1949, Hellier 1962, Miller 1965, Zimmerman 1969, Franks et al. 1972, Chittenden and McEachron 1976, Hoese and Moore 1977, Benson 1982, Cornelius 1984), but occasionally enter freshwater or brackish rivers and creeks (Swift et al. 1977, Lee et al. 1980, Loftus and Kushlan 1987).

Substrate: Juveniles and adults have mostly been found over bottoms of mud, oyster beds, sand, shell, sandy mud, silt, and sand with shell (Lee 1937, Reid 1955, Gunter and Hall 1965, Miller 1965, Swingle 1971). Juveniles have been reported not to use seagrass beds (Zimmerman 1969), although adults have been found in areas with seagrass and detritus substrates.

Physical/Chemical Characteristics:
Temperature - Eggs and Larvae: Eggs have been observed in both laboratory and field studies over a temperature range of 28.0° to 34.0°C (Gunter 1945, Ward 1957, Bryan 1971, Perret et al. 1971, Wang and Raney 1971, Christmas and Waller 1973). Yolk sac larvae have been observed in the field from 15.0° to 34.9°C (Gunter 1945, Christmas and Waller 1973, Tarver and Savoie 1976).

Temperature - Juveniles and Adults: Both juveniles and adults have been observed in the field from 5.0° to 39.0°C (Hellier 1962, Miller 1965, Perret et al. 1971, Swingle 1971, Wang and Raney 1971, Dunham 1972, Franks et al. 1972, Christmas and Waller 1973, Gallaway and Strawn 1974, Perret and Caillouet 1974, Juneau 1975, Tarver and Savoie 1976, Barrett et al. 1978, Benson 1982). The maximum acceptable temperature is probably 37.0°C, with 39.0°C being close to the upper lethal limit for this species (Gallaway and Strawn 1974). The preferred temperature range appears to be 19.0° to 25.0°C (Benson 1982).

Salinity - Eggs and Larvae: Eggs have been observed in both laboratory and field studies in salinities ranging from 1.8 to 36.4‰ (Gunter 1945, Ward 1957, Bryan 1971, Perret et al. 1971, Wang and Raney 1971, Christmas and Waller 1973). Yolk sac larvae have been collected from brooding males in salinities ranging from 2.0 to 36.0‰ (Bryan 1971, Perret et al. 1971, Wang and Raney 1971, Christmas and Waller 1973, Cornelius 1984).

Salinity - Juveniles and Adults: Free swimming juveniles have been collected from 0 to 56‰ salinity. They are reported to prefer <10‰ (Perret et al. 1971, Wang and Raney 1971, Christmas and Waller 1973, Cornelius 1984). Adults are euryhaline, and are common from 0.0 to 45‰ (Gunter 1945, Gunter 1947, Gunter 1956, Simmons 1957, Hoese 1960, Hellier 1962, Miller 1965, Bryan 1971, Perret 1971, Swingle 1971, Dunham 1972, Frank et al. 1972, Christmas and Waller 1973, Perret and Caillouet 1974, Swingle and Bland 1974, Juneau 1975, Tarver and Savoie 1976, Swift et al. 1977, Barrett et al. 1978, Cornelius 1984), but occur in salinities as high as 60‰ (Simmons 1957). They have been reported to show some preference for 15.0 to 30.0‰ salinities, and are increasingly less common below 15‰ (Gunter 1945, Perret et al. 1971, Swingle 1971, Franks et al. 1972, Christmas and Waller 1973, Swingle and Bland 1974).

Dissolved Oxygen: The hardhead catfish has been collected in waters with a dissolved oxygen (DO) content range of 2.7 to 11.1 parts per million (ppm) (Bryan 1971, Barrett et al. 1978). It is sometimes found in habitats characterized by low DO (Benson 1982).

Movements and Migrations: The hardhead catfish generally decreases in abundance in bays and estuaries along the northern Gulf of Mexico and Texas coast during fall and winter as it moves to deeper waters of the Gulf or sometimes within an estuary system to overwinter. It then returns to shallows during spring and summer (Gunter 1945, Miller 1965, Swingle 1971, Franks et al. 1972, Landry and Strawn 1973, Steele 1985). Older age class fish are reported to migrate while many of the younger ones remain in the bays (Swingle 1971). Migration to the Gulf can begin as early as September with the lowest numbers in bay systems occurring from November to February (Swingle 1971, Wagner 1973). Abundance increases with temperature (Wagner 1973, Tarver and Savoie 1976) with returns to the bays and estuaries beginning from March to April. Peak abundance is observed from April and May to as late as October along with a high influx of young-of-the-year fish (Chambers and Sparks 1959, Arnold et al. 1960, Hellier 1962, Hoese et al. 1968, Zimmerman 1969, Perret et al. 1971, Christmas and Waller 1973, Wagner 1973, Perret and Caillouet 1974, Juneau 1975, Chittenden and McEachron 1976, Juneau and Pollard 1981, Sheridan 1983, Cornelius 1984). Migration may be triggered by photoperiod (Steele 1984, Steele 1985).

**Reproduction**
Mode: This species has separate male and female sexes (gonochoristic), and fertilization occurs externally. Fertilized eggs and post-hatch larvae are mouthbrooded by adult males.

Spawning: In the Gulf of Mexico, spawning takes place from May to September in waters 0.6 to 1.2 m deep. It occurs in shallow waters of secondary and primary bays, and Gulf inlets (Lee 1937, Gunter 1945, Gunter 1947, Reid 1955, Ward 1957, Kelley 1965, Bechtel and Copeland 1970, Bryan 1971, Wagner 1973). Spawning may also occur in nearshore areas of the Gulf of Mexico. Although no spawning has been observed in this area, ripe females with large ovarian eggs have been taken there in 21.9 to 27.4 m depths during July (Hildebrand 1954). Eight young with yolk sacs whose total lengths (TL) were approximately 45 mm were collected in the surf on Galveston Island in July (Pattillo pers. observ.). Furthermore, the absence of adults has been noted in some inshore areas during the spawning season (Springer and Woodburn 1960, Dugas 1970).

Spawning females have slightly everted hemorrhagic genital openings (Gunter 1947), and enlarged pelvic fins which may serve to enhance fertilization (Lee 1937). Females with enlarging pelvic fins are seen as early as March and through July and do not totally disappear until after October (Gunter 1945). Motile sperm in males has been noted from early March until the middle of July (Ward 1957). It has been suggested that eggs are initially deposited in sandy depressions. The males fertilize the eggs and then pick them up into their mouths to brood them (Gunter 1947, Jones et al. 1978). Brooding males have enlarged branchial and buccal cavities to accommodate eggs or larvae, and their mouths are hemorrhagic in appearance (Lee 1937, Reid 1955, Zimmerman 1969). Brooding males are observed from May to August (Lee 1937, Gunter 1945, Gunter 1947, Reid 1955, Breuer 1957, Zimmerman 1969, Dugas 1970, Bryan 1971, Christmas and Waller 1973, Swift et al. 1977). The numbers of eggs or larvae reported found in brood males range from 1 to 48 and do not appear to be related to the length of the male (Lee 1937, Gunter 1945, Gunter 1947, Reid 1955, Reid 1957). Males do not feed during the brooding period which lasts about 60 days (Lee 1937, Gunter 1947, Jones et al. 1978).

Fecundity: Females produce 14 to 64 mature ova each season, along with numerous small, nonfunctional eggs. The left ovary is slightly larger and typically has 3 to 6 more eggs than the right (Lee 1937, Gunter 1945, Gunter 1947, Reid 1955, Ward 1957, Jones et al. 1978). Females may spawn more than once a season (Gunter 1945).

**Growth and Development**

Egg Size and Embryonic Development: Eggs are demersal. Ripe ovarian eggs are greenish, slightly oval or elliptical, and measure 12-19 mm in diameter (Lee 1937, Gunter 1947, Reid 1955, Ward 1957, Jones et al. 1978). Many small nonfunctional eggs are attached to ripe eggs and to each other by a thin, colorless, adhesive film that is lost as development proceeds. Non-functional eggs may serve as food for males that fast while brooding (Gunter 1947, Ward 1957). Eggs reach the gastrula stage after about 29 hours, and hatching probably occurs in about 30 days (Ward 1957, Jones et al. 1978).

Age and Size of Larvae: Hatching size ranges from 29 to 45 mm TL and occurs primarily in June (Bryan 1971, Gallaway and Strawn 1974, Cornelius 1984). The duration of the larval stage ranges from about 2 to 4 weeks in the wild and up to 55 days under laboratory conditions (Jones et al. 1978). Although mouth brooded young are considered to be in the larval stage, their fin ray complement is complete before yolk absorption, and therefore, a true larval stage is not considered to exist (Jones et al. 1978). The yolk supply is used up by 50 mm TL (Gunter 1945).

Juvenile Size Range: Juveniles are released by male parents from June to August (Swingle 1971, Christmas and Waller 1973, Gallaway and Strawn 1974). The standard length (SL) of juveniles when released ranges from 33 to 58 mm (Gallaway and Strawn 1974) and 41 to 62 mm TL (Gunter 1945, Swingle 1971, Christmas and Waller 1973). Juveniles in the wild have been observed to grow 10 mm/month from July to October; however, cooler water temperatures drastically reduce the growth rate during winter months (Christmas and Waller 1973).

Age and Size of Adults: Minimum sizes noted for sexually mature adults are 135 mm TL and 126 SL for females, and 142 mm SL and 201 mm TL for brood males (Lee 1937, Gunter 1947). Maximum reported sizes are 635 mm TL and 330 mm SL (Reid 1955, Barrett et al. 1978) with average sizes of 110 mm TL and fork lengths (FL) of 100 to 160 mm (Perret et al. 1971, Chittenden and McEachron 1976). Adults rarely exceed 1.154 kg in weight (Gallaway and Strawn 1974). The average life span is 2 to 3 years (Swingle 1971, Chittenden and McEachron 1976).

**Food and Feeding**

Trophic mode: This species is carnivorous throughout its development. Both juveniles and adults are opportunistic, nocturnal bottom feeders utilizing a wide range of feeding modes such as scavenging, carnivory, and ectoparasitism (Miles 1949, Darnell 1958, Hildebrand 1958, Hellier 1962, Hoese 1966, Harris and Rose 1968, Odum 1971, Diener et al. 1974, Dugas 1975, Benson 1982).

Food Items: The hardhead catfish feeds primarily on crustaceans (shrimp and crabs), and insects. Molluscs are also an important diet item. This species may pass through three feeding stages in its development: zooplankton, especially copepods, are most important for individuals <100 mm TL; benthic micro-invertebrates are most important for individuals between 100 and 200 mm TL; crabs and fishes gradually assume importance in fish >200 mm TL (Darnell 1958). Specific diet items that have been reported include: bottom debris and detritus; plant tissue, algae, polychaetes, gastropods, bivalves (*Rangia cuneata* and *Congeria leucophaeta*), ostracods, isopods, copepods, cirripedia, amphipods, mysids, penaeid shrimp including brown shrimp and pink shrimp, grass shrimp, blue crabs, xanthid (mud) crabs, insects, arachnids, menhaden, anchovies, silversides, mullets, juvenile hardhead catfish, various eggs and cysts, hermit crabs, nudibranchs, fish bones, and scales actively taken from living fish (Gunter 1945, Miles 1949, Reid 1955, Darnell 1958, Hellier 1962, Hoese 1966, Harris and Rose 1968, Hildebrand 1958, Diener et al. 1974, Hoese and Moore 1977, Swift et al. 1977, Levine 1980). In addition, hardhead catfish feeding in the surf zone of South Carolina have been found to consume retantians, mole crabs, and isopods (DeLancey 1989).

**Biological Interactions**

Predation: The hardhead catfish is not a major forage species (Fontenot and Rogillio 1970). It has been reported as prey for longnose gar, cobia, bull shark, jewfish, ladyfish, spotted seatrout, and red drum (Gunter 1945, Miles 1949, Darnell 1961, Branstetter 1981).

Factors Influencing Populations: Studies have demonstrated that sounds produced by the hardhead catfish could enable it to avoid obstructions, and probably predators, at close range. These sounds may also be used to communicate during breeding and nocturnal schooling (Breder 1968, Tavolga 1962, 1971, 1977). Nematodes have been observed to parasitize hardhead catfish in blister-like swellings under the skin of the caudal region (Gunter 1945).

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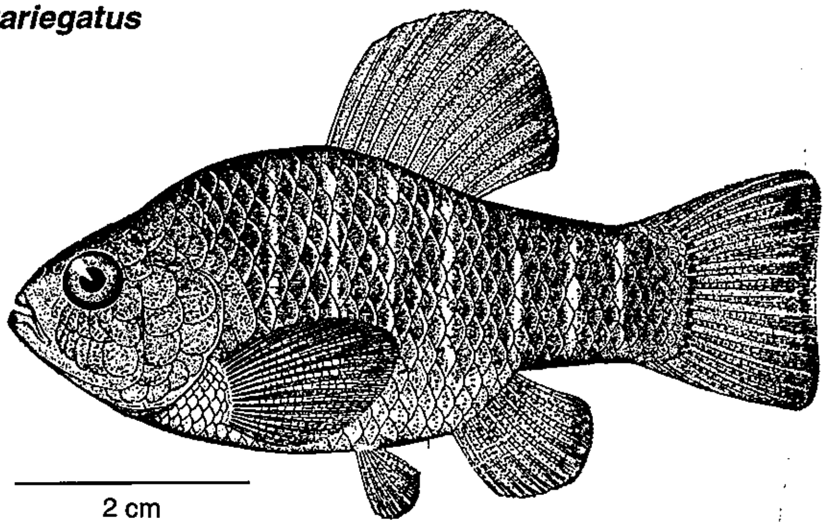
## Sheepshead minnow

***Cyprinodon variegatus***
**Adult**




(from Jordan 1925)

**Common Name:** sheepshead minnow
**Scientific Name:** *Cyprinodon variegatus*
**Other Common Names:** Variegated minnow (Hildebrand 1919); sheepshead killifish (Harrington and Harrington 1961); sheepshead pupfish (Blair et al. 1968); broad killifish, and chubby (Breuer 1957).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Atheriniformes
Family: Cyprinodontidae

### Value

Commercial: This fish has some commercial value as bait (Simpson and Gunter 1956, Perschbacher and Strawn 1986), but little information is available on its use.

Recreational: This species' recreational value is limited to its use as bait by anglers, and as a forage for game fish species. In addition, it is occasionally kept as an aquarium fish.

Indicator of Environmental Stress: The sheepshead minnow is used extensively as a bioassay organism by U.S. Environmental Protection Agency (EPA) and others for acute, partial-chronic, and chronic bioassays in order to set water quality standards. Testing is primarily for effects of organochlorides and organophosphorus compounds on the estuarine community, but this species is also useful in the evaluation of the hepatocarcinogenic risks of chemicals in contaminated coastal waters (Schimmel et al. 1974, Schimmel and Hansen 1974, Goodman et al. 1979, Karara and Hayton 1984, Couch and Courtney 1987, Hale 1989, Hutchinson and Williams 1989, Miller et al. 1990).

Ecological: The sheepshead minnow and other cyprinodontids are important in the control of salt water mosquitoes (Hildebrand 1919, Harrington and Harrington 1961) and also in the export of energy from the marsh by serving as food for birds and larger fish (Hildebrand 1919, Simmons 1957, Perschbacher and Strawn 1986). Burrowing behavior by this and other species of marsh fish during cold weather may adversely affect nesting success of wading birds by making these fish less available to avian predation (Frederick and Loftus 1993). The sheepshead minnow is able to thrive in marginal shallow water habitats, and therefore utilizes areas devoid of other fish species (Shipp 1986).

### Range

Overall: The range for this species extends along the Atlantic coast, from Maine to Yucatan, Mexico, and throughout the West Indies to northern South America (Blair et al. 1968, Hoese and Moore 1977, Hardy 1978, Lee et al. 1980).

Within Study Area: Within U.S. Gulf of Mexico estuaries, this fish can be found from the Rio Grande, Texas, to Florida Bay, Florida (Table 5.22) (Odum and Caldwell 1955, Springer and Woodburn 1960, Tabb and Manning 1961, Finucane 1966, Moe et al. 1966, Blair et al. 1968, Wang and Raney 1971, Hoese and Moore 1977, Hardy 1978, Lee et al. 1980).

### Life Mode

Eggs are demersal (Kuntz 1914, Schimmel and Hansen 1974, Hardy 1978). Larvae, juveniles, and adults are markedly diurnal (Breder 1959, Ruebsamen 1972). They have been observed to school, especially when frightened (Hildebrand and Schroeder 1928, Martin

Table 5.22. Relative abundance of sheepshead minnow in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ◉ | ○ | ◉ | ○ | ○ |
| Ten Thousand Islands | ○ | ○ | ○ | ○ | ○ |
| Caloosahatchee River | ○ | ○ | ○ | ○ | ○ |
| Charlotte Harbor | ○ | ○ | ○ | ○ | ○ |
| Tampa Bay | ● | ◉ | ● | ◉ | ◉ |
| Suwannee River | ● | ● | ● | ● | ● |
| Apalachee Bay | ● | ● | ● | ● | ● |
| Apalachicola Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| St. Andrew Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Choctawhatchee Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Pensacola Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Perdido Bay | ○ | ○ | ○ | ○ | ○ |
| Mobile Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Mississippi Sound | ◉ | ○ | ○ | ○ | ○ |
| Lake Borgne | ○ | ○ | ○ | ○ | ○ |
| Lake Pontchartrain | ○ | ○ | ○ | ○ | ○ |
| Breton/Chandeleur Sounds | ○ | ○ | ○ | ○ | ○ |
| Mississippi River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Barataria Bay | ● | ◉ | ◉ | ◉ | ◉ |
| Terrebonne/Timbalier Bays | ○ | ○ | ○ | ○ | ○ |
| Atchafalaya/Vermilion Bays | ○ | ○ | ◉ | ○ | ○ |
| Calcasieu Lake | ○ | ○ | ◉ | ○ | ○ |
| Sabine Lake | ◉ | ◉ | ◉ | ◉ | ◉ |
| Galveston Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Brazos River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Matagorda Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| San Antonio Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Aransas Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Corpus Christi Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Laguna Madre | ● | ● | ● | ● | ● |
| Baffin Bay | ◉ | ◉ | ● | ◉ | ◉ |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

1972), and are demersal in shallow coastal and inland waters (Reid 1955, Harrington and Harrington 1961, Springer and Woodburn 1960, Tabb and Manning 1961, Peterson 1990).

**Habitat**

Type: All life stages are estuarine and are restricted to bays and coastal inland areas, preferring quiet, shallow waters. They are found in salt marshes, sloughs, coves, bays, creeks, canals, and ditches (Hildebrand and Schroeder 1928, Simpson and Gunter 1956, Breuer 1957, Gunter 1958, Gunter 1967, Strawn and Dunn 1967, Franks 1970, Martin 1972, Swift et al. 1977, Loftus and Kushlan 1987). Sheepshead minnows are uncommon in heavily vegetated marsh areas (Loftus and Kushlan 1987). Larvae often occupy the water's edge while larger individuals (7 mm) may stay on the bottom (Ward and Armstrong 1980). This fish is generally found in depths ranging from 0-1.5 m (Raney et al. 1953, Phillips and Springer 1960).

Substrate: All life stages occur over bottoms areas where vegetation is generally, but not strictly, absent. Bottoms can consist of rock, sand, mud, detritus mud, or mud with shell fragments (Reid 1955, Simpson and Gunter 1956, Franks 1970, Martin 1972, Swift et al. 1977, Loftus and Kushlan 1987), occasionally with turtle grass, shoal grass, or algae present (Hudson et al. 1970).

Physical/Chemical Characteristics:

Temperature - Eggs: Egg development has been observed to occur at 17.4-27.5°C (Renfro 1960) and >26°C (Schimmel and Hansen 1974). Optimal development occurs at 22.8-28.9°C (Ward and Armstrong 1980).

Temperature - Larvae, Juveniles, and Adults: These life stages are all eurythermal. Their reported temperature range in Texas is 8.8-34.9°C (Gunter 1945, Simmons 1957, Strawn and Dunn 1967, Pineda 1975), 5.0-33.5°C in Mississippi (Christmas and Waller 1973; Franks 1970), and 7.2-43.0°C in Florida (Reid 1954, Odum and Caldwell 1955, Kilby 1955, Phillips and Springer 1960, Harrington and Harrington 1961, Hudson et al. 1970, Wang and Raney 1971, Subrahmanyam and Drake 1975). The sheepshead minnow has been observed to be resistant to near freezing conditions, at least for short periods (Gunter and Hildebrand 1951, Simpson and Gunter 1956). Laboratory and field observations found that it begins burrowing into the substrate between 7° and 9° C possibly to escape predation (Loftus and Kushlan 1987, Frederick and Loftus 1993).

Salinity: The sheepshead minnow is a euryhaline species recorded from freshwater to hypersaline conditions in all life stages. Observations suggest a preference for salinities of 10-25.0‰ and 21.0-30.0‰, being less common above this range than below (Gunter 1945, Gunter 1950, Reid 1954, Kilby 1955, Odum and Caldwell 1955, Phillips and Springer 1960, Tabb and Manning 1961, Franks 1970, Hudson et al. 1970, Swingle 1971, Wang and Raney 1971, Martin 1972, Christmas and Waller 1973, Pineda 1975, Subrahmanyam and Drake 1975, Swift et al. 1977, Cornelius 1984, Nordlie 1985). It has been collected from an overall salinity range of 0-142.4‰. The high extreme of this range is probably very close to the upper tolerance limit for this species (Gunter 1945, Simpson and Gunter 1956, Simmons 1957, Renfro 1960, Hoese 1960, Gunter 1967, Martin 1972, Ward and Armstrong 1980, Nordlie 1985). However, it rarely invades salinities higher than 80‰, possibly due to the lack of food at such high salinities (Hildebrand 1957). Environmental factors experienced during growth and development may affect the ability of different populations to withstand salinity variations (Martin 1968).

Dissolved Oxygen: The sheepshead minnow appears to have a strong tolerance of hypoxia (Peterson 1990). It has been found in Chesapeake Bay in waters with a dissolved oxygen (DO) content ranging from 1 to 6 ppm, and 20 to 90% saturation (De Silva et al. 1962). It has also been taken from anoxic waters where the DO content ranged from 0 to 0.81 ppm (Odum and Caldwell 1955). "Obligate gulping" of air is believed to be used in order to relieve oxygen stress.

Movements and Migrations: This species remains in estuaries throughout the year (Rogers and Herke 1985). Observed movements appear to be influenced by seasonal fluctuations in temperature. As temperatures begin to drop in the fall there is a general movement to warmer, slightly deeper waters. It has been noted that at this time individuals can be taken by trawls in these deeper waters where none were present during warmer months (Gunter 1945, Simpson and Gunter 1956, Breuer 1957, Springer and Woodburn 1960).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic), with equal (or nearly so) sex ratios (Hildebrand 1919, Raney et al. 1953, Warlen 1964). Fertilization is external.

Spawning: This species has an extended spawning season lasting from February to October and probably throughout the year in warmer waters (Kuntz 1914, Hildebrand 1919, Gunter 1950, Kilby 1955, Raney et al. 1953, Martin 1972, Ruebsamen 1972, DeVlaming et al. 1978). Ripe females have been collected in water temperatures ranging from 15 to 28.5°C (Ruebsamen 1972). Drops in salinity may initiate spawning activity (Martin 1972). Spawning can occur at depths of 2.5-61 cm in shallow arms of small bays, large tide pools, mangrove lagoons, roadside ditches, and pools in shallow, gently flowing streams over bottoms of sand, black silt, or mud. Males occupy territories up to 0.3-0.6 m in diameter and may or may not construct nest pits. Pits, when constructed, are over sand, gravel, or soft mud bottoms with a detritus overlay, and are 10-15 cm in diameter, 2.5-3.8 cm deep, and are centrally located in well groomed, oval shaped territories. This territory is defended by the male against all but ripe females. Spawning may take place within or outside of the territories, but not usually within the nest pit. Spawning territories are typically situated adjacent to banks or up to 3 m from shore and are usually associated with submerged logs or rocks. The density of territories may approach 100 per 0.9 $m^2$ area (Raney et al. 1953, Simpson and Gunter 1956, Hardy 1978, Ward and Armstrong 1980).

Fecundity: Sheepshead minnows are fractional spawners. Fecundity varies with each spawn and each female. Single females spawn a number of times during a single season at intervals of 1-7 days with an average of 4 spawnings per nest entry, and deposit 1-3 eggs per spawning (Kuntz 1914, Hildebrand 1919, Hardy 1978). Spawning throughout the year is possible in southern parts of the range (DeVlaming et al. 1978). In one laboratory study, the number of eggs produced over a 28 day period per female *in vitro* ranged from 2 to 1,028 and averaged 186 (Schimmel and Hansen 1974). Another study reported from 2 to 24 eggs spawned by a single female on thirty occasions from April 9 through August 16 with the possibility that the actual number may have exceeded observations (Hildebrand 1919). The ovary from a single female in this study contained 140 oocytes with at least 50% mature.

**Growth and Development**

Egg Size and Embryonic Development: Eggs are demersal, develop oviparously, and are adhesive or semi-adhesive by means of minute threads which stick to plants, the sides of aquaria, each other, and the bottom substrate. Eggs are spherical in form (1.0-1.73 mm in diameter), yellowish in color, and highly translucent. The egg membrane is thick and heavy with a visible perivitelline space between it and the vitelline membrane. Small groups of minute oil globules are scattered over the surface of the yolk sphere that normally rests at the upper pole. Incubation time can vary from 4-12 days: 12 days at 17.4-25.5°C and 110‰ salinity; 5-6 days at laboratory temperature; 5 days at 30°C; 4-5 days at 28°C and 30‰ salinity. Hatching typically occurs in spring and summer (Kuntz 1914, Hildebrand 1919, Hubbs and Drewry 1959, Renfro

1960, Schimmel and Hansen 1974, Hardy 1978).

Age and Size of Larvae: Newly hatched larvae have a total length (TL) of 4 mm. The yolk is relatively large, and the dorsal and ventral fin folds are continuous. Larvae are slightly yellowish in color and the posterior half of their body is marked by lighter and darker vertical bands. At five days after hatching the yolk is almost completely absorbed and larvae are ≥5 mm TL. The general color is still yellowish with vertical bands slightly more conspicuous. On the sixth day, with the larvae averaging 8 mm in length and about 4 mg in weight, they begin active free swimming (Usher and Bengtson 1981). At 9 mm many adult characters are apparent. The vertical bands are present, but not fully developed. Individuals are considered juveniles beginning at 12 mm (Kuntz 1914, Hildebrand 1919, Hildebrand and Schroeder 1928, Schimmel and Hansen 1974).

Juvenile Size Range: During the juvenile life stage, the back becomes markedly elevated, the body depth proportionally greater, and the caudal fin more rounded than in the adult. Coloration is quite characteristic, although the general color is lighter in the adult. Juveniles reach maturity *in vitro* at 3 months with sex dichromatism and ripe females occurring at 27 mm (Kuntz 1914, Schimmel and Hansen 1974). A field study in Louisiana observed growth to be about 5 mm/month from March through October (Ruebsamen 1972).

Age and Size of Adults: Reported size averages for each sex in Texas are 45.0 mm TL for males, and 46.5 mm TL for females (Simpson and Gunter 1956). The largest published size is 93 mm (Gunter 1945).

**Food and Feeding**

Trophic Mode: The sheepshead minnow is a primary consumer, and is often termed herbivorous, detritivorous, and, infrequently, larvivorous and omnivorous.

Food Items: Diet principally consists of plant material, diatoms and other algae, detritus, amphipods, copepods, and mosquito larvae and pupae. The remains of insects, fish, sponge, annelid fragments, and pelecypods have also been reported. Sand and mud are also conspicuous stomach contents, suggesting benthic feeding (Hildebrand and Schroeder 1928, Gunter 1950, Simpson and Gunter 1956, Springer and Woodburn 1960, Harrington and Harrington 1961, Martin 1970, Odum 1971, Ruebsamen 1972, Schimmel and Hansen 1974, Subrahmanyam and Drake 1975, Levine 1980, Perschbacher and Strawn 1986).

**Biological Interactions**

Predation: Known fish predators include spotted seatrout, Atlantic croaker, and red drum (Gunter 1945, Darnell 1958). Because they often occupy shallow water marsh habitat, sheepshead minnows are prey for several species of wading birds (Frederick and Loftus 1993).

Factors Influencing Populations: This species has the ability to tolerate a broad range of environmental parameters, allowing it to survive under extreme conditions in marginal shallow water habitats that may be devoid of other fish species (Shipp 1986). The onset of cooler water temperatures can initiate burrowing or movement to deeper, warmer waters during the fall and winter.

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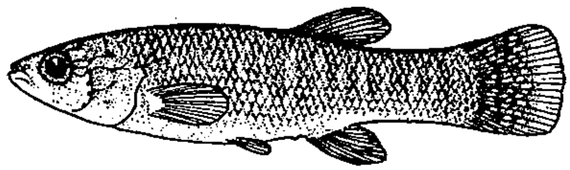
# Gulf killifish

***Fundulus grandis***
**Adult**




(from Eddy 1969)

**Common Name**: gulf killifish
**Scientific Name**: *Fundulus grandis*
**Other Common Names**: Chub, finger mullet, top minnow, bullminnow, mudminnow, mudfish (Gunter 1945, Hoese and Moore 1977, Waas et al. 1983).
**Classification** (Rosen 1964, Rosen and Patterson 1969, Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Atheriniformes |
| Family: | Cyprinodontidae |

### Value

Commercial: This species has some commercial value as a live bait fish. Supplies are derived entirely from wild populations where they are trapped or seined. Fish have been reported to sell at $0.65 per dozen (Waas et al. 1983), but total dollar value of this industry is unknown since, due to its limited size, no statistics are available (Simpson and Gunter 1956, Hoese and Moore 1977, Perschbacher and Strawn 1986, Waas and Strawn 1983). Several studies have examined the feasibility of commercial production of gulf killifish and found it could be economically profitable (Trimble et al. 1981, Tatum et al. 1982, Waas et al. 1983, MacGregor et al. 1983).

Recreational: Gulf killifish are used along the Gulf coast, especially in Alabama, by recreational fishermen who prize this species as a live bait for flounder, red drum, sand seatrout, and spotted seatrout (Simpson and Gunter 1956, Hoese and Moore 1977, Waas et al. 1983, Perschbacher and Strawn 1986).

Indicator of Environmental Stress: The gulf killifish has been used occasionally as an indicator organism (Courtney and Couch 1984). Studies by the U.S. Environmental Protection Agency (EPA) and others suggest it may be a responsive, useful estuarine species in research on the effects of water-soluble fractions of fuel oil, organochlorides, and carcinogens (Ernst and Neff 1977, Courtney and Couch 1984). The National Marine Fisheries Service (NMFS) has used this species to study the effects of acidified water on estuarine life (McFarlane and Livingston 1983, Courtney and Couch 1984). Bioaccumulation of contaminants and liver lesions in gulf killifish have been found to be correlated with substrate contaminant levels in Tampa Bay (McCain et al. 1996).

Ecological: The gulf killifish is important in the export of energy from salt marshes by serving as food for larger fish and piscivorous birds (Jenni 1969, Perschbacher and Strawn 1986), and in the control of salt marsh mosquito populations through predation (Harrington and Harrington 1961).

### Range

Overall: Distribution is continuous from Laguna de Tamiahua, Veracruz, Mexico throughout the Gulf of Mexico and along the Atlantic coast of northeastern Florida up to the Mantangas River. It is also found in Cuba (Rivas 1948, Blair et al. 1968, Kushlan and Lodge 1974, Relyea 1983, Duggins et al. 1989). It is closely related to the mummichog (*F. heteroclitus*) (Duggins et al. 1989, Bernardi and Powers 1995), which occurs in estuaries of the U.S. east coast as far south as Indian River, Florida (Nelson et al. 1991).

Within Study Area: Within U.S. Gulf of Mexico estuaries, the gulf killifish occurs from Florida Bay, Florida to the Rio Grande, Texas (Table 5.23) (Springer and

Table 5.23. Relative abundance of gulf killifish in 31 Gulf of Mexico estuaries (Nelson et al. 1992, Van Hoose pers. comm.).

| *Estuary* | *Life stage* A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ○ | ○ | ○ | ○ | ○ |
| Ten Thousand Islands | ○ | ◉ | ◉ | ◉ | ◉ |
| Caloosahatchee River | ○ | ○ | ○ | ○ | ○ |
| Charlotte Harbor | ◉ | ◉ | ◉ | ◉ | ◉ |
| Tampa Bay | ○ | ○ | ○ | ○ | ○ |
| Suwannee River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Apalachee Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Apalachicola Bay | ○ | ○ | ○ | ○ | ○ |
| St. Andrew Bay | ○ | ○ | ○ | ○ | ○ |
| Choctawhatchee Bay | ○ | ○ | ○ | ○ | ○ |
| Pensacola Bay | ○ | ○ | ○ | ○ | ○ |
| Perdido Bay | ○ | ○ | ○ | ○ | ○ |
| Mobile Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Mississippi Sound | ◉ | ◉ | ◉ | ◉ | ◉ |
| Lake Borgne | ◉ | ○ | ○ | ○ | ○ |
| Lake Pontchartrain | ○ | ○ | ○ | ○ | ○ |
| Breton/Chandeleur Sounds | ○ | ○ | ○ | ○ | ○ |
| Mississippi River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Barataria Bay | ● | ● | ● | ● | ● |
| Terrebonne/Timbalier Bays | ● | ● | ● | ● | ● |
| Atchafalaya/Vermilion Bays | ◉ | ◉ | ◉ | ◉ | ◉ |
| Calcasieu Lake | ○ | ○ | ◉ | ○ | ○ |
| Sabine Lake | ◉ | ◉ | ◉ | ◉ | ◉ |
| Galveston Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Brazos River | ◉ | ○ | ◉ | ○ | ○ |
| Matagorda Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| San Antonio Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Aransas Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Corpus Christi Bay | ○ | ○ | ○ | ○ | ○ |
| Laguna Madre | ◉ | ◉ | ◉ | ◉ | ◉ |
| Baffin Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| | A | S | J | L | E |

Relative abundance:

- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:

- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

Woodburn 1960, Powell et al. 1972, Price and Schlueter 1985, Comp 1985).

**Life Mode**

Eggs are demersal and adhesive (Relyea 1983). Larvae, juveniles, and adults are nektonic in shallow coastal waters 0.6 to 2.0 m in depth (Gunter 1945, Reid 1955, Springer and Woodburn 1960, Franks 1970, Swingle 1971). This species forms schools, with 15 to 20 individuals typical while feeding (Relyea 1983). It has also been observed to congregate in large numbers after dark in shallows near mangroves (Harrington and Harrington 1961).

**Habitat**

Type: All life stages are estuarine residents. They inhabit shallow waters near the shores of oyster bars, tidal ponds, sloughs, salt water creeks, bayous, marsh pools, and coastal inland ponds (Gunter 1945, Gunter 1950, Reid 1955, Simpson and Gunter 1956, Renfro 1960, Gunter 1967, Wagner 1973, Hoese and Moore 1977, Swift et al. 1977). They have been reported from fresh to hypersaline habitats (Simpson and Gunter 1956, Renfro 1960, Swingle 1971).

Substrate: All life stages occur over bottoms where vegetation is generally, but not strictly, absent. Bottoms can consist of hard muddy sand, mud, silt, clay, detritus, or shell, and occasionally with seagrass or algae present. They are also common among mangrove prop roots and emergent marsh vegetation (Gunter 1945, Reid 1955, Simpson and Gunter 1956, Renfro 1960, Springer and Woodburn 1960, Harrington and Harrington 1961, Tabb and Manning 1961, Strawn and Dunn 1967, Franks 1970, Swingle 1971, Swift et al. 1977, Greeley and MacGregor 1983, Thayer et al. 1987).

Physical/Chemical Characteristics:

Temperature - Eggs: Spawning and egg development have been recorded from 4° to 33°C (Hubbs and Drewry 1959, Tatum et al. 1978, Waas and Strawn 1983).

Temperature - Larvae: Larvae have been reared in culture ponds at temperatures ranging from 22° to 35.5°C (Tatum et al. 1978, Waas and Strawn 1983).

Temperature - Juveniles and Adults: Adult and juvenile stage fish are eurythermal, and have been reported from waters ranging from 2° to 34.9°C (Gunter 1945, Franks 1970, Perret et al. 1971, Wang and Raney 1971, Christmas and Waller 1973, Pineda 1975, Tatum et al. 1978, Courtney and Couch 1984). They have been able to withstand prolonged exposure to 38°C *in vitro* (Waas 1982). A lethal low temperature of -1.5°C has been reported by Umminger (1971).

Salinity - Eggs: Egg development has occurred from 0 to 80‰ (Hubbs and Drewry 1959, Tatum et al. 1978, Waas 1982, Perschbacher et al. 1990). The highest hatching percentages occur from 0 to 35‰ (Perschbacher et al. 1990).

Salinity - Larvae: Best larval growth and survival occurs in the 5 to 40‰ range (Perschbacher et al. 1990). Observations indicate a preference for lower salinity waters ranging from 5 to 18.3‰ (Gunter 1950, Gunter 1967, Franks 1970, Swingle 1971, Christmas and Waller 1973, May 1977, Courtney and Couch 1984).

Salinity - Juveniles and Adults: Both adult and juvenile life stages are euryhaline, and have been found in waters with salinities of 0.0 to 76.1‰ (Gunter 1945, Gunter 1950, Simmons 1957, Reid 1954, Hoese 1960, Gunter, 1967, Franks 1970, Swingle 1971, Wang and Raney 1971, Christmas and Waller 1973, Wagner 1973, Pineda 1975, Swift et al. 1977, Tatum et al. 1978).

Movements and Migrations: Reported movements have been associated with feeding. The gulf killifish moves onto marshes with flooding tides to feed, and returns on the outgoing tide to tidal streams (Harrington and Harrington 1961, Perschbacher and Strawn 1986, Perschbacher et al. 1990), and shoreline flats (Reid 1954). One study reports movement to deeper waters during cold weather (May 1977).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic), and fertilization is external (Able and Hata 1984).

Spawning: Spawning occurs in estuaries in shallow water among dense beds of marsh vegetation that are typically flooded only during the bi-weekly high tides (Simmons 1957, Harrington and Harrington 1961, Greeley and MacGregor 1983). Eggs are deposited in clusters on submerged vegetation, plant roots, or on the substrate itself (Waas 1982). Spawning periods appear to be regulated primarily by temperature, with photoperiod, food availability, tides, and circadian mechanisms acting as indirect regulators (Tatum et al. 1978, Waas 1982, MacGregor et al. 1983, Waas and Strawn 1983, Hsiao and Meier 1989). Spawning peaks have been reported in spring, summer, and fall. A shift in spawning season from early spring through summer in the northern and western Gulf to the cooler late fall through spring in south Florida is apparent with recorded seasons in the study area being: April-September in Corpus Christi Pass, Texas; March-June in Copano and Aransas marshes, Texas (Gunter 1945); April-May at Blackjack Peninsula, Texas (Gunter 1950); March-April and August-September in Trinity Bay, Texas (Waas 1982); March-September in Mississippi Sound, Alabama (MacGregor et al. 1983); June-July in Mobile Delta, Alabama (Swingle 1971); late fall through early spring in the Tampa Bay area (Springer and Woodburn 1960); and April-September at Cedar Key, Florida (De Vlaming et al. 1978). Evidence also exists of bimodal and year round spawning in some areas (Gunter 1945, Gunter 1950, Kilby 1955, Swingle 1971, Ruebsamen 1972, Christmas and Waller 1973, Subrahmanyam and Drake 1975, De Vlaming et al. 1978, Waas 1982, Waas and Strawn 1983). Spawning is apparently more prevalent in the evening than in the day (Tatum et al. 1978).

Fecundity: Gulf killifish are fractional spawners and spawn many times per season (De Vlaming et al. 1978, Waas 1982, Waas and Strawn 1983). Usually 10 to 20 eggs are deposited per oviposition, but this species has been found to have the potential to produce as many as 1200 eggs over a spawning season, with the number of eggs correlated with length of the female (Tatum 1978, Waas 1982, Waas and Strawn 1983). Frequency of spawning is unknown and so actual fecundity can not be determined, but one study conducted over a period of 165 days (March through mid-August) showed a daily deposition range of 0.01-1.18 eggs for females averaging 9.6 g (Tatum et al. 1982). Other *Fundulus* species have been found to spawn almost daily (Waas 1982, Waas and Strawn 1983).

**Growth and Development**

Egg Size and Embryonic Development: All growth and development occurs within the estuary. Eggs are pale yellow translucent spheres with vacuoles concentrated at one pole. The color of fertilized eggs changes from yellow to gray as the embryos develop. Eggs are relatively large and range in size from 1.0 to 2.1 mm in diameter, averaging approximately 2.0 mm (Tatum et al. 1978, Tatum et al. 1982, Waas 1982, Waas and Strawn 1983). Embryonic development is oviparous with egg hatching determined by incubation temperature (Courtney and Couch 1984). Hatching has been observed at 9 to 14 days after fertilization at 26 to 31°C and 30‰, 14 to 28 days at 12.5 to 33°C and 5 to 10‰, 15 to 28 days at 12.5‰, and 21 days at 20°C (Hubbs and Drewry 1959, Ernst and Neff 1977, Tatum et al. 1978, Tatum et al. 1982, Waas 1982, Courtney and Couch 1984). Moderate salinities do not appear to affect development and growth. Eggs may be able to withstand exposure to air, an adaptation to fluctuating water levels in coastal marshes (Loftus and Kushlan 1987).

Age and Size of Larvae: Little information is available on the age and size of gulf killifish larvae.

Juvenile Size Range: In a captive rearing study, fish 4 to 6 weeks old had grown to an average weight of 0.1 g in a temperature range of 12.5 to 33°C and salinities of 5 to 10‰ (Tatum et al. 1978). After 52 days, these fish had reached a mean weight and total length of 2.0 g (range: 0.8-7.2 g) and 56 mm (range: 40-84 mm). Temperatures during this period ranged from 22° to 35.5°C, and salinity varied from 11 to 16‰.

Age and Size of Adults: Field studies of gulf killifish show age class I fish range from 18 to 30 mm standard length (SL). Fish in class II average 68 mm SL and attain reproductive maturity during this time when they reach 40 to 50 mm total length (TL). Adults range in size from 40 to 141 mm TL and weigh up to 45.0 g. These fish survive into class III size, but rarely into class IV (Gunter 1945, Gunter 1950, Reid 1955, Simpson and Gunter 1956, Renfro 1960, Springer and Woodburn 1960, Franks 1970, Swingle 1971, Christmas and Waller 1973, Waas 1982, Waas et al. 1983). The gulf killifish is one of the largest species of *Fundulus* occurring in southern Florida coastal marshes (Loftus and Kushlan 1987).

**Food and Feeding**

Trophic Mode: Gulf killifish are opportunistic predators, but they can also feed omnivorously. Feeding is throughout the water column during daylight hours (Ruebsamen 1972, Tatum et al. 1982, Relyea 1983, Rozas and LaSalle 1990). Young fish are detritivores, but become more carnivorous with increased age and size.

Food Items: The diet of the gulf killifish varies with the habitat in which it is feeding (Rozas and LaSalle 1990). Crustaceans and insects form a large portion of this fish's diet. Food items include: mosquitoes, isopods, amphipods, tanadaceans, pelecypods, gastropods, annelids, polychaetes, insects, fishes, crabs, larval grass shrimp, fiddler crabs, hermit crabs, detritus, substrate, vascular plant tissue, and some algae probably as a consequence of amphipod grazing (Simpson and Gunter 1956, Springer and Woodburn 1960, Harrington and Harrington 1961, Odum 1971, Ruebsamen 1972, Subrahmanyam and Drake 1975, May 1977, Levine 1980, Relyea 1983, Perschbacher and Strawn 1986, Rozas and LaSalle 1990).

**Biological Interactions**

Predation: Predators include wading birds and larger piscivorous fishes (Jenni 1969, Perschbacher and Strawn 1986).

Factors Influencing Populations: The incidence of parasitism by *Eimeria funduli* (Protozoa: Eimeriidae) has been reported over a broad area of the range of the gulf killifish (Solangi and Ogle 1981). Although heavily infected fish can have 80 to 85% of both liver and pancreatic tissues replaced by *E. funduli* oocytes, the disease does not appear to cause mortality in infected fish maintained in the laboratory. Growth rate, however, is considerably reduced, which could adversely affect the reproductive potential of local populations, and commercial production of this species for bait (Solangi and Ogle 1981).

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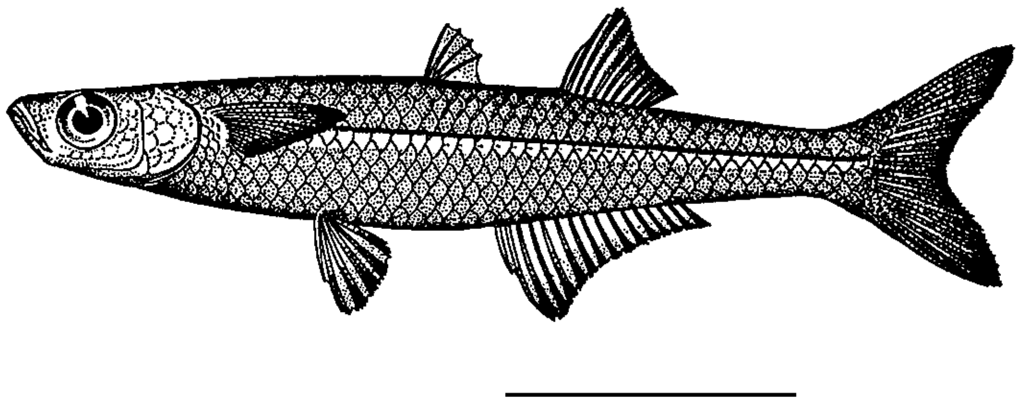
***Menidia* species**
**Adult**



2 cm (from Bigelow and Schroeder 1953)

**Common Name**: silversides
**Scientific Name**: *Menidia* species
**Other Common Names**: inland silverside, tidewater silverside, Mississippi silverside, waxen silverside, glassy silverside, glassminnow, hardhead (Bigelow and Schroeder 1953, Massman 1954, Kilby 1955, Springer and Woodburn 1960, Hubbs et al. 1971, Middaugh et al. 1985, Robins et al. 1991).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Perciformes
Family: Atherinidae

Two species of *Menidia* commonly occur in estuaries of the Gulf of Mexico: the inland silverside (*M. beryllina*), and the tidewater silverside (*Menidia peninsulae*) (Johnson 1975, Chernoff et al. 1981, Robins et al. 1991). These were not recognized as distinct species until fairly recently (Robins et al. 1980, Chernoff et al. 1981). The formerly recognized inland freshwater species, *M. audens*, is now considered synonymous with *M. beryllina* (Lee et al. 1980, Chernoff et al. 1981). Other recognized species in the Gulf of Mexico region include the key silverside (*M. conchorum*) (Duggins et al. 1977, Robins et al. 1991), and Texas silverside (*M. clarkhubbsi*) (Echelle and Mosier 1982, Robins et al. 1991). The Atlantic silverside (*M. menidia*) is found in estuaries of the U.S. east coast (Bigelow and Schroeder 1953, Nelson et al. 1991), but not in the Gulf of Mexico (Lee et al. 1980).

*Menidia beryllina* and *M. peninsulae* can be distinguished by the morphology of the rearward extension of the swim bladder (Echelle and Echelle 1997). This structure is long and transparent in *M. beryllina*, short and opaque in *M. peninsulae*, and intermediate in *M. clarkhubbsi* and hybrid individuals. These species can also be distinguished by the distance between the dorsal and anal fins relative to standard length (Chernoff et al. 1981, Middaugh and Hemmer 1987a).

The *Menidia* species were considered together in *Volume I* of this series (Nelson et al. 1992) because of their ecological similarities, and because many published studies do not completely distinguish between them. In this life history summary, information on individual species is noted where their identity is known. Where species identity is uncertain, information is attributed to "*Menidia*", "*Menidia* species" or "silversides".

**Value**

Commercial: Silversides have little commercial value other than providing forage for commercially important fish, but they are reported to be delicious when properly cooked (Kendall 1902, Garwood 1968, Benson 1982, Ross pers. comm.).

Recreational: Silversides are important forage for game fish, and are also sometimes used as bait (Simmons 1957, Garwood 1968, Benson 1982, Hubbs 1982).

Indicator: Eggs and larvae have been used to study the toxic effects of chlorine as a biocide (Morgan and Prince 1977). Silversides are considered good indicators for oil pollution (Solangi 1980) and have been used as bioassay organisms by the U.S. Environmental Protection Agency (EPA) (Poole 1978).

Ecological: Silversides are among the most abundant nearshore surface fishes. They are secondary con-

Table 5.24. Relative abundance of silversides (*Menidia* species) in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ● | ● | ● | ● | ● |
| Ten Thousand Islands | ◉ | ◉ | ◉ | ◉ | ◉ |
| Caloosahatchee River | ● | ● | ● | ● | ● |
| Charlotte Harbor | ● | ● | ● | ● | ● |
| Tampa Bay | ● | ● | ● | ● | ● |
| Suwannee River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Apalachee Bay | ● | ● | ● | ● | ● |
| Apalachicola Bay | ● | ● | ● | ● | ● |
| St. Andrew Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Choctawhatchee Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Pensacola Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Perdido Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Mobile Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Mississippi Sound | ● | ● | ◉ | ○ | ○ |
| Lake Borgne | ◉ | ◉ | ◉ | ◉ | ◉ |
| Lake Pontchartrain | ◉ | ◉ | ◉ | ◉ | ◉ |
| Breton/Chandeleur Sounds | ○ | ○ | ○ | ○ | ○ |
| Mississippi River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Barataria Bay | ◉ | ◉ | ● | ◉ | ◉ |
| Terrebonne/Timbalier Bays | ◉ | ◉ | ◉ | ◉ | ◉ |
| Atchafalaya/Vermilion Bays | ◉ | ○ | ◉ | ○ | ○ |
| Calcasieu Lake | ◉ | ◉ | ◉ | ◉ | ◉ |
| Sabine Lake | ◉ | ◉ | ◉ | ◉ | ◉ |
| Galveston Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Brazos River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Matagorda Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| San Antonio Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Aransas Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Corpus Christi Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Laguna Madre | ● | ● | ● | ● | ● |
| Baffin Bay | ● | ● | ● | ● | ● |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

sumers, and are important forage fishes for top carnivores in the nearshore area (Simmons 1957, Hellier 1962, Garwood 1968, Shipp 1979, Hubbs 1982, Benson 1982, Shipp 1986). They are considered useful as biological control agents of mosquitoes and gnats (Hubbs et al. 1971, Middaugh et al. 1985).

### Range

Overall: The range of *Menidia beryllina* extends from Quincy, Massachusetts to Vera Cruz, Mexico along the coast and in estuaries, bays and sounds, and in freshwater rivers and impoundments. In inland waters, they are found from the Mississippi Valley to Reelfoot Lake, Tennessee, and the Red and Arkansas River drainages in Oklahoma. *M. beryllina* has been introduced and established in reservoirs in Texas and California (Tilton and White 1964, Martin and Drewry 1978, Lee et al. 1980, Middaugh et al. 1985). *M. peninsulae* occurs from the east coast of Florida to eastern Mexico, in moderate to high salinity estuarine and coastal waters (Johnson 1975).

Within Study Area: Within U.S. Gulf of Mexico estuaries, *Menidia beryllina* occurs from Florida Bay, Florida to the Rio Grande, Texas. They are ubiquitous residents of shallow estuarine waters (Tilton and White 1964, Christmas and Waller 1973, Martin and Drewry 1978, Middaugh et al. 1985) (Table 5.24). *M. peninsulae* has a disjunct distribution in estuaries of the Gulf of Mexico, from Florida to Mississippi, and Texas to Mexico, apparently absent from the lower salinity estuarine waters of Lousiana (Johnson 1975, Chernoff et al. 1981, Middaugh and Hemmer 1984, Middaugh and Hemmer 1987a). The unisexual *M. clarkhubbsi* complex has been described from estuarine waters of Texas (Echelle and Mosier 1982), and is reported to occur from Texas to Alabama (Echelle et al. 1989b). The key silverside, *M. conchorum*, is endemic to the Florida Keys (Duggins et al. 1977).

### Life Mode

*Menidia* eggs are demersal. Larvae, juveniles, and adults are nektonic and pelagic, and form schools (Hildebrand 1922, Kilby 1955, Chambers and Sparks 1959, Arnold et al. 1960, Martin and Drewry 1978, Wurtsbaugh and Li 1985). All stages have diurnal activity, although one Florida study reports feeding occurring primarily at night (Darnell 1958, Zimmerman 1969, Odum 1971, Ruebsamen 1972, Krull 1976, Middaugh et al. 1985, Wurtsbaugh and Li 1985).

### Habitat

Type: Silversides are resident species in estuaries (Wagner 1973). Most specimens are typically collected in the top 30-45 cm of the water column and near vegetated shorelines (Kilby 1955, Breuer 1957, Darnell 1958, Hoese 1965, Wilson and Hubbs 1972, Wagner

1973, Benson 1982). Habitats include lagoons, estuaries, bays, marshes, beach passes, ponds, rivers, canals, and lakes (Gunter 1945, Bailey et al. 1954, Gunter 1958, Arnold et al. 1960, Springer and Woodburn 1960, Hellier 1962, Tilton and White 1964, Hoese 1965, Parker 1965, Perret et al. 1971, Wilson and Hubbs 1972, Christmas and Waller 1973, Wagner 1973, Cornelius 1984, Loftus and Kushlan 1987). Habitat partitioning among *M. beryllina*, *M. peninsulae*, and *M. clarkhubbsi* has been noted in a study in Copano Bay, Texas (Echelle and Echelle 1997). *M. peninsulae* were found primarily in seaward bays and connected tidal pools with mesohaline, polyhaline, and euhaline salinities. *M. beryllina* were predominant in freshwater streams and bays, isolated pools, and tidal creeks with limnetic, oligohaline, and mesohaline salinities. Both species, their hybrids, and *M. clarkhubbsi* co-occured in shallow bays and tidal pools with mesohaline salinities.

Substrate: Little preference for bottom type has been demonstrated for *Menidia* species, with collections made over sand, mud, shell, clay, clay-shell, clay-sand, and silt-clay (Simmons 1957, Hoese and Jones 1963, Swingle 1971, Benson 1982). One report does state abundances are greatest over bottoms with a high sand content and low percentage of organics. Silversides are particularly common near inundated terrestrial plants and aquatic vegetation such as *Thalassia* (Hildebrand 1922, Kilby 1955, Hoese and Jones 1963, Zimmerman 1969, Franks 1970, Fisher 1973, Swingle and Bland 1974), and are often associated with some sort of structure such as islands, piers, and oyster reefs (Benson 1982).

Physical/Chemical Characteristics: *Menidia* species are considered to be eurythermal and euryhaline (Gunter 1956, Renfro 1960, Franks 1970, Middaugh et al. 1985), but temperature and salinity are factors affecting their distribution (Kilby 1955, Renfro 1960, Springer and Woodburn 1960, Swingle 1971). In general, *M. beryllina* is considered to be most abundant at salinities ≤19‰, whereas *M. peninsulae* is found primarily at ≥15‰ (Middaugh et al. 1986).

Temperature - Eggs: Eggs of *Menidia beryllina* have been observed to develop from 13.2° to 34.2°C (Hildebrand 1922, Garwood 1968, Hubbs et al. 1971, Fisher 1973, Hubbs 1982, Middaugh et al. 1985). High survival was recorded from 17.0° to 33.5°C and optimum survival occurred from 20.0° to 25.0°C. Upper lethal limit for eggs is about 35.0°C (Hubbs et al. 1971).

Temperature - Larvae: Larvae of *Menidia beryllina* have been raised under laboratory conditions and collected in the field over a temperature range of 21° ± 1°C to 30° ± 1° (Hildebrand 1922, Garwood 1968, Hubbs et al. 1971, Bengtson 1985).

Temperature - Juveniles: Juvenile *Menidia* have been collected in the wild from 5.0° to 33°C (Garwood 1968, Franks 1970, Perret et al. 1971, Pineda 1975, Bonin 1977). Peaks in numbers have been reported at 26.5° and 21.8°C (Bonin 1977). In one study in Mississippi Sound, temperature ranges in which different juvenile *Menidia* size classes were found are: 26.4° to 28.4°C for fish whose total length (TL) was 14 to 22 mm; 21.0° to 31.8°C for 23 to 36 mm TL; and 21.0° to 32.5°C for 40 to 44 mm TL (Garwood 1968).

Temperature - Adults: Adult *Menidia* sampled in Gulf of Mexico estuaries have been found from 5.0°C to 34.9°C (Chambers and Sparks 1959, Renfro 1960, Franks 1970, Perret et al. 1971, Christmas and Waller 1973, Perret and Caillouet 1974, Pineda 1975, Tarver and Savoie 1976, Barrett et al. 1978, Middaugh et al. 1985)

Salinity - Eggs: Eggs of *Menidia* species have been observed in the field at salinities ranging from 0.0 to 31.5‰ (Fisher 1973, Garwood 1968, Hubbs et al. 1971). One laboratory study of *M. beryllina* (reported as *M. audens*) from Lake Texoma, a freshwater reservoir, noted salinity affecting temperature tolerance limits of eggs: no survival at 100% seawater (33‰); normal range of 17° to 33°C at 25% seawater; 19° to 33° at 50% seawater; and only 22° to 31.3°C at 75% seawater (Hubbs et al. 1971). In other words, *M. beryllina* eggs become more stenothermal as salinity increases. Middaugh et al. (1986) collected adult Menidia from northwest Florida, and compared the survival of *M. beryllina* and *M. peninsulae* embryos incubated at an array of salinities. *M. beryllina* were euryhaline, with 73-78% survival at 5, 15, and 30‰. *M. peninsulae* embryos had 90% hatch at 5‰, but only 65% hatch at 30‰, suggesting that it is the less euryhaline species at this life stage.

Salinity - Larvae: The recorded salinity range for *Menidia* larvae is 0.0 to 30‰, with higher concentrations of larval *M. beryllina* occurring at 2 to 8‰ (Garwood 1968, Martin and Drewry 1978, Bengtson 1985).

Salinity - Juveniles: Juvenile *Menidia* have been collected in the wild from 0.0 to 34.5‰ salinity (Gunter 1945, Gunter 1950, Garwood 1968, Franks 1970, Pineda 1975, Bonin 1977, Martin and Drewry 1978). In Mississippi Sound, juvenile *Menidia* are reported to occur by size class in the following salinities: 3.3 to 19.4‰ for fish 14 to 22 mm TL; 2.2 to 23.8‰ for 23 to 36 mm TL; and 2.2 to 28.3‰ for 40 to 47 mm TL (Garwood 1968).

Salinity - Adults: Adult *Menidia* are reported to be abundant up to 45‰ (Simmons 1957), and present in collections made in hypersaline conditions at 120‰ (Copeland 1967). They have been collected in waters with 0 to 120‰ salinity (Gunter 1945, Gunter 1950, Simmons 1957, Renfro 1960, Copeland 1967, Franks 1970, Perret et al. 1971, Swingle 1971, Christmas and Waller 1973, Perret and Caillouet 1974, Swingle and Bland 1974, Pineda 1975, Tarver and Savoie 1976, Barrett et al. 1978, Cornelius 1984). Reported salinity ranges of occurrence include 5.0 to 9.9‰ (Tarver and Savoie 1976); 0.0 to 4.9‰ and 15.0 to 19.9‰ (Swingle 1971); 10.0 to 24.9‰ (Perret et al. 1971); 21.0 to 30.0‰ (Cornelius 1984); and 22.5‰ or higher (Franks 1970). However, these historical reports of disparate salinity ranges are probably due to different habitat affinities among the now-recognized *Menidia* species. *M. beryllina* is considered to be the more euryhaline species, occurring from fresh to marine salinities, whereas *M. peninsulae* is found primarily from estuarine to marine salinties (Echelle and Mosier 1982). In a study of Copano Bay, Texas, *M. peninsulae* was predominant in seaward bays and connected tidal pools (salinity range 13.5-32.5‰, mean 18.9‰). *M. beryllina* were predominant in freshwater streams and bays (salinity range 0.1-2.3‰, mean 0.8‰), isolated pools (salinity range 2.3-20‰, mean 7.5‰), and tidal creeks (salinity range 3.5-7.8‰, mean 5.1‰). Both species, their hybrids, and *M. clarkhubbsi* co-occured in shallow bays and tidal pools (salinity range 6.0-18.5‰, mean 11.4‰) (Echelle and Echelle 1997).

Dissolved Oxygen and pH: *M. beryllina* can tolerate dissolved oxygen (DO) concentrations as low as 1.7 parts per million (ppm) (Middaugh et al. 1985), but have also been collected at 9.5 and 11.0 ppm DO (Barrett et al. 1978). Collections have been made in a pH range of 7.2 to 9.4 (Middaugh et al. 1985).

Movements and Migrations: Silversides are non-migratory estuarine residents (Benson 1982, Middaugh et al. 1985). Diel inshore and offshore movements are probably related to predator avoidance and feeding (Darnell 1958, Krull 1976, Wurtsbaugh and Li 1985). As juveniles grow, they are reported to move into shallower waters (Darnell 1958).

**Reproduction**

Mode: Spawning of *Menidia* species is by external fertilization of broadcast milt and roe, and egg development is oviparous (Fisher 1973). Sexes of *M. beryllina* and *M. peninsulae* are separate (gonochoristic), but sex ratios in these species may be skewed in response to environmental conditions. In a study near Santa Rosa Island, Florida, *M. peninsulae* spawned during cool conditions (14.1-24.2°C) February through April were 70-94% female, whereas those spawned during warm conditions later in the year were 35-60% female (Middaugh and Hemmer 1987b, Echelle and Echelle 1997). This temperature-dependent expression of sex may be a reproductive adaptation to favor growth of females during optimum conditions, and allow maturation within a year (Middaugh and Hemmer 1987b). Small populations of a unisexual all-female gynogenetic species complex (*M. clarkhubbsi*) have been described from Texas (Echelle and Mosier 1982). These fish produce diploid eggs without genetic recombination, and embryonic development is initiated by spawning with one of the bisexual *Menidia* species, without genetic contribution from the sperm. The resulting progeny are clones of the parental *M. clarkhubbsi* individual. This "species" may have originated from hybrids between *M. beryllina* and a now-extinct progenitor species similar to *M. peninsulae* (Echelle and Echelle 1997). *M. beryllina* x *M. peninsulae* hybrids are known to occur in low frequency in waters where the two species are sympatric, with habitat affinities intermediate to the two parental species. Hermaphroditic individuals have also been reported (Yan 1984).

Spawning: Spawning of *Menidia beryllina* (reported as *M. audens*) occurs during the day in the late morning (Hubbs et al. 1971), and takes place in Gulf of Mexico estuaries in spring and fall as a bimodal peak. Occasional spawning throughout the year has also been reported. Ripe adults usually appear by March, but sometimes as early as February, and are collected throughout the year in some areas. Seasonal peaks usually occur in May to June and September to January (Hildebrand 1922, Gunter 1945, Gunter 1950, Simmons 1957, Hellier 1962, Hoese 1965, Garwood 1968, Swingle 1971, Ruebsamen 1972, Christmas and Waller 1973, Wagner 1973, Gallaway and Strawn 1974, Swingle and Bland 1974, Pineda 1975, Hubbs 1982). Salinity has little effect on spawning condition of *M. beryllina*, which is probably triggered instead by rising temperatures or possibly changes in water levels (Hoese 1965, Garwood 1968, Hubbs 1982, Middaugh et al. 1985). Evidence of spawning was found over a salinity range of 3.6 to 31.5‰ and a temperature range of 15.0° to 32.7°C, but slowed or ceased at 30.0°C (Garwood 1968, Hubbs 1982, Middaugh 1985). Spawning of *M. beryllina* is probably most prevalent in tidal freshwater or brackish water in the upper parts of estuaries (Martin and Drewry 1978), and occurs in shallow waters with gently sloping bottoms having an abundance of rooted aquatic and/or inundated terrestrial plants, tree roots, and dead leaves (Hildebrand 1922, Wilson and Hubbs 1972, Fisher 1973). It has also been reported in a low to medium salinity tidal pass in Louisiana (Sabins and Truesdale 1974). *M. peninsulae* is primarily a nocturnal spawner, and peak spawning activity coincides with interruptions in current velocity (Middaugh and Hemmer 1984). In a study near Santa Rosa Island, Florida, spawning activity of

*M. peninsulae* extended from February to July, with peaks March through June, at temperatures 16.7 to 30.8°C (Middaugh and Hemmer 1987a). Spawning activity peaked during "equatorial tides", when tidal height and current were at their minima, possibly an adaptation to enhance fertilization success. Spawning occurred in shallow water, 10 - 60 cm deep, and spawned eggs adhered to the red algae *Ceramium byssoideum* over rocky substrate (Middaugh and Hemmer 1987a).

Fecundity: Silversides are fractional spawners that spawn several times per season, and sometimes all year (Hildebrand 1922, Hellier 1962, Fisher 1973). Female *Menidia beryllina* in one study deposited 10 to 20 eggs in a single spawning pass, and were not observed to repeatedly broadcast eggs. Females stripped of ripe eggs yielded 10 to 200 eggs per individual (Fisher 1973). Fecundity is size dependent, with average sized females (standard length (SL) 75 mm) producing approximately 835 eggs daily, large females about 2000 eggs, and small females about 200 eggs. Over a spawning period of 91 to 122 days, an average sized *M. beryllina* female has the capacity to produce 75,985 to 101,879 eggs, a large female 132,860 to 178,210 eggs, and a small female 45,000 to 61,000 eggs (Hubbs 1982). Spawners are usually age class-1 fish, but class-0 fish have been found to spawn occasionally (Fisher 1973, Hubbs 1982).

**Growth and Development**

Egg Size and Embryonic Development: Eggs of *Menidia beryllina* are demersal with gelatinous threads that attach to vegetation, other objects, and to each other on or near bottom (Hildebrand 1922, Martin and Drewry 1978). They have a clear yellowish appearance with a large oil globule occupying a central position and variously distributed smaller globules ranging from a few to several (Hildebrand 1922, Hubbs 1982). The chorion has a tuft of 4 to 9 adhesive filaments one of which is enlarged and much longer than the others, about 30 to 50 mm in total length. Eggs are not quite spherical when first spawned and range about 0.75 to 1.0 mm in diameter (Hildebrand 1922, Martin and Drewry 1978). Cleavage is meroblastic and equal with the second cleavage at right angles to the first (Martin and Drewry 1978). Hatching occurs in 10 days at 27.5°C and 5 days in warmer temperatures (Hubbs et al. 1971, Hubbs 1982). Larvae are present through the spring, and in summer and fall months (Martin and Drewry 1978).

Age and Size of Larvae: *Menidia beryllina* larvae are about 3.5-4.0 mm TL at hatching (Hildebrand 1922, Martin and Drewry 1978). They have an oval yolk sac with a single oil globule in the anterior end. In a laboratory feeding experiment, yolk depletion and starvation occurred in 3 to 4 days at 30°C, and 2 to 3 days at 15°C (Hubbs et al. 1971, Martin and Drewry 1978). The body is elongate and slender with an extremely short gut and an anus about 1/4 of way from tip of snout to rear of caudal finfold (Martin and Drewry 1978). They are highly transparent with 3 to 11 melanophores on the dorsal surface of the head, and a cluster above the gut and dorsal surface of the yolk. At 7.8 mm TL, about 15 caudal rays and 8 anal ray bases become visible. The first dorsal fin is rudimentary and other median fins have a full complement of rays tending toward the adult fin shape. The pelvic fins are formed. Larvae are aggregating by 8 to 10 mm TL, and schooling by 11 to 12 mm TL. The first dorsal fin is formed by 11 to 12 mm TL(Martin and Drewry 1978). The end of this stage is at about 11 to 12 mm TL (Garwood 1968, Martin and Drewry 1978).

Juvenile Size Range: In Mississippi Sound, the size range for juvenile stage *Menidia* is about 12 to 49 mm TL (Garwood 1968). Length-frequency data are unreliable for a growth estimate, but one study of *Menidia* in Tampa Bay indicated 5-7 mm per month from June to November, and that early-spawned juveniles grew about 8 mm SL per month from June to September. Lengths of 75 to 85 mm SL were achieved after 1 year of growth (Springer and Woodburn 1960). Winter cold evidently inhibits growth (Martin and Drewry 1978).

Age and Size of Adults: Silversides may reach sexual maturity by 45 mm TL or 33 mm SL (Hellier 1962, Garwood 1968, Martin and Drewry 1978). Males are smaller than females with average sizes of 50.9 and 55.0 mm TL for males and 59.5 and 61.0 mm TL for females being reported (Hildebrand 1922, Gunter 1945). Maturity is usually reached by 1 year, but sometimes as early as 5 months (Martin and Drewry 1978, Hubbs 1982). Weight ranges from 0.1 to 7.5 g for fish 15 to 87 mm SL with a 95 mm TL fish weighing 11.4 g and a 55 mm TL fish weighing 2.84 g (Franks 1970, Barrett et al. 1978). The largest reported size is 125 mm TL (Simmons 1957). The life span *Menidia* is usually one year, with some survivals to 2 years (Gunter 1945, Martin and Drewry 1978, Hubbs 1982). Total length (TL) can be estimated from standard length (SL) for silversides by multiplying SL by 1.2 (Hubbs 1982).

**Food and Feeding**

Trophic Mode: Silversides are carnivorous, secondary consumers feeding mainly during daylight hours especially in the early morning with some additional afternoon feeding by adults (Darnell 1958, Middaugh et al. 1985, Wurtsbaugh and Li 1985). One study of *Menidia beryllina* in Louisiana reports equal feeding intensity both day and night (Ruebsamen 1972). *M. peninsulae* are reported to feed primarily during the day (Middaugh and Hemmer 1984). Trophic partitioning between

*Menidia* species has been noted (Lee et al. 1980, Bengtson 1984, Bengtson 1985).

Food Items: Various larval and adult crustaceans are the predominant food items of *Menidia* (Odum 1971, Levine 1980). Silversides less than 16 mm SL feed primarily on the larval stages of copepods and other crustaceans (Odum 1971). Larval *M. beryllina* have been successfully reared on *Artemia* nauplii, nutritionally similar to known natural foods such as the copepod *Acartia* (Bengtson 1985). Juveniles 15 to 42 mm SL are known to feed on mollusc veliger larvae. Detritus is a major item in small size classes, but is fairly common in larger ones as well, although declining in importance (Darnell 1958, Ruebsamen 1972, Carr and Adams 1973, Diener et al. 1974). Detritus is probably obtained as suspended material rather than from the benthos (Carr and Adams 1973). Isopods and amphipods form the bulk of food in all size classes with isopods and veligers declining in fish larger than 40 to 54 mm TL to be replaced by insects, especially chironomid larvae, pupae and adults (Darnell 1958, Levine 1980). Larger fish also consume more megalops larvae, copepods, and mysids than smaller size classes (Carr and Adams 1973). Schizopods are consumed by all size classes, but mainly by intermediate size fish. Fish form a small but significant diet item (Levine 1980). Fish prey include bay anchovy, gulf menhaden, silversides, and gulf pipefish (*Syngnathus scovelli*). Miscellaneous items consumed include sand, filamentous algae, vascular plant material, rotifers, annelids, ostracods, arachnids, eggs, cysts, and fish remains (Darnell 1958, Ruebsamen 1972, Levine 1980).

**Biological Interactions**

Predation: Silversides are important forage fishes for many commercial and recreational fishes and other top trophic level carnivores (Simmons 1957, Garwood 1968, Hubbs 1982). Reported predators include gar (*Lepisosteus* species), catfish (*Ictalurus* species), hardhead catfish, silversides, spotted seatrout, red drum, white bass (*Morone chrysops*), largemouth bass (*Micropterus salmoides*), and crappie (*Pomoxis* species) (Simmons 1957, Darnell 1958, Garwood 1968, Hubbs et al. 1971, Diener et al. 1974, Hubbs 1982, Rozas and Hackney 1984, Wurtsbaugh and Li 1985). Near Santa Rosa Island, Florida, pinfish have been reported to prey on newly-spawned eggs of *M. peninsulae* adhering to red algae (Middaugh and Hemmer 1987a).

Factors Influencing Populations: Hybridization between *Menidia peninsulae* and *M. menidia* has been reported in northeastern Florida (Johnson 1975), and hybridization between *M. beryllina* and *M. peninsulae* is known to occur in Texas estuaries (Echelle and Echelle 1997). The clonal lineages of the *M. clarkhubbsi* complex may be ephemeral, because of lack of genetic variation and recombination, accumulation of deleterious alleles, and inability to adapt to changing environmental conditions (Echelle and Echelle 1997). However, this asexual life history strategy provides a short-term reproductive advantage, and enables utilization of intermediate habitats. Trophic competition and partitioning has been demonstrated between *M. menidia* and *M. beryllina* in Rhode Island estuaries. The later spawning time and slower growth rate of *M. beryllina* may be an adaptation to the lower zooplankton abundance later in the season (Bengtson 1984, Bengtson 1985). However, *in situ* experiments in Rhode Island suggest that the size-specific survival of *M. beryllina* larvae may depend more on the suite of predators present than on a limited zooplankton forage base (Gleason and Bengtson 1996). The key silverside (*M. conchorum*) is being considered as a candidate species under the federal Endangered Species Act because of its rare status (NMFS 1997, Jordan pers. comm.).

**Personal communications**

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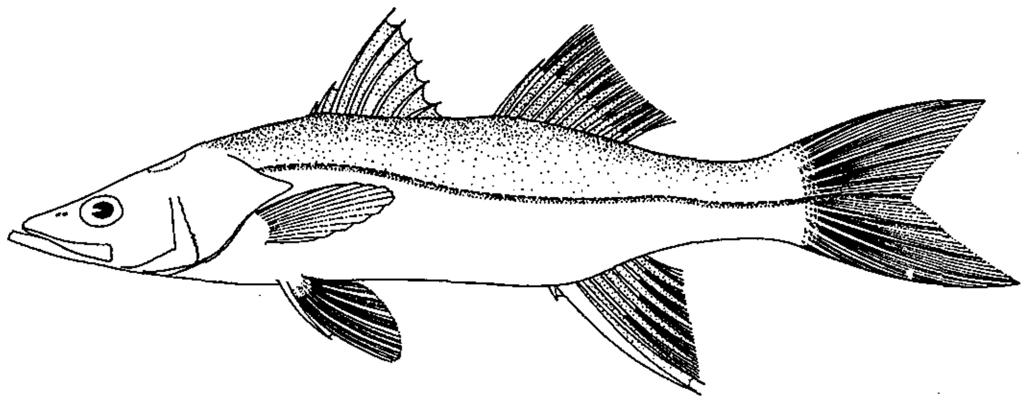
## Common snook

***Centropomus undecimalis***
**Adult**



10 cm (from Fischer 1978)

**Scientific Name**: *Centropomus undecimalis*
**Common Name**: common snook
**Other Common Names**: gulf pike, salt water pike, linesider, snook robalo (Higgins and Lord 1926, Hoese and Moore 1977, Rivas 1986); *crossie blanc* (French), *robalo comun*, *robalo blanco* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Perciformes
Family: Centropomidae

### Value

Commercial: The common snook is harvested throughout much of its range (Hildebrand 1958, Tucker 1986). In the U.S., it was caught commercially on a small scale in Texas and Florida at one time, but declining numbers led to a ban on commercial landings in Florida in 1958, and to its virtual disappearance in Texas with the last commercially landed fish reported there in 1961 (Higgins and Lord 1926, Baughman 1943, Hildebrand 1958, Marshall 1958, Volpe 1959, Tucker 1986, Matlock and Osburn 1987). It is caught and sold mostly fresh in Mexico, Central and South America, and in the Caribbean (Fischer 1977). Harvest is by gill nets, cast nets, and hook and line. The common snook is also considered a possible mariculture species (Roberts 1990).

Recreational: This is a popular gamefish, putting up spectacular fights as well as being good eating (Baughman 1943, Marshall 1958, Volpe 1959, Martin and Shipp 1971, Ager et al. 1976, Hoese and Moore 1977, Tucker et al. 1985, Tucker 1986). The common snook readily accepts natural or artificial bait on hook and line, and is also caught by spearing (Marshall 1958, Ager et al. 1976). Population declines since the 1930's have resulted in reduced catches by anglers along the Gulf coast (Hildebrand 1958, Seaman and Collins 1983, Tucker 1986, Matlock and Osburn 1987). This decline has resulted in it being classified as a species of special concern by the state of Florida (Tucker 1986, Johnson 1987). The Florida Department of Natural Resources maintains a closed season on snook during both the winter and summer months, a bag limit, and a minimum size limit to relieve fishing pressure (Seaman and Collins 1983, Kunneke and Palik 1984, NOAA 1985). All species of *Centropomus* are covered by the Florida regulations (Taylor pers. comm.). In Texas, recreational catches of snook decreased considerably from the 1940's through the 1960's. Catches of snook along the Texas coast currently represent less than 0.1% of the recreational landings (Matlock and Osburn 1987). Texas maintains size limits and bag limits for snook (TPWD 1993).

Indicator of Environmental Stress: Reductions in snook populations may be due in part to environmental alteration and degradation, reduced freshwater discharge to estuaries, sewage and industrial pollution, and insecticides (Marshall 1958, Killam et al. 1992).

Ecological: The common snook is considered a high trophic level carnivore, preying mostly on fish (Springer and Woodburn 1960, Harrington and Harrington 1961, Shafland and Koehl 1979).

### Range

Overall: The common snook is distributed in tropical and subtropical waters from North Carolina to as far south as Rio de Janeiro, Brazil (Marshall 1958, Rivas 1962, Lee et al. 1980, Seaman and Collins 1983). It

Table 5.25. Relative abundance of common snook in 31 Gulf of Mexico estuaries (Nelson et al. 1992, Taylor pers. comm.).

| *Estuary* | *Life stage* A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ○ | | ○ | | |
| Ten Thousand Islands | ◉ | ◉ | ◉ | √ | √ |
| Caloosahatchee River | ○ | | ◉ | ○ | |
| Charlotte Harbor | ◉ | ○ | ◉ | √ | √ |
| Tampa Bay | ◉ | ◉ | ○ | √ | √ |
| Suwannee River | √ | | | | |
| Apalachee Bay | √ | | | | |
| Apalachicola Bay | √ | | | | |
| St. Andrew Bay | √ | | | | |
| Choctawhatchee Bay | √ | | | | |
| Pensacola Bay | √ | | | | |
| Perdido Bay | | | | | |
| Mobile Bay | | | | | |
| Mississippi Sound | | | | | |
| Lake Borgne | | | | | |
| Lake Pontchartrain | | | | | |
| Breton/Chandeleur Sounds | | | | | |
| Mississippi River | | | | | |
| Barataria Bay | √ | | | | |
| Terrebonne/Timbalier Bays | | | | | |
| Atchafalaya/Vermilion Bays | | | | | |
| Calcasieu Lake | | | | | |
| Sabine Lake | | | | | |
| Galveston Bay | √ | | √ | | |
| Brazos River | | | | | |
| Matagorda Bay | √ | | √ | | |
| San Antonio Bay | | | | | |
| Aransas Bay | √ | √ | √ | √ | √ |
| Corpus Christi Bay | √ | √ | √ | √ | √ |
| Laguna Madre | √ | √ | ○ | √ | √ |
| Baffin Bay | | | | | |
| | A | S | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

occurs along the eastern coast of central America, throughout the Caribbean, along the Gulf coast from Mexico to Port Aransas, Texas, and along peninsular Florida from Pensacola Bay to the Mosquito Lagoon area and the St. Johns River (Table 1) (Lunz 1953, Marshall 1958, Yerger 1961, Linton and Rickards 1965, Merriner et al. 1970, Martin and Shipp 1971, Dahlberg 1972, Cooley 1974, Ager et al. 1976, Hoese and Moore 1977, Tucker 1986). Centers of abundance occur in the Caribbean, southwestern Gulf of Mexico, and mangrove belts of southern Florida (Odum 1971, Gilmore et al. 1983, Tucker 1986). Mitochondrial DNA analyses indicate that Caribbean stocks are distinct from Florida stocks (Tringali and Bert 1996).

Within Study Area: The common snook is relatively common along the west coast of Florida as far north as the Homosassa River area (Table 5.25). It is found only occasionally along the northern coast of the Gulf of Mexico (Cooley 1974). In Texas, it is only abundant in the lower Laguna Madre, and is rarely found north of Port Aransas (Baughman 1943, Cooley 1974, Matlock and Osburn 1987). There is one report of a single juvenile captured off Grand Terre Island, Louisiana (Guillory et al. 1985). Mitochondrial DNA analyses indicate that Caribbean stocks are distinct from Florida stocks (Tringali and Bert 1996). Mitochondrial DNA analyses indicate that snook from the Atlantic and Gulf coasts of Florida comprise distinct stocks, and may therefore warrant consideration as separate management units (Tringali and Bert 1996).

**Life Mode**

Eggs and early larvae are pelagic and planktonic (Ager et al. 1976, Tucker 1986). As snook mature into juveniles and adults they become pelagic and nektonic (NOAA 1985). Juveniles and adults are usually found in schools (Bruger 1981, Tucker 1986). All life stages exhibit diurnal activity.

**Habitat**

Type: This fish is considered to be estuarine dependent (Tolley et al. 1987). Eggs and larvae are found in the shallow open waters of river mouths, beach inlets and passes, and estuarine passes in polyhaline to euhaline salinities (Volpe 1959, Linton and Rickards 1965, Moe 1972, Ager et al. 1976, Shafland and Koehl 1979, Lau and Shafland 1982, Tucker 1986). They have been raised in the laboratory in euhaline salinities, but can survive and develop in freshwater by 14 days after hatching (Shafland and Koehl 1979, Lau and Shafland 1982, Tucker 1986). Larvae probably hatch in shallow open waters off beaches, inlets, and passes, and make their way inshore to estuarine nursery grounds (Linton and Rickards 1965). Larvae have been collected in the summer in Naples Bay, Florida, associated with the bottom, which may allow them to take advantage of two-layered circulation as the mechanism for transport into the upper reaches of estuaries (Tolley et al. 1987).

Juvenile snook inhabit neritic and estuarine areas. They prefer protected bodies of water, usually of small surface area and shallow water depth, when small (Springer and Woodburn 1960), and seagrass beds when larger (Gilmore et al. 1983). Shoreline vegetation is also considered a possible important element as juveniles also occur in areas with vegetation other than seagrass (McMichael et al. 1989). They have been collected in ditches, tidal pools, headwaters of creeks, ponds, bays, and shorelines in freshwater to euhaline salinities in water depths from 0.3 to 1.2 m (Lunz 1953, Marshall 1958, Springer and Woodburn 1960, Tabb and Manning 1961, Gunter and Hall 1965, Linton and Rickards 1965, Merriner et al. 1970, Martin and Shipp 1971, Breuer 1972, Dahlberg 1972, Fore and Schmidt 1973, Ager et al. 1976, Hoese and Moore 1977, McMichael et al. 1989). In southwest Florida, Fore and Schmidt (1973) reported that primary nursery areas were brackish, shallow, warm tidal streams and dredged canals with slow currents, soft bottoms, and little submerged vegetation, but often with shoreline stands of red or white mangrove. McMichael et al. (1989) described a similar habitat for juvenile snook in the Tampa Bay area. On the Florida east coast, Gilmore et al. (1983) reported that juveniles with standard lengths (SL) that average 27.5 mm are typically found in freshwater tributaries. They begin to move from stream banks and bank vegetation to deeper water or salt marshes at 60 mm SL, 40 to 70 days old. Juveniles move from this habitat at an average size of 67 mm SL, showing up in seagrass beds after reaching lengths of 100 to 150 mm SL. Their residence here is from 1 to 6 months with most fish leaving at 300 mm SL.

Adults are found in estuarine and neritic waters. They inhabit Gulf passes, channels, beaches, river mouths, mangrove or salt marshes, brackish estuarine waters, and tidal ponds, lakes, and streams (Higgins and Lord 1926, Marshall 1958, Tabb and Manning 1961, Gunter and Hall 1963, Odum 1971, Kushlan and Lodge 1974, Ager et al. 1976, Hoese and Moore 1977). They have been reported in waters from 0.3 to 3.66 m in depth and in salinities ranging from fresh to euhaline (Baughman 1943, Gunter and Hall 1963, Cooley 1974, Kushlan and Lodge 1974, Loftus and Kushlan 1987). In summer, they have been reported in offshore areas such as coral reefs as far as 70 miles west of Key West, Florida, in the Dry Tortugas National Park (Schmidt pers. comm.).

Substrate: Juveniles and adults have been found over bottoms of clay, mud, mud-sand, sand, sand with rocks, detritus with mud and sand, and sand with shell (Breuer 1957, Marshall 1958, Gunter and Hall 1963, Gunter and Hall 1965, Bruger 1981, McMichael et al. 1989).

Physical/Chemical Characteristics:
Temperature: The common snook is very sensitive to temperature, with detrimental effects occurring at approximately 15°C or lower (Marshall 1958, Gilmore et al. 1983).

Temperature - Eggs: Eggs have not been observed in the wild, but they have been successfully spawned and developed at 28° ± 1° C (Shafland and Koehl 1979, Lau and Shafland 1982, Tucker 1986).

Temperature - Larvae: Larvae propagated in laboratories have been successfully reared at 24.6 to 32.4°C (Shafland and Koehl 1979, Lau and Shafland 1982, Tucker 1986). Snook larvae have been collected from Naples Bay, Florida, in temperatures ranging from 28.7° to 31.4°C (Tolley et al. 1987). In a hatchery study, snook larvae reared at 24°C did not survive, and development rates increased with incubation temperature. Optimum yolk utilization efficiency and larval growth occurred at 26°C (Limouzy 1993).

Temperature - Juveniles and Adults: Juveniles and adults have been collected in waters with a temperature range of 14.2° to 35.6°C (Marshall 1958, Springer and Woodburn 1960, Tabb and Manning 1961, Gunter and Hall 1963, Linton and Rickards 1965, Merriner et al. 1970, Martin and Shipp 1971, Dahlberg 1972, Cooley 1974, Shafland and Foote 1983, McMichael et al. 1989). Temperature tolerance may differ throughout the common snook's range due to such parameters as genetic stock, salinity, size, and diet (Howells et al. 1990). In laboratory experiments on the effect of falling temperature, juveniles ceased feeding at 14.2°C, lost equilibrium at 12.7°C, and died at 12.5°C (Shafland and Foote 1983). Other studies suggest a lower lethal temperature for juvenile snook of 9°C in salt water (19‰) and 10°C in freshwater (Howells et al. 1990). Abnormal behavior has been reported below 14.2°C, with death occurring from 9 to 17°C. The lower lethal limit for small juveniles has been reported as 9 to 14°C, while that of sub-adults and adults probably approaches the lower end of a 6 to 13°C range, making them somewhat more tolerant of colder temperatures than fingerlings (Marshall 1958, Springer and Woodburn 1960, Gunter and Hall 1963, Shafland and Foote 1983, Howells et al. 1990). Many field studies have reported snook as lethargic, stunned, or killed as a result of winter freezes (Marshall 1958, Cooley 1974). Gunter (1941) reported a severe winter kill of snook along the Texas coast due to cold weather in 1940.

Salinity - Eggs and Larvae: Eggs and larvae have been raised in the laboratory in salinities from 30 to 38‰ (Shafland and Koehl 1979, Lau and Shafland 1982, Tucker 1986). Both appear to prefer polyhaline to euhaline salinity ranges and are unable to develop in fresh water. Larvae at 14 days of development can be successfully transferred to fresh water and are considered euryhaline at this point (Ager et al. 1976, Shafland and Koehl 1979). Field studies show a significant relationship between larval size and salinity, with larger larvae occurring in lower salinities (Tolley et al. 1987). Snook larvae have been collected from Naples Bay, Florida, in salinities ranging from 14.8 to 33.5‰ (Tolley et al. 1987).

Salinity - Juveniles and Adults: Both juveniles and adults are euryhaline, and have been reported from a salinity range of 0.0 to 36‰ (Hildebrand 1958, Marshall 1958, Springer and Woodburn 1960, Tabb and Manning 1961, Tabb et al. 1962, Gunter and Hall 1963, Gunter and Hall 1965, Bryan 1971, Martin and Shipp 1971, Dahlberg 1972, Fore and Schmidt 1973, Cooley 1974, Kushlan and Lodge 1974, Gilmore et al. 1983, McMichael et al. 1989). Adult snook are more often associated with moderate to higher salinities within this range (Marshall 1958, Fore and Schmidt 1973, Seaman and Collins 1983, Palik and Kunneke 1984). On the east coast of Florida, juvenile snook <50mm consistently occur at lower salinities, whereas those >150mm are generally found in higher salinity waters (Gilmore et al. 1983). Snook are relatively widespread in freshwater areas in Florida, and have been collected in Lake Okeechobee, coastal rivers, the Big Cypress Swamp, and at several locations in the Everglades (Loftus and Kushlan 1987). Physiological studies of juveniles indicate they can osmoregulate at salinities between 0 and 45‰ in a manner similar to other brackish water fishes (Quintero and Grier 1985). More than 70% of seing-caught and 90% of trawl-caught specimens taken in the Little Manatee River from 1988 to 1991 were taken at salinities less than 5‰. Maximum numbers were taken during October and November. Changes in blood osmolality and gill morphology of juvenile snook after acclimation at various salinities (0, 15, 30, and 40‰) has been studied (Quinterro and Torres 1993). The chloride cells within the gills appeared to be metabolically active regardless of the acclimation salinity.

Dissolved Oxygen: Dissolved oxygen (DO) level may limit the distribution of this fish in confined or isolated marsh habitats (Gilmore et al. 1983). Juvenile snook have been collected in impounded wetland habitats associated with the Indian River Lagoon with DO levels of less than 1.0 ppm (no ref). Peterson and Gilmore (1991) found an ontogenetic change in a juvenile snook's ability to survive reduced oxygen levels which correlated well with the habitat shift noted by Gilmore et al. (1983). Small juveniles may also use aquatic surface respiration to utilize the well-oxygenated surface film during hypoxic events (Peterson et al. 1991).

Movements and Migrations: Snook is a relatively non-migratory, inshore species (Volpe 1959, Moe 1972). Apparently this fish has a broad inshore range and moves freely in this area, as conditions permit, in short coastwise movements (Moe 1972, Tucker 1986). Eggs and larvae are carried by currents or swim to nursery areas where they remain until maturity. It has been suggested that the optimal salinity for activity changes with development in juveniles from freshwater to isosmotic levels to match, or even determine, their gradual migration to higher salinities (Perez-Pinzon and Lutz 1991). Movements from estuaries and fresh water tributaries to spawning areas just offshore can be considered a limited spawning migration (Moe 1972, Tucker 1986). Some southerly movements in response to falling water temperature have been noted (NOAA 1985). Juvenile snook exhibit a habitat specificity which changes as the fish grow older, resulting in localized movements. Adult habitat requirements are not as narrow as those of juveniles, although limited movement occurs throughout the life cycle (Gilmore et al. 1983). In a study of Tampa Bay, Florida, most juvenile snook were concentrated in two tributaries, the Alafia and Little Manatee Rivers (CES 1992). Adult snook were also concentrated in tributaries, except in the spring when they were scattered throughout nearshore areas of Tampa Bay. In another study of Little Manatee River, Florida, most juveniles were found along the shoreline at two marginal creek/cove sites (Matheson and Rydene 1993).

**Reproduction**

Mode: This species can be considered a protandric hermaphrodite, suggested by skewed sex ratios that significantly favor small males, and the absence of age 0 and 1 females (Taylor and Grier 1993, Taylor pers. comm.). Comparisons of the chromosomes of males and females do not show differences in chromosomatic size or number (Ruiz-Carus 1993). The banding patterns on the chromosomes supported the hypothesis of protandric hermaphroditism. Examination of more than 4,100 snook gonads confirmed that snook undergo sex reversal (Taylor and Grier 1993). For all snook ≤500mm and under age 4 the sex ratio was skewed in favor of males (6.1M:1.0F), whereas for fish ≥800mm and over age 7 the sex ratio favors females (1.0M:3.2F). Direct evidence from pond-held juvenile males demonstrates that female common snook are derived from post-mature males (Taylor pers. comm.). Fertilization is external, by broadcast of milt and roe.

Spawning: In Florida, spawning occurs from May to mid-November with peak spawning periods from June to July along the southeast and southwest coasts, and in August along the east central coast. These peaks may vary among locations. In a study of snook in Tampa Bay, a diel and lunar sampling protocol was used to determine peak periods of various reproductive activities (Roberts et al. 1988). The gonadosomatic index of adult snook and the catch per unit effort (CPUE) of larvae were highest during the new moon period in June and July. Eggs were most abundant during late evening and early morning hours. Some spawning may occur year round in the warmer parts of the range (Marshall 1958, Volpe 1959, Ager et al. 1976, Moe 1972, Tucker 1986). In south Texas, the primary spawning period is June to August (Matlock and Osburn 1987). One female with roe was reported from Corpus Christi, Texas in July (Baughman 1943). Snook can spawn repeatedly during a single season (Fore and Schmidt 1973, Seaman and Collins 1983). Fish ready to spawn congregate in schools in shallow, saline, open waters just offshore in such areas as river mouths, estuarine passes, and along open beaches in the vicinity of inlets. Actual spawning is most likely to occur in shallow nearshore waters (Marshall 1958, Volpe 1959, Linton and Rickards 1965, Moe 1972, Ager et al. 1976, Bruger 1981, Gilmore et al. 1983). Salinities of >20‰ are necessary to activate sperm for successful spawning (Ager et al. 1976, Shafland and Koehl 1979).

Fecundity: Spawning females produce large numbers of eggs; a female with a fork length (FL) of 584 mm contained about 1,440,000 eggs (Volpe 1959). Fecundity has been tentatively estimated at 20,412 eggs/kg body weight, with some fractional spawning being reported (Marshall 1958, Ager et al. 1976). Common snook can be considered batch-synchronous, i.e., they can spawn once every 3 to 4 days for about 152 days from mid-April to mid-September in Florida waters. Batch fecundity is approximately 850,000 eggs, and if there are 38 spawning events per season, total fecundity for a 800 mm FL female could be 32,000,000 eggs per year (Taylor pers. comm.).

**Growth and Development**

Egg Size and Embryonic Development: Development is oviparous. Eggs are 0.68 to 0.73 mm in diameter, spherical, yellowish-white in color with transparent yolk material containing a single well defined oil globule that ranges from 0.17 to 0.30 mm in diameter. Hatching rates reported in laboratory experiments are 16-18 hours at 28°C and 24 to 30 hours at 27.8° to 30.6°C. Fertilized eggs float in salt water with a salinity of >20‰ (Ager et al. 1976, Lau and Shafland 1982, Tucker 1986).

Age and Size of Larvae: Larvae are 1.4 to 1.5 mm SL at hatching and have a large yolk sac that contains a large oil globule in the anterior portion, and a transparent finfold present around most of the body (Lau and Shafland 1982, Tucker 1986). Their length increases to about 2.1 mm SL by 36 hours after hatching (AH) (Lau and Shafland 1982). At this time eyes are becoming pigmented, the mouth begins to develop, the yolk sac is absorbed, and the gut increases in diameter and is partitioned (Lau and Shafland 1982). Eyes and jaws are complete 32 to 48 hours AH and the digestive system is functional by 72 hours AH (Shafland and Koehl 1979, Tucker 1986). At approximately 96 hours AH, larvae are 2.2 to 2.3 mm SL, the oil globule is completely absorbed, and the swimbladder is visible above the gut. Notochord flexion begins from 3.6 to 3.8 mm SL, and is usually complete by 4.5 mm. Caudal fin is visible by 3.2 mm SL; pelvic fin buds visible between 5.0 to 5.5 mm SL, pelvic girdle completely ossified by 8.6 mm SL and heavily lined with teeth (Lau and Shafland 1982). The larval stage ends with scale development at 13.8 to 16.4 mm SL, 34 days AH (Lau and Shafland 1982). Growth rate for larvae varies. Newly hatched larvae at 28°C±1°C grow 1.02 mm/day for a few hours, slowing rapidly to about 0.15 mm/day when about 2.4 mm SL. Growth rate then increases gradually with increasing size from 0.15 to 0.50 mm/day in snook between 3.5 to 22.0 mm SL (Lau and Shafland 1982). The osteological develpment of larval snook is described in detail by Potthoff and Tellock (1993).

Juvenile Size Range: The minimum size described for juveniles is 13.8 mm SL (Lau and Shafland 1982). The caudal skeleton is ossified by 21.9 mm SL, and by 26.4 mm SL melanophores begin to form along lateral line, darkening it and the fins. Juveniles have appearance of small adults at this point (Lau and Shafland 1982). The reported growth rate for juveniles in the wild is 0.5-1.2 mm/day (Fore and Schmidt 1973, Gilmore et al. 1983, McMichael et al. 1989) with a reported average of 0.6-0.7 mm/day for the first eight months of life (McMichael et al. 1989). Juveniles are 163 mm FL at the end of their first winter, and 342 mm FL by the end of their second (Volpe 1959). Some juveniles mature by the end of their second year, but most are not mature until their third year when they reach a FL of 500 mm (Marshall 1958, Volpe 1959).

Age and Size of Adults: Marshall (1958) reported minimum sizes for adults of 337 mm FL for females, and 338 mm FL for males. Predicted size and age for Florida gulf coast snook at 50% maturity are 401 mm FL at 1.93 years for males, and 499 mm FL at 2.64 years for females (Taylor pers. comm.). Estimates for Florida east coast snook at 50% maturity are 379 mm FL at 2.26 years for males, and 644 mm FL at 3.68

years for females. Volpe (1959) reported a maximum life span of about 7 years. However, Taylor et al. (1993) reported that males can live 13 years and attain 925 mm TL, and females 19 years and 1,105 mm TL. In the Everglades region, 4 and 5 year old fish comprise 59% of the snook population. The sex ratio is approximately 3:1, males to females (Gilmore et al. 1983).

**Food and Feeding**

Trophic Mode: The common snook is an opportunistic carnivore that tends to be piscivorous, with its specific diet varying among habitats (Seaman and Collins 1983). The common snook is a visual predator that forages throughout the water column and on the bottom, often in narrow passes accompanied by strong currents (Springer and Woodburn 1960, Fore and Schmidt 1973, Seaman and Collins 1983, Manooch 1984, NOAA 1985).

Food Items: Larvae are considered stenophagous. They are planktivores preying chiefly on copepods and their eggs and larvae. They also feed on other invertebrate eggs, crab zoea, foraminifera, algae, and plant tissue (Harrington and Harrington 1961). In a laboratory rearing study, larvae began feeding when 2 to 3 days old, and accepted rotifers, newly hatched *Artemia*, and copepod nauplii between 53 and 130 microns in size (Shafland 1977). Late postlarvae also feed on neonatal *Gambusia* (Gilmore et al. 1983, Shafland 1977). Juveniles become piscivorous at 25 to 30 mm TL with fish constituting a major portion of their diet by 56 mm SL (Springer and Woodburn 1960, Shafland and Koehl 1979). Food organisms of juvenile snook include bay anchovy, pinfish, sailfin molly (*Poecilia latipinna*), western mosquitofish (*Gambusia affinis*), sheepshead minnow, gobies, silversides, red drum, killifishes, grass shrimp, plant tissue, insects, and other fishes. Smaller specimens have also been reported eating small crustacea and zooplankton (Springer and Woodburn 1960, Harrington and Harrington 1961, Bryan 1971, Fore and Schmidt 1973, Gilmore et al. 1983). Field studies of juvenile snook in Tampa Bay suggest that feeding occurs during daytime hours (McMichael et al. 1989). Adults consume mostly fish, crabs, and shrimp, but crayfish, and some plant tissue are also utilized (Marshall 1958, Fore and Schmidt 1973). Fish constitute the most important component with the following reported from diet studies: menhaden, mojarras, mullet, pinfish and other sparids, anchovies, pigfish, sailfin and other mollys, western mosquitofish and other *Gambusia* species (Marshall 1958, Bryan 1971, Odum 1971). Crabs found in adult snook stomachs are mostly from the family Portunidae and include blue crab (*Callinectes sapidus*), *C. ornatus*, *Portunus gibbesii*, and *P. sayi*. Mud crabs (Xanthidae) and hermit crabs (Paguridae) are also part of the common snook's diet (Fore and Schmidt 1973).

**Biological Interactions**

Predation: It is during the larval and juvenile stages that the common snook is vulnerable to predation by other piscivorous species (Seaman and Collins 1983).

Factors Influencing Populations: Habitat requirements and temperature are probably the most important factors determining the range of snook in U.S. waters (Cooley 1974, Ager et al. 1976, Hoese and Moore 1977). The preferred habitats, mangrove and salt marshes, are not extensive in the northwestern Gulf of Mexico which, along with the need for relatively warm temperatures, probably accounts for the relative scarcity of this species. This habitat is similar to that of the tarpon, *Megalops atlanticus*, which, like the snook, is declining in numbers, giving support to the hypotheses of habitat destruction and/or environmental change as factors in their decline (Marshall 1958, Rivas 1962, Odum 1971, Cooley 1974, Hoese and Moore 1977, Peterson and Gilmore 1991). Interaction with other species include habitat overlapping and parasitism. Possible competition may exist between snook and associated fish such as tarpon, ladyfish, spotted seatrout, silver perch, and bank sea bass (Linton and Rickards 1965). An unidentified nematode has been reported parasitizing the mesentery and stomach wall of snook, but apparently with no ill effects (Marshall 1958). Other reported parasites are *Philometra centropomi* in the nasal mucosa and *Prosthenhystera obesa* in the gall bladder (Seaman and Collins 1983). Snook have also been identified as a host for *Lymphocystis* virus. Larval recruitment and/or juvenile survival may be enhanced by increased upland runoff or marsh flooding (Tilmant et al. 1989). The presence of juveniles in low salinity areas may be a survival adaptation to exploit areas that are largely free of piscine predators (Fore and Schmidt 1973). The Texas Parks and Wildlife Department, in cooperation with Texas A&M University and the University of Texas, has been experimenting with hatchery propagation of snook as a means to stock Texas bays (Vega pers. comm.). Studies of hatchery rearing of snook have also been conducted in Florida (Mote 1993).

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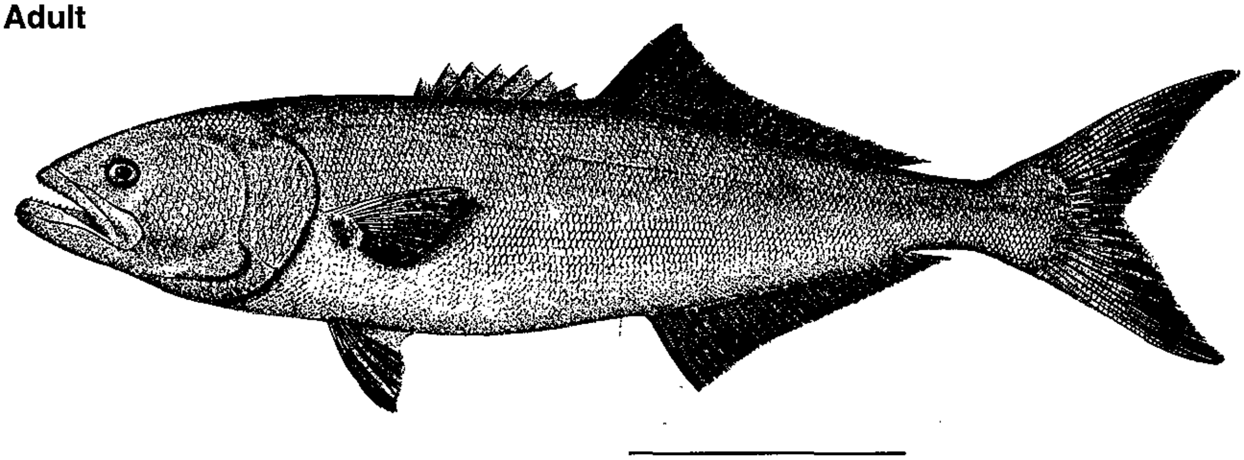
# Bluefish

***Pomatomus saltatrix***
**Adult**




(from Goode 1884)

**Common Name**: bluefish
**Scientific Name**: *Pomatomus saltatrix*
**Other Common Names**: blue, tailor, snapper, elf, fatback, snap mackerel, skipjack, snapping mackerel, horse mackerel, greenfish, skip mackerel, chopper, Hatteras blue (Wilk 1977); *tassergal* (French), *anchova de banco* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Perciformes |
| Family: | Pomatomidae |

**Value**

Commercial: In the Gulf of Mexico, the bluefish is considered an incidental commercial species, with most catches occurring in coastal waters (Lund 1961, Barger et al. 1978, Benson 1982). In the Gulf of Mexico during 1992, approximately 134.3 mt of bluefish were harvested with over 85 per cent coming from Florida (Newlin 1993). It was once common enough to support a small fishery in east Texas waters, but has not been of commercial interest there since the 1930's (Gunter 1945, Hoese 1958, Newlin 1993). In Alabama, it is a relatively minor component of that state's commercial fishery, contributing only 7.7 mt in 1992 (Swingle 1971, Newlin 1993). Louisiana landed 12.2 mt and Mississippi landings were too small to be reported (Newlin 1993). Haul seines, gill nets, and hook and line are the primary types of gear used. In Florida, bluefish is generally not the targeted species, but is used to supplement catches of other species (GMFMC 1981). Harvest is limited to fish over 10 inches, and catches are largely by trammel nets in waters off the Gulf beaches. In recent years, incidental catch in shrimp trawls have made up 25% of the Florida harvest. Catches are made by pound nets, gill nets, purse seines, long haul seines, beach seines, and hook and line here and in other areas of the range of this fish (Walford et al. 1978, GMFMC 1981). The market price is generally low, with the average price per pound to fishermen only $0.27 in 1992 (Newlin 1993), but they can supplement the income of commercial fishermen when more desirable species are unavailable (Manooch 1984). Bluefish are usually marketed fresh due to poor freezing quality.

Recreational: This is an important game species in both U.S. and Mexican waters. Its recreational importance far outweighs its commercial value, especially on the Atlantic seaboard (Hildebrand 1957, Lund 1961, Swingle 1977, Barger et al. 1978, Benson 1982). Its voracity makes it an exciting game fish and it is also an excellent food fish when eaten fresh (Hoese and Moore 1977). Fishery information for the Gulf of Mexico showed a total catch of 501,000 bluefish in 1992 (NMFS 1993). Most of the recreational catch occurs in coastal waters within 3 miles of shore. Angling methods include surf casting; float fishing from piers, docks, bridges, and jetties; and trolling, casting, live bait fishing, and chumming from boats (Walford et al. 1978).

Indicator of Environmental Stress: Bluefish bioaccumulate contaminants such as polychlorinated biphenyls (PCB) into various adipose tissues from the water column and through the marine food chain (Sanders and Haynes 1988, Eldridge and Meaburn 1992). Studies by the National Marine Fisheries Service (NMFS), the Food and Drug Administration (FDA), and Environmental Protection Agency (EPA) have found concentrations of PCB in large bluefish (>500

Table 5.26. Relative abundance of bluefish in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | *Life stage* A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ○ | | √ | | |
| Ten Thousand Islands | ○ | | √ | | |
| Caloosahatchee River | | | | | |
| Charlotte Harbor | ○ | | ○ | | |
| Tampa Bay | ○ | | √ | | |
| Suwannee River | ○ | | ○ | | |
| Apalachee Bay | ○ | | ○ | | |
| Apalachicola Bay | ○ | | ○ | | |
| St. Andrew Bay | ◉ | | ○ | | |
| Choctawhatchee Bay | ◉ | | ○ | | |
| Pensacola Bay | ○ | | ○ | | |
| Perdido Bay | ○ | | ○ | | |
| Mobile Bay | ○ | | ○ | | |
| Mississippi Sound | ○ | | ○ | | |
| Lake Borgne | | | | | |
| Lake Pontchartrain | | | | | |
| Breton/Chandeleur Sounds | | | √ | | |
| Mississippi River | √ | | √ | | |
| Barataria Bay | | | ○ | | |
| Terrebonne/Timbalier Bays | | | √ | | |
| Atchafalaya/Vermilion Bays | | | √ | | |
| Calcasieu Lake | | | √ | | |
| Sabine Lake | | | √ | | |
| Galveston Bay | | | ○ | | |
| Brazos River | | | ○ | | |
| Matagorda Bay | | | √ | | |
| San Antonio Bay | √ | | | | |
| Aransas Bay | √ | | √ | | |
| Corpus Christi Bay | √ | | √ | | |
| Laguna Madre | | | | | |
| Baffin Bay | | | | | |
| | A | S | J | L | E |

| Relative abundance: | | Life stage: |
|---|---|---|
| ● | Highly abundant | A - Adults |
| ◉ | Abundant | S - Spawning |
| ○ | Common | J - Juveniles |
| √ | Rare | L - Larvae |
| blank | Not present | E - Eggs |

mm FL) that exceed the limit of 2 µg/g set by the FDA. This has prompted investigation to determine if states with bluefish fisheries need to control the consumption of large individuals by recreational and subsistence fishermen that regularly eat these fish, and how to minimize human exposure by regulating the bluefish harvest (Sanders and Haynes 1988, Eldridge and Meaburn 1992).

Ecological: The bluefish is a pelagic marine predator, and is primarily a visual feeder (Olla et al. 1970, Olla and Studholme 1972). The bluefish is probably in competition with other pelagic predators such as striped bass (*Morone saxatilis*), Spanish mackerel (*Scomberomorous maculatus*), king mackerel (*S. cavalla*), seatrout and weakfish (*Cynoscion* species), and little tunny (*Euthynnus alletteratus*).

**Range**

Overall: The bluefish occurs in temperate coastal waters of the Atlantic and Indian Oceans, and is one of the most widespread of the U.S. coastal and estuarine fishes (Fischer 1978). Along the U.S. east coast, bluefish occur from Cape Cod to Florida (Lund 1961, Wilk 1977). It is occasionally found as far north as Nova Scotia, and occurs throughout the Gulf of Mexico from Florida to Mexico, but are absent from Central America. Along the Atlantic coast of South America, bluefish occur from Argentina to Colombia. It is also found off Cuba, Bermuda, and the Azores, in the eastern Atlantic off the Canary Islands, and from Portugal to Senegal. Its range includes the Mediterranean and Black Seas as well. It is found off Africa from Angola to South Africa. Distribution in the Indian Ocean includes the East coast of southern Africa, Madagascar, Malay Peninsula, Tasmania, and southern and western Australia where it is reported abundant off southern Queensland and New South Wales. There is a single report in the eastern Pacific off the coast of Chile (Lund 1961). Based on the seasonal and spatial distribution of bluefish larvae, it has been hypothesized that two spawning populations exist on the U.S. east coast, one spawning in the spring south of Cape Hatteras, and one in the summer in the Mid-Atlantic bight (Kendall and Walford 1979).

Within Study Area: Within U.S. Gulf of Mexico estuaries, this species occurs from Florida Bay, Florida to the Rio Grande, Texas (Table 5.26) (Lund 1961, Wilk 1977). It is less abundant overall in the Gulf of Mexico than along the Atlantic coast (Walford et al. 1978). Bluefish occur in coastal waters off of Texas, Louisiana (Hoese and Moore 1977), Mississippi, Alabama, and the west coast of Florida (Hardy 1978, GMFMC 1981, Manooch 1984, NOAA 1985). Larval bluefish in the northern Gulf of Mexico are reported to occur primarily between 88° and 93° longitude, and to be relatively uncommon in the eastern Gulf off of the Florida coast (Ditty and Shaw 1995). Recreational catch data suggest that bluefish are more common off of Louisiana and Texas, and less common along the Florida Gulf coast (Ditty and Shaw 1995).

**Life Mode**

Both eggs and larvae are pelagic and planktonic (Lippson and Moran 1974, Norcross et al. 1977). Juveniles and adults are pelagic and nektonic. This is a migratory species in which both large juveniles and adults school, but usually separately. Adults are diurnal, and are active all daylight hours (Pullen 1962, Parker 1965, Olla et al. 1970, Olla and Studholme 1972, Hardy 1978, Barger et al. 1978, Benson 1982). Swimming speed increases at dawn and decreases during the late afternoon and evening (Walford et al. 1978).

**Habitat**

Type: This species inhabits temperate and warm temperate zones, generally in continental shelf waters (Wilk 1977). Eggs and larvae are found in continental shelf waters, usually over depths <100m. Larvae move inshore sometime during their first growing season and are occasionally found in the mouth of bays. They were collected from water depths ranging from 34 to 183 m in one study, with all but one captured in waters >49 m deep (Moe 1972, Lippson and Moran 1974, Norcross et al. 1974, Barger et al. 1978, Benson 1982). Eggs and larvae are found in euhaline (marine) salinities (Barger et al. 1978, Benson 1982). Juveniles have been reported from both inshore and offshore areas in clear and turbid waters. Inshore collections include such habitats as along ocean beaches, lagoons, sounds, bays, barrier island passes, estuaries, and bayous.

Juveniles are known to enter estuaries, and may remain there for several months at a time on the U.S. east coast (Juanes et al. 1993, McBride et al. 1993). Movement into these areas may benefit survival and growth due to shelter and food resources (Gunter 1945, Arnold et al. 1960, Pullen 1962, Zimmerman 1969, Perret et al. 1971, Franks et al. 1972, Norcross et al. 1974, Hardy 1978, Benson 1982). Early juveniles (14.0-16.5 mm) can be found as far as 96 km offshore. Juveniles are usually found above the thermocline, with a reported depth range of 1.1 to 26 m deep (Clark et al. 1969, Zimmerman 1969, Franks et al. 1972, Norcross et al. 1974, Hardy 1978). Juveniles have also been collected considerable distances up rivers in New England (Norcross et al. 1974, Hardy 1978). Salinities from which juveniles are reported range from fresh to euhaline (Gunter 1945, Pullen 1962, Parker 1965, Perret et al. 1971, Franks et al. 1972, Hardy 1978).

Adults have been captured in nearshore areas of barrier islands and their passes, and along island beaches on the Gulf side, but are not common in low-salinity estuarine areas. Adults may move into or near estuaries to feed (Simmons 1957, Franks et al. 1972, Swingle 1977, Benson 1982). They prefer shallow water, near dropoffs from shoal and banks (Shipp 1986). However, they may occur in water as deep as 100 m (Lund 1961, Franks et al. 1972, Hardy 1978), and during the spawning season, they have been reported up to 148 km offshore in the Mid-Atlantic Bight (Norcross et al. 1974). In Texas, they are sometimes found in association with schools of gulf menhaden (Breuer 1949).

Substrate: Juveniles have been found over bottoms of shell and sandy shell with hard packed mud (Pullen 1962, Zimmerman 1969). Bottom types for all life stages are probably many and varied due to the pelagic and wide ranging nature of this species.

Physical/Chemical Characteristics:

Temperature - Eggs: In one laboratory study, eggs fertilized *in vitro* were successfully incubated in a temperature range of 18 to 22.2°C, with an average temperature of 20.0°C until hatching (Deuel et al. 1966). Eggs in the wild occur from 18 to 26.3°C (Norcross et al. 1974).

Temperature - Larvae: In one study of 18 specimens, larval bluefish were reported in the Gulf of Mexico over a temperature range of 23.2 to 26.4°C (Barger et al. 1978, Benson 1982). Ditty and Shaw (1995) collected 70 larval bluefish in the northern Gulf of Mexico at a mean temperature of 24.6°C, with a range of 22.4 to 26.9°C. Minimum temperature has been suggested as 21°C (Hardy 1978).

Temperature - Juveniles: Juveniles have been recorded in temperatures from 14.8 to 31.2°C in the Gulf of Mexico (Gunter 1945, Pullen 1962, Perret et al. 1971, Wang and Raney 1971, Franks et al. 1972, Hardy 1978). Water temperatures below 10°C are considered lethal for this life stage (Lund and Maltezos 1970), but these temperatures generally don't occur in the Gulf of Mexico.

Temperature - Adults: The temperature range recorded for adults is 18-21.0°C (Deuel et al. 1966, Franks et al. 1972, Norcross et al. 1974). Swimming speed is significantly affected by temperature with stressful behavior noted below 11.9°C and above 29.8°C (Olla and Studholme 1971). Adults can survive temperatures as low as 7.5°C temporarily (Lund and Maltezos 1970).

Salinity - Eggs: In one laboratory study, eggs fertilized *in vitro* were successfully incubated in a salinity of 32.5‰ until hatching (Deuel et al. 1966). Eggs in the wild occur from 26.6 to 34.9‰, but are found most often in 30‰ or greater (Norcross et al. 1974).

Salinity - Larvae: In one study of 18 specimens, larval bluefish were reported in the Gulf of Mexico over a salinity range of 35.7 to 36.6‰ (Barger et al. 1978). Ditty and Shaw (1995) collected 70 larval bluefish in the northern Gulf of Mexico at a mean salinity of 33.0‰, with a range of 26.7 to 36.3‰. They have been collected in salinities as high as 38‰ in the Atlantic Ocean (Kendall and Walford 1979).

Salinity - Juveniles: Juveniles have been recorded over a salinity range of 8.0 to 36.2‰ in the Gulf of Mexico (Gunter 1945, Pullen 1962, Perret et al. 1971, Wang and Raney 1971, Franks et al. 1972, Hardy 1978).

Salinity - Adults: Salinity preference for adults seems to be 26.6 to 34.9‰ (Benson 1982), but they exhibit an overall range of 7.0-36.5‰, with only rare occurrences above 35‰ (Simmons 1957, Deuel et al. 1966, Franks et al. 1972, Hardy 1978).

Movements and Migrations: Larval bluefish in the northern Gulf of Mexico are reported to reach peak abundance in April, and November-December (Ditty et al. 1988). Young of the year bluefish move inshore sometime during their first growing season, and some are found in estuaries and their tributaries (Norcross et al. 1974, Hardy 1978, Benson 1982). Age class 0 fish arrive in Texas coastal waters during late November when they are 48-56 mm standard length (SL) (Hoese 1965), and some evidently enter bay systems (Gunter 1945, Pullen 1962, Perret et al. 1971, Benson 1982). Adults are caught off the Texas coast primarily from April to September, with peaks in July and August, and appear to be entirely absent during December and January (Springer and Pirson 1959). Adults move seasonally in groups loosely collected into aggregates that can be 6 to 8 km long (Hardy 1978). They generally move north in spring and summer, and south in fall and winter (Moe 1972, Wilk 1977). In the Gulf of Mexico, they remain offshore during much of the year, moving inshore during the summer in Louisiana, late summer and fall in Mississippi, and fall in Florida and the northwestern Gulf. Florida bluefish remain inshore until spring, with large numbers still found off southern Florida in March and some present throughout the year (Springer and Woodburn 1960, Deuel et al. 1966, Perry 1970, Hoese 1977). Seasonal migrations appear to be linked to water temperature and possibly photoperiod (Lund and Maltezos 1970, Olla and Studholme 1971). In the Atlantic, fall migration appears to be triggered when temperatures fall to 13 to 15°C. In this area, fall migration is believed to go in two directions (Lund and Maltezos 1970): juveniles are essentially shore fish and move southward along the coast staying with the warmer water and will enter inner bays, whereas adults are pelagic and move offshore to find warmer water in which to overwinter (Lund and Maltezos 1970). Movements between offshore and inshore waters are irregular and may be a response to wind induced changes in water temperature (Reid 1954, Lund and Maltezos 1970). Migrating bluefish have been reported to enter public beach waters and nip at swimmers (de Sylva 1976, IGFA 1991).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic), but hermaphroditism has not been examined. Fertilization is external by broadcast of milt and roe, and no accessory organs are present (Wilk 1977).

Spawning: The bluefish is an offshore ocean spawner (Lippson and Moran 1974). Gulf of Mexico populations appear to spawn over the continental shelf, as they do in the Atlantic off the eastern U.S. (Moe 1972, Lippson and Moran 1974, Norcross et al. 1974, Barger et al. 1978). The spawning period varies depending on location. Spawning in the northern Gulf of Mexico may be bimodal, occurring in both spring and fall. Fall spawning occurs from late September through early November (Hildebrand 1957, Barger et al. 1978, Finucane et al. 1980). Spring spawning is known to occur in waters off the Louisiana coast (Barger et al. 1978). Spawning locations may be associated with hydrologically dynamic areas, such as the estuarine/oceanic frontal zone of the Mississippi River plume (Ditty and Shaw 1995). It has been inferred, but not consistently demonstrated, that such frontal zones offer a nutritional advantage to larval fish. In the Atlantic on the U.S. east coast, spawning is reported in the spring 55 to 148 km offshore in salinities of 25.6 to 32.5‰, and water temperatures of 14 to 25.6°C (Deuel et al. 1966, Norcross et al. 1974, Hardy 1978). In this area, optimal temperature and salinity for spawning were 25.6°C and 31‰, and little spawning was reported at 18°C and 31.7‰, and 20.5°C and 26.6‰. The majority of spawning in the Chesapeake Bay area is reported to occur at temperatures above 22°C and surface salinities of 31‰ or greater (Deuel et al. 1966, Norcross et al. 1974).

Fecundity: The number of eggs produced is a function of size and age (Wilk 1977). In Atlantic waters of the U.S. east coast, a 528 mm female contained about 900,000 maturing eggs while a 585 mm female contained about 1,100,000 eggs.

**Growth and Development**

Egg Size and Embryonic Development: Fertilized eggs are 0.90-1.20 mm in diameter, with a single oil globule present 0.22-0.30 mm in diameter (Deuel et al. 1966, Lippson and Moran 1974). The egg capsule is thin, but tough, and is transparent and colorless. Yolk is a pale amber and the oil globule is a deeper amber. Perivitelline space is about one sixth the egg radius. Development is oviparous and cell division proceeds rapidly. Regular movements are first noticed about 37 hours after fertilization (AF) with mass hatching occurring between 44 to 46 hours AF at 18.5 to 22.2°C, and 46 to 48 hours AF at 18.0 to 22.2° (Deuel et al. 1966, Lippson and Moran 1974, Norcross et al. 1974). Egg incubation time at 25° C has been estimated at 30 to 36 hours (Ditty and Shaw 1995).

Age and Size of Larvae: Newly hatched larvae are 2.0-2.4 mm total length (TL) and grow to 2.9 mm TL during their first day. The yolk sac is absorbed by about 4 mm TL. Incipient fin rays are evident by 6 mm TL, and countable by 8 mm TL. Fin development is complete by 13 to 14 mm TL marking the end of the larval stage (Deuel et al. 1966, Lippson and Moran 1974, Norcross et al. 1974).

Juvenile Size Range: The minimum length of this stage is about 14 mm SL (Lippson and Moran 1974, Norcross et al. 1974). Maturity occurs during the second year when fish are about 300 to 350 mm fork length (FL) (Deuel et al. 1966). A 200 mm TL female with nearly mature eggs was reported from Mexican waters (Hildebrand 1957). Testes mature slightly earlier than ovaries in fish of similar size (Wilk 1977).

Age and Size of Adults: In the Gulf of Mexico, adult bluefish have been estimated up to 8 years old, and up to 767 mm FL (Barger 1990), based on otolith analysis. Initial growth in the Gulf of Mexico is considered to be rapid. Barger (1990) provides VonBertalanffy growth parameters for Gulf of Mexico and southeast U.S. bluefish. On the U.S. east coast, bluefish up to 9 years old have been aged through scale analyses, but larger and presumably older fish have been reported that may be as old as 14 years (Wilk 1977). Sizes for different year classes range as follows; 230 mm FL at 1+ year; 400 mm FL at 2+ years; 490 mm FL at 3+ years (1.816 kg); 580 mm FL at 4+ years (3.178 kg); 640 mm FL at 5+ years (4.086 kg); 690 mm FL at 6+ years (4.540 kg); and 710 mm FL at 7+ years (5.448 kg) (Wilk 1977). A size of about 860 mm FL and 8.455 kg is suggested for fish reaching 14 years of age (Wilk 1977), and a fish caught in North Carolina waters weighed 14.40 kg (IGFA 1991).

**Food and Feeding**

Trophic Mode: The bluefish is a voracious, pelagic, marine predator that visually feeds on a variety of fishes and invertebrates throughout the water column (Olla et al. 1970, Olla and Studholme 1972, Benson 1982). It has earned nicknames such as "marine piranah" and "chopper" because fish will move in large schools through shoals of bait fish in a feeding frenzy (IGFA 1991). Schools of bluefish can be located at a distance by hovering seagulls that are eating forage fish driven to the surface by feeding bluefish (Olla et al. 1970). During these feeding frenzies, bluefish are known to even strand themselves on shore while in pursuit of prey that have fled inshore (IGFA 1991).

Food Items: Larval and early juvenile bluefish feed mostly on copepods, and gradually shift to fish and crab larvae (Marks and Conover 1993). Copepods are the most common prey type in fish <60 mm TL. Crab larvae are initially consumed by bluefish < 40 mm TL, while the onset of piscivory occurs in the 30-70 mm TL size range. As bluefish grow, they tend to consume increasingly larger teleost prey. The shift in food items corresponds to the period of inshore migration, making the change in diet coincident with a habitat shift (Marks and Conover 1993). The prey of adult bluefish include annelid worms, mysids, shrimps, crabs, lobsters, squid, lampreys, small sharks, eels, herrings, anchovies, killifishes, silversides, halfbeaks, bluefish, pipefish, sciaenids, jacks, flatfish, searobins, mackerels, mullets, cods, sea bass, porgies, wrasses, puffers, butterfish, sand lances, cusk-eels, lizardfish, and eelpouts (Miles 1949, Richards 1976, Benson 1982). Bluefish feeding activities drive prey species near the waters surface, where they are vulnerable to predation by piscivorous birds (Safina 1990a, Safina 1990b).

**Biological Interactions**

Predation: Only such large predators as sharks, tunas, swordfish, and wahoo pose threats to these fast swimmers (Medved and Marshall 1981).

Factors Influencing Populations: Fin rot has been noted as a disease to which this species is particularly vulnerable. Known parasites include isopods, copepods, cestodes, trematodes, nematodes, and protozoans (Wilk 1977).

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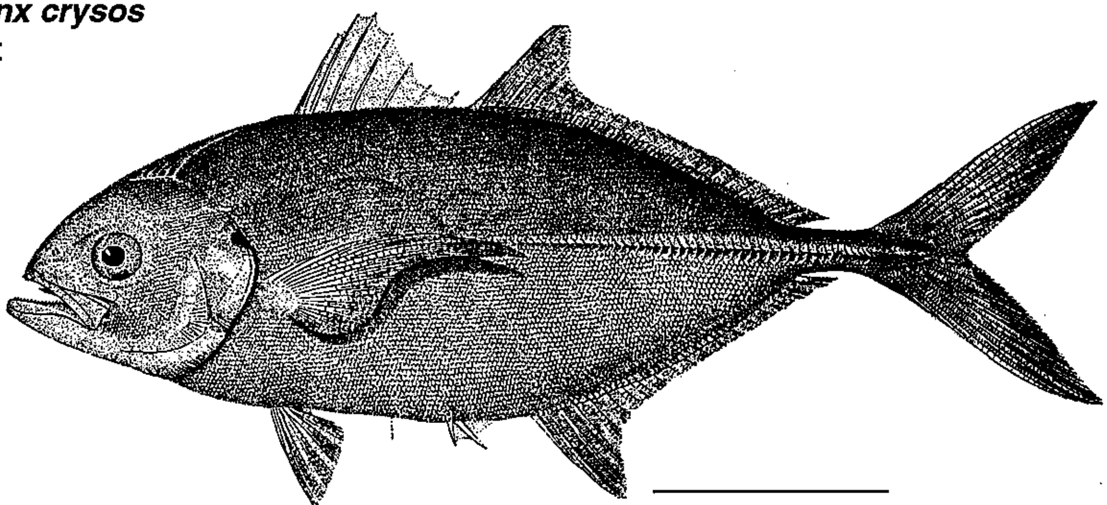
# Blue runner

*Caranx crysos*
**Adult**




(from Goode 1884)

**Common Name**: blue runner
**Scientific Name**: *Caranx crysos*
**Other Common Names**: jager boca, bau, deep water cavaly (McKenney et. al. 1958); *carangue coubal* (French), *cojinuda negra* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Perciformes
Family: Carangidae

**Value**
Commercial: The blue runner is one of the most commercially important species of the jacks, but stocks still remain relatively unexploited (Heald 1970, Goodwin and Johnson 1986). Annual landings of blue runner in the northeast Gulf of Mexico have been reported as approximately 600 metric tons (Heald 1970). Beach and haul seines are the primary gear used to catch blue runner, and catches occur off the coasts of Louisiana and Florida (Heald 1970). Large incidental catches occur during commercial red drum purse seining operations off of Gulf of Mexico barrier islands (Overstreet 1983). This species has traditionally been used as bait, but has gained popularity as a fresh or frozen food fish, with small amounts being exported to the Caribbean area (Shaw and Drullinger 1990). In Puerto Rico, Trinidad, and the West Indies, blue runner is an important food fish (McKenney et. al. 1958), and is marketed either fresh or salted (Shaw and Drullinger 1990). Recruitment to the fishery occurs at age III (NOAA 1985, Goodwin and Johnson 1986).

Recreational: Blue runner is fished recreationally, primarily in the late spring and summer, in coastal areas from jetties and small boats (McKenney et al. 1958, Sutherland 1977, Shipp 1986). An estimated 1,079,000 were caught by anglers in the Gulf of Mexico during 1991 (Van Voorhees et al. 1992). It is used extensively as bait along the southeast coast of the United States (McKenney et al. 1958, NOAA 1985), especially for larger reef fishes such as amberjacks, and for deep sea fishing for sailfish (McKenney et al. 1958).

Indicator of Environmental Stress: The blue runner is not typically used in studies of environmental stress.

Ecological: The blue runner is a carnivorous species, feeding throughout the water column (NOAA 1985).

**Range**
Overall: This fish is widely distributed in the western Atlantic Ocean from Nova Scotia to Brazil, and throughout the Gulf of Mexico (McKenney et al. 1958, Fischer 1978, Johnson 1978, Goodwin and Johnson 1986). It also occurs in the Caribbean, the West Indies, and Bermuda. The areas of greatest abundance of blue runner are the tropical waters along the southeast coast of the United States along the western side of the Gulf Stream and between the Florida current and the shore, throughout the West Indies, and seasonally throughout the Gulf of Mexico (McKenney et al. 1958, Allison 1961, Johnson 1978, Goodwin and Johnson 1986). It is particularly common along the lower east coast of Florida (MacKenney et al. 1958).

Within Study Area: Blue runner occur seasonally from Tampa Bay, Florida to the Rio Grande, Texas (Goodwin and Finucane 1985, Goodwin and Johnson 1986,

Table 5.27. Relative abundance of blue runner in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | √ | | √ | | |
| Ten Thousand Islands | ○ | | ○ | | |
| Caloosahatchee River | | | | | |
| Charlotte Harbor | ○ | | ○ | | |
| Tampa Bay | ○ | | ○ | | |
| Suwannee River | ○ | | ○ | | |
| Apalachee Bay | ○ | | ○ | | |
| Apalachicola Bay | ○ | | ○ | | |
| St. Andrew Bay | ◉ | | ○ | | |
| Choctawhatchee Bay | ○ | | ○ | | |
| Pensacola Bay | ○ | | ○ | | |
| Perdido Bay | ○ | | ○ | | |
| Mobile Bay | ○ | | ○ | | |
| Mississippi Sound | ○ | ◉ | ◉ | ◉ | ◉ |
| Lake Borgne | | | | | |
| Lake Pontchartrain | | | | | |
| Breton/Chandeleur Sounds | | | | | |
| Mississippi River | | | | | |
| Barataria Bay | | | ○ | | |
| Terrebonne/Timbalier Bays | | | √ | | |
| Atchafalaya/Vermilion Bays | | | | | |
| Calcasieu Lake | | | | | |
| Sabine Lake | | | | | |
| Galveston Bay | √ | | √ | | |
| Brazos River | | | | | |
| Matagorda Bay | | | | | |
| San Antonio Bay | | | | | |
| Aransas Bay | | | | | |
| Corpus Christi Bay | | | | | |
| Laguna Madre | | | | | |
| Baffin Bay | | | | | |
| | A | S | J | L | E |

*Life stage* (columns)

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

Adams pers. comm., Nelson et al. 1992). Within U.S. estuaries of the Gulf of Mexico, the blue runner appears to be most common along the west coast of Florida (Table 5.27) (Heald 1970, Fischer 1978), and not generally common in estuaries west of the Mississippi River (Shaw and Drullinger 1990, Adams pers. comm., Cambell pers. comm., Rice pers. comm.). However, larval data suggest that blue runner are common in coastal marine waters west of the Mississippi River (Ditty pers. comm.)

**Life Mode**

This is a pelagic, fast-swimming species (Goodwin and Johnson 1986). Early life stages are planktonic. Late juveniles form small schools in and at the edges of the Florida Current (McKenney et. al. 1958). Adults usually form schools, although larger individuals will remain solitary (Nichols 1938, Goodwin and Finucane 1985).

**Habitat**

Type: The blue runner is neritic and oceanic inhabiting primarily tropical and warm waters surrounding continents or large islands (McKenney et. al. 1958, Goodwin and Johnson 1986). In the Atlantic Ocean off the southeastern U.S., larvae and juveniles inhabit offshore waters in association with the Gulf Stream (Berry 1959). The larvae of blue runner are present in the Gulf Stream from May through November and are in greatest abundance from mid-June to mid-August (Fable et al. 1981, Shaw and Drullinger 1990). Larvae are found in the Gulf of Mexico from April through August (Ditty et al. 1988), and the greatest numbers occur in the central region, where they are found in waters over the continental shelf (Shaw and Drullinger 1990). Juveniles occur over deep water, but are usually present in the upper 100 m of the water column (McKenney et al. 1958). However, they have been known to occur in depths of 180 m or greater (Johnson 1978). Individuals greater than 100 mm SL inhabit the shelf and nearshore waters of the Atlantic coast, and peak in abundance during June and July (Berry 1959, Dooley 1972, Johnson 1978, Goodwin and Johnson 1986). Early juveniles are associated with floating objects such as sargassum seaweed or jellyfish, and acquire a cryptic coloration during this period (Nichols 1938, Lindall et al. 1973, Johnson 1978, NOAA 1985, Shipp 1986).

Substrate: Because this species is pelagic, it occurs over a wide variety of substrates (NOAA 1985).

Physical/Chemical Characteristics:

Temperature: Recently hatched larvae (<2.5 mm SL) occur in water surface temperatures of 28.8°-30.1° C (Shaw and Drullinger 1990), while larvae of all sizes occur in thermal habitats of 20.4-32°C (Johnson 1978, Shaw and Drullinger 1990). Juveniles are found at

20.4°-29.4°C (Johnson 1978). Adults inhabit areas where the temperature ranges from 20.0-30.8°C.

Salinity: The blue runner inhabits polyhaline to euhaline areas depending on life stage. Offshore spawning suggests that eggs occupy areas of marine salinities. Newly hatched larvae occur in salinities of 25.0-36.2‰ (Shaw and Drullinger 1990). Larvae occupy salinities ranging from 24.8-37.7‰, with most larvae found below 33‰ (Shaw and Drullinger 1990). Juveniles are taken in 35.2-36.0‰, and adults inhabit areas ranging from 26.0 to 36.2‰ (Johnson 1978).

Migrations and Movements: In the Caribbean Sea and Atlantic Ocean, larval and early juvenile blue runner are carried to the Florida coast and then northward by the Antilles Current and Gulf Stream, respectively. Juveniles 80-140 mm in length may migrate to inshore waters of the Atlantic coast or move eastward with the currents (Berry 1959, Dooley 1972). Adults and juveniles favor the northern Gulf of Mexico during warm months (Berry 1959). Adults and larger fish migrate southward or move offshore during colder months (December to June) (Berry 1959, Johnson 1978, NOAA 1985). Adults probably migrate offshore during the spawning season to reproduce (Goodwin and Finucane 1985).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe.

Spawning: Based on the collection of larvae in the Gulf of Mexico, spawning occurs from January to August in offshore waters, but some evidence indicates spawning may occur throughout the year in some areas of the Gulf (Goodwin and Finucane 1985). Along the southeast Atlantic coast of the United States, spawning occurs from early April to early September (Berry 1959). The greatest period of activity occurs during June, July, and August (Goodwin and Finucane 1985). Larvae are most abundant in the Gulf Stream mid-June to mid-August (McKenney et al. 1958, Berry 1959, Johnson 1978, Ditty et al. 1988), but are captured throughout the year in some areas of the Gulf (Goodwin and Finucane 1985). Spawning location, based on occurrence of larvae, is offshore and occurs in water depths >40m (Ditty pers. comm., Shaw and Drullinger 1990).

Fecundity: Reported fecundity varies from 41,000 ova in a 288 g fish to 1,546,000 ova in a 1,076 g fish. Goodwin and Finucane (1985) have developed curvilinear equations to estimate fecundity.

**Growth and Development**

Egg Size and Embryonic Development: Little information is available on blue runner eggs, but the closely related *Caranx mate* has clear, spherical, pelagic eggs with a yolk diameter of 0.66±0.02 mm (Shaw and Drullinger 1990).

Age and Size of Larvae: Blue runner larvae are not well known, but the larvae of the closely related *Caranx mate* range 1.32 to 1.70 mm SL when they hatch, and average length is 1.46 mm SL (Shaw and Drullinger 1990).

Juvenile Size Range: Transformation to the juvenile stage occurs around 12 mm (Ditty pers. comm.). The most noticeable changes in the structural development of a blue runner occur in two stages. The first stage happens between 8-12 mm and the second between 45-60 mm (McKenney et. al. 1958). Blue runner is a fast growing species. Approximately 75% of their maximum size is attained by age 3 to 4 years (Johnson 1978, Goodwin and Johnson 1986).

Age and Size of Adults: Males mature by a length of 225 mm SL, but females do not mature until approximately 247 mm SL. The largest recorded blue runner is 711 mm FL (Johnson 1978, Goodwin and Johnson 1986). Estimates of maximum weight approach 2.73 kg. The blue runner is a moderately long-lived species, with a possible life span of up to 11 years. Goodwin and Johnson (1986) have developed a growth equation for this species.

**Food and Feeding**

Trophic Mode: The blue runner is a carnivorous predator, feeding on fish, crustaceans, and other invertebrates (McKenney et al. 1958, NOAA 1985). Larval and early juveniles are carnivorous planktivores capable of foraging throughout the water column.

Food Items:
Larvae forage almost entirely on cyclopoid copepods. Juveniles also feed on calanoid copepods. At lengths greater than 10.0 mm, juvenile blue runner eat amphipods, larval fish, decapod larvae, ostracods, and fish eggs; however, copepods remain the main diet constituent (McKenney et al. 1958, Dooley 1972). Adults feed throughout the water column on fishes, crustaceans, and other invertebrates (NOAA 1985).

**Biological Interactions**

Predation: Juveniles are evidently preyed on by surface-feeding shore birds such as terns (McKenney et al. 1958).

Factors Influencing Populations: Schools of carangid fish have been found in association with schools of red drum (Overstreet 1983). Commercial fishermen use this knowledge to set nets for drum, and catch blue runner as well.

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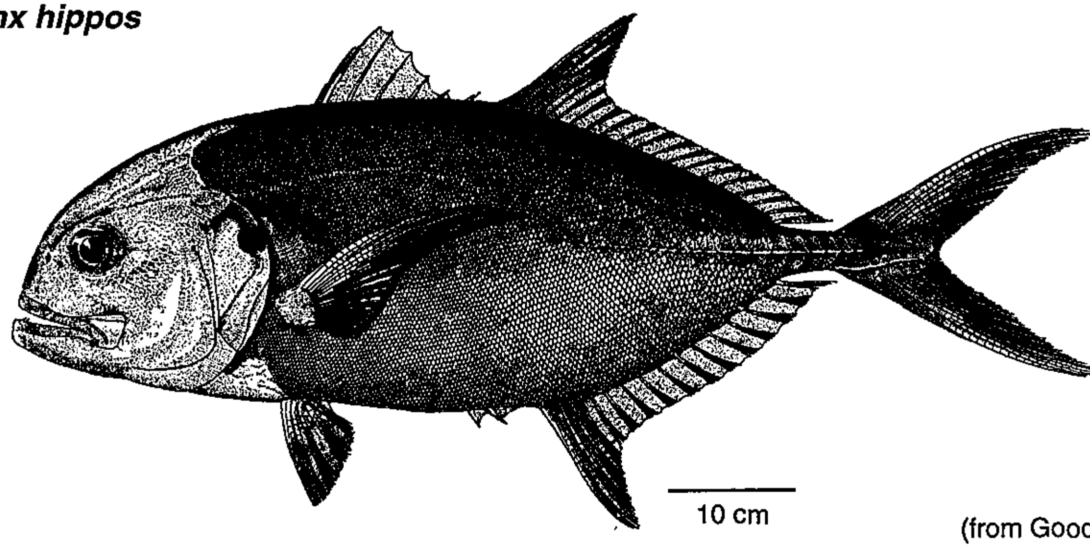
## Crevalle jack




(from Goode 1884)

**Common Name**: crevalle jack
**Scientific Name**: *Caranx hippos*
**Other Common Names**: jack, common jack, yellowtail jack, hardtail jack, amber jack, crevalle, jack crevalle, runner, Jenny Lind, rudder fish (Hildebrand and Schroeder 1928, Reid 1955, Springer and Woodburn 1960, Gunter and Hall 1963, Gunter and Hall 1965); *carangue crevalle* (French), *jurel común* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Perciformes |
| Family: | Carangidae |

**Value**

Commercial: The meat of this fish is generally considered to be medium quality, and is therefore not particularly sought by commercial fishermen. The commercial fishery in the U.S. portion of the Gulf of Mexico is primarily in western Florida, where they are caught mostly by haul seine and gillnet, but also by purse seine, handline, and trolling. In Venezuela, it is caught mainly by purse seines, handlines, "mandingas," and traps. It is commonly found in Panama markets where it is esteemed as a food fish and brings a good price (Benson 1982, Hildebrand and Schroeder 1928, Fischer 1978, Johnson et al. 1985).

Recreational: An estimated 1,725,000 crevalle jacks were caught by recreational fishermen in the Gulf of Mexico during 1991 (Van Voorhees et al. 1992). The crevalle jack is known for its hard fighting ability and many anglers enjoy this challenging fish, but it is regarded as a nuisance by some since it takes considerable time to land on light tackle (Tabb and Manning 1961, Hoese and Moore 1977, Benson 1982). Despite general opinion, it can be very good when properly prepared and cooked (Johnson et al. 1985). This is the most common of the large carangid fishes caught by recreational fisherman on the west coast of Florida (Reid 1954).

Indicator of Environmental Stress: The crevalle jack is not typically used in studies of environmental stress.

Ecological: This is a large, pelagic carnivore that preys mainly on other fish (Hildebrand and Schroeder 1928, Breuer 1949, Perret et al. 1971, Swingle and Bland 1974).

**Range**

Overall: The range for this species includes the western Atlantic from Nova Scotia to Uruguay, and tropical and temperate waters around the world, primarily in shallow continental waters. There is one record only from the Bahamas and a few from the West Indies, where it is probably uncommon. It is relatively more common in the northern part of its range (Hildebrand and Schroeder 1928, Bigelow and Schroeder 1953, Berry 1959, Hoese and Moore 1977, Fischer 1978, Johnson 1978).

Within Study Area: This jack is present throughout the Gulf of Mexico. It is common in Texas and Louisiana waters and parts of the west coast of Florida (Hoese and Moore 1977, Fischer 1978) (Table 5.28).

**Life Mode**

This is a large pelagic fish common in offshore waters. It is most active during the day in the upper water column. Both adults and juveniles are schooling, but

Table 5.28. Relative abundance of crevalle jack in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ◉ | | ◉ | | |
| Ten Thousand Islands | ○ | | ○ | | |
| Caloosahatchee River | ○ | | ○ | | |
| Charlotte Harbor | ◉ | | ○ | | |
| Tampa Bay | ◉ | | ◉ | | |
| Suwannee River | ○ | | ○ | | |
| Apalachee Bay | ○ | | ○ | | |
| Apalachicola Bay | ○ | | ○ | | |
| St. Andrew Bay | ○ | | ○ | | |
| Choctawhatchee Bay | ○ | | ○ | | |
| Pensacola Bay | ○ | | ○ | | |
| Perdido Bay | ○ | | ○ | | |
| Mobile Bay | ○ | | ○ | | |
| Mississippi Sound | ○ | ○ | ○ | ○ | ○ |
| Lake Borgne | | | ○ | | |
| Lake Pontchartrain | | | ○ | | |
| Breton/Chandeleur Sounds | ○ | | ○ | | |
| Mississippi River | | | ○ | | |
| Barataria Bay | ○ | | ○ | | |
| Terrebonne/Timbalier Bays | √ | | ○ | | |
| Atchafalaya/Vermilion Bays | | | ○ | | |
| Calcasieu Lake | | | ○ | | |
| Sabine Lake | √ | | √ | | |
| Galveston Bay | √ | | ○ | | |
| Brazos River | | | ○ | | |
| Matagorda Bay | ○ | | ○ | | |
| San Antonio Bay | ○ | | ○ | | |
| Aransas Bay | ○ | | ○ | | |
| Corpus Christi Bay | ○ | | ○ | | |
| Laguna Madre | ○ | | ◉ | | |
| Baffin Bay | ○ | | ○ | | |
| | A | S | J | L | E |

*Life stage* (column heading)

| Relative abundance: | | Life stage: |
|---|---|---|
| ● | Highly abundant | A - Adults |
| ◉ | Abundant | S - Spawning |
| ○ | Common | J - Juveniles |
| √ | Rare | L - Larvae |
| blank | Not present | E - Eggs |

some large adults are solitary (Arnold et al. 1960, Springer and Woodburn 1960, Perret et al. 1971, Swingle 1971, Christmas and Waller 1973, Swingle and Bland 1974, Benson 1982).

**Habitat**

Type: Eggs and larvae are pelagic and offshore in marine salinities, and may be associated with offshore currents (Berry 1959, Benson 1982). Larvae are present in the Gulf of Mexico March through November, reaching peak abundance June through August (Ditty et al. 1988). Juveniles probably migrate inshore during the early juvenile stage (about 21 mm), and are frequently associated with floating debris and sargassum weed. Crevalle jack selectively inhabit inshore waters during the later part of the juvenile stage, usually in shallow, brackish areas and occasionally entering fresh water. Juveniles are found in bays, gulf passes, sounds, estuaries, brackish lakes and ponds, canals, and rivers, in salinities ranging from fresh to hypersaline (Hildebrand and Schroeder 1928, Gunter 1945, Reid 1955, Simmons 1957, Darnell 1958, Berry 1959, Arnold et al. 1960, Springer and Woodburn 1960, Tabb and Manning 1961, Gunter and Hall 1963, Hoese 1965, Kelley 1965, Bechtel and Copeland 1970, Franks 1970, Perret et al. 1971, Swingle 1971, Dahlberg 1972, Christmas and Waller 1973, Swingle and Bland 1974, Barret et al. 1978, Lee et al. 1980, Benson 1982, Shipp 1986).

Adults are pelagic and are associated with waters of the continental shelf and continental islands (Berry 1959). They are found in a wide range of depths from shallow inshore to oceanic waters (Benson 1982), and in salinities ranging from fresh to hypersaline (Johnson 1978). Collections have also been made in brackish estuarine waters, upstream in coastal rivers, and commonly in shallow flats (Johnson 1978, Adams pers. comm.). In Texas, they occur in the nearshore area from February or March through October and sometimes November, with variable peaks in abundance (Springer and Pirson 1958). Larger adults remain offshore and are seldom taken in bays and other inshore waters (Gunter 1945, Christmas and Waller 1973, Lindall et al. 1973, Benson 1982).

Substrate: Since this is a pelagic schooling fish, it is not associated with a particular bottom type, but it has been recorded from bottoms of mud, sand, shelly sand, and hard packed bottoms with a mud and algae film (Reid 1955, Gunter and Hall 1963, Benson 1982).

Physical/Chemical Characteristics:

Temperature - Larvae: Larvae have been recorded from water temperatures of 20.0 to 29.0°C (Johnson 1978).

Temperature - Juveniles and Adults: Juveniles and adults have been collected over a temperature range of 15.0 to 38.0°C (Gunter 1945, Gunter and Hall 1963, Franks 1970, Roessler 1970, Perret et al. 1971, Wang and Raney 1971, Christmas and Waller 1973, Perret and Caillouet 1974, Juneau 1975, Tarver and Savoie 1976, Barret et al. 1978). The lower lethal temperature limit for juveniles is around 7.4-10.0°C (Hoff 1971, Gilmore et al. 1978). Their apparent preference is 25.0-29.9°C (Perret et al. 1971). Adults are most common in temperatures of 18 to 33.6°C (Gunter 1945, Johnson 1978).

Salinity - Larvae: Larvae have been recorded in salinities of 35.2 to 36.7‰ (Johnson 1978).

Salinity - Juveniles and Adults: Both adults and juveniles are considered euryhaline and have been found in waters with salinities ranging from 0.0 to 60.0‰ (Gunter 1942, Gunter 1945, Reid 1955, Gunter 1956, Simmons 1957, Gunter and Hall 1963, Gunter and Hall 1965, Dugas 1970, Franks 1970, Roessler 1970, Perret et al. 1971, Swingle 1971, Wang and Raney 1971, Dahlberg 1972, Christmas and Waller 1973, Perret and Caillouet 1974, Swingle and Bland 1974, Juneau 1975, Tarver and Savoie 1976, Barrett et al. 1978). In one study, fish 30 to 285 mm in total length (TL) were mostly caught in salinities above 30.0‰ (Gunter 1945). In another study, the majority of fish ranging from 20 to 180 mm TL with an average size of 60 mm TL were collected from 10.0 to 19.9‰ (Perret et al. 1971).

Dissolved Oxygen: Juveniles have been collected in waters with a dissolved oxygen (DO) range of 4.0 to 7.5 parts per million (ppm) (Barrett et al. 1978).

Movements and Migrations: Little is known about movements and migrations of this species, but they probably involve a complex pattern of spawning and developmental migrations, and temperature induced movements. Adults migrate offshore to spawn, but a concerted migration is improbable due to the extended spawning season (Gunter 1945, Berry 1959, Moe 1972, Johnson 1978, NOAA 1985). Larvae are associated with the northern movements of the Gulf Stream (Berry 1959). Early juveniles, 21-55 mm standard length (SL), migrate inshore. Juveniles enter bays and estuaries from the Gulf when the water temperature is above 20.0°C, and they have reached 90 to 285 mm TL in size (Gunter 1945, Benson 1982). They probably migrate south or move into warmer, offshore waters during colder months (Berry 1959). In Florida, the crevalle jack has been observed in shallow water at all times of the year except during winter months (Reid 1954). Juveniles and adults have been recorded along the Atlantic coast and in the Gulf of Mexico from April through November. However, they are most common in coastal waters of the Gulf from June to October (Joseph 1952, Joseph and Yerger 1956, Bass and Hitt 1978).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe.

Spawning: Spawning evidently occurs over the outer shelf in oceanic waters greater than 40 m in depth (Ditty pers. comm.), and probably to the south of the Florida Straits (Berry 1959, Hoese 1965, Fahay 1975, Benson 1982). The spawning season in the western Atlantic is thought to be March to September (Berry 1959).

Fecundity: Actual fecundity is unknown. In one study, the ovaries of a 520 mm TL female with well developed eggs were 110 by 60 mm (Beebe and Tee-Van 1928).

**Growth and Development**

Egg Size and Embryonic Development, and Age and Size of Larvae: The actual spawning locations of crevalle jack are not well known, and little is known about the development of eggs and larvae (Berry 1959, Johnson 1978).

Juvenile Size Range: Metamorphosis to the juvenile stage occurs around 12 mm SL (Ditty pers. comm.). The growth rate is reported to increase after juveniles reach a length of 50 mm (Nichols 1937, Johnson 1978). Age and size at sexual maturity remain uncertain. Males with developed testes have been collected when 540 to 690 mm SL in size (Berry 1959), and a 406 mm SL female was recorded as having well developed eggs (Beebe and Tee-Van 1928).

Age and Size of Adults: Specific maximum sizes for this species are uncertain. Lengths of 1010 mm TL and weights up to 25 kg have been documented, but unsubstantiated reports have recorded fish measuring more than 150 cm TL and weighing 32 kg (Berry 1959, Fischer 1978, Shipp 1986). Adult females are typically larger than males of a given age (Berry 1959).

**Food and Feeding**

Trophic Mode: This species is a diurnal carnivore, apparently preying on small schooling fish of the coastal zone (Hildebrand and Schroeder 1928, Saloman and Naughton 1984).

Food Items: This species has been observed in Florida feeding wildly along shorelines on larval fishes consisting mostly of ladyfish, anchovies, and cyprinodonts (Tabb and Manning 1961). Small jacks have been found to prey mostly on a variety of clupeids, while medium size fish usually ate clupeids and sparids, and large fish consumed various clupeids, carangids, and sparids (Saloman and Naughton 1984). Large fish appear to be more opportunistic than smaller ones, but food availability seems to a major factor in determining diet since it changes between sizes, seasons, areas, and years. Gulf menhaden is a favorite food (Breuer 1949, Swingle and Bland 1974) as well as scaled sardine, anchovies, Spanish sardine, Atlantic bumper, pinfish, halfbeaks, crevalle jacks, and Atlantic cutlassfish. After fish, crustaceans such as penaeid shrimp or portunid crabs are the second most important prey item depending on area. In addition, numerous other fish are consumed as well as squid, bivalves, gastropods, echinoderms, sea grasses, algae, sand, and wood (Darnell 1958, Odum 1971, Benson 1982, Saloman and Naughton 1984).

**Biological Interactions**

Predation: Known predators include larger, fast swimming predators such as great barracuda and blackfin tuna (Berry 1959).

Factors Influencing Populations: Parasites observed on this species include: Nematodes- *Ascaris* sp.; Cestodes- *Tetrarhyncus bisculatus; Trematodes- Distomum appendiculatum, D. tenue, Gasterostomum arcuatum*, and *G. gracilescens* (Linton 1904).

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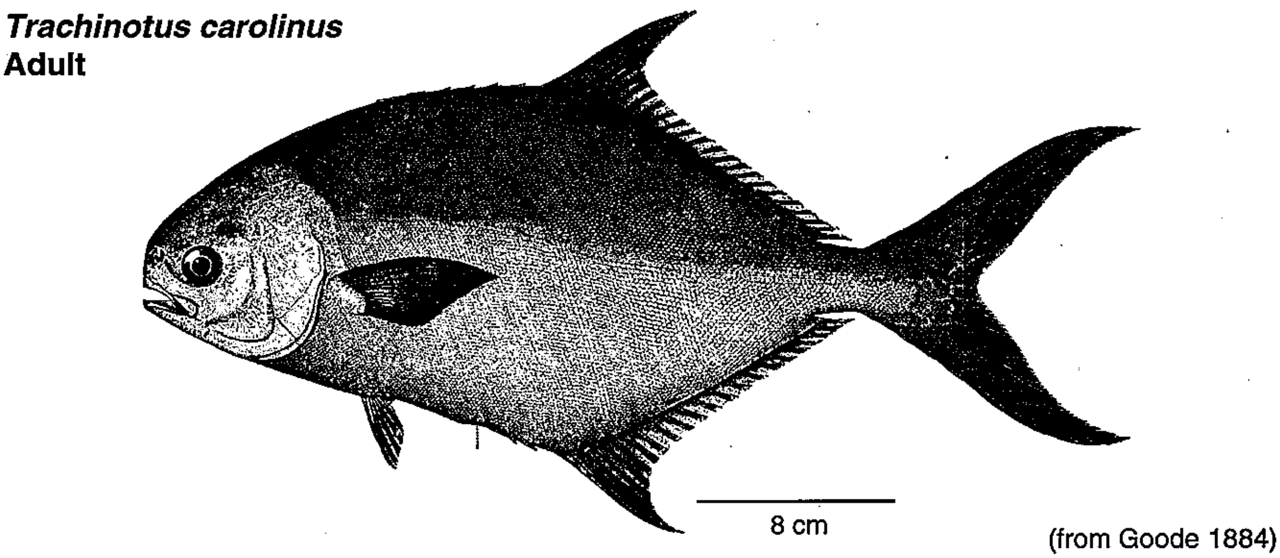
# Florida pompano




(from Goode 1884)

**Common Name:** Florida pompano
**Scientific Name:** *Trachinotus carolinus*
**Other Common Names**: pompano, common pompano, Atlantic pompano, sunfish, *pampano amarillo* (Spanish), *pompaneau sole* (French) (Hildebrand and Schroeder 1928, Gunter 1945, Arnold et al. 1960, Gunter and Hall 1965, Hoese 1965, Parker 1965, Berry and Iversen 1967, Fischer 1978, Benson 1982, NOAA 1985).
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Perciformes |
| Family: | Carangidae |

**Value**
Commercial: This fish is highly desired due to its excellent flavor and high market value. Although catches are not large and are often unpredictable, the Florida pompano supports an important fishery along the South Atlantic and Gulf of Mexico coasts, with Florida the leading producer. Most fish caught in Florida are landed during winter on the west coast from Monroe County to Charlotte County, primarily south of Cape Romano. Commercially harvested fish enter the market at total lengths (TL) of 250-360 mm and 0.5-0.7 kg. They were historically harvested mostly by trammel nets, but with the advent of nylon monofilament most are now taken by gill nets (Hildebrand and Schroeder 1928, Gunter 1945, Fields 1962, Berry and Iversen 1967, Finucane 1969a, Iversen and Berry 1969, Bellinger and Avault 1970).

Recreational: Florida pompano are a favorite fish among anglers due to their high quality as a food fish and their fighting ability on light tackle. An estimated 269,000 fish were caught by anglers during 1991 in the Gulf of Mexico (Van Voorhees et al. 1992). Pompano are usually caught by bottom fishing offshore, or by casting from shore or boat (Gunter 1945, Berry and Iversen 1967, Iversen and Berry 1969, Bellinger and Avault 1970).

Indicator of Environmental Stress: Florida pompano are not typically used in studies of environmental stress.

Ecological: The Florida pompano is found in coastal and estuarine waters, where it is a generalized carnivore feeding primarily on benthic prey. Juveniles can be a dominant species of the surf zone (Gunter 1958, Bellinger and Avault 1971, Benson 1982).

**Range**
Overall: The Florida pompano is found in the coastal waters from Cape Cod, Massachusetts to southeastern Brazil. It is widely distributed but uncommon among islands of the West Indies, being most abundant along continental waters. It is also uncommon north of Cape Hatteras, and the highest abundance occurs along the Florida coast (Hildebrand and Schroeder 1928, Fields 1962, Berry and Iversen 1967, Iversen and Berry 1969, Gilbert 1986, Shipp 1986).

Within Study Area: This species occurs throughout the Gulf of Mexico, but is most abundant along the west coast of Florida from Florida Bay to Charlotte Harbor (Table 5.29) (Hoese and Moore1977, Fischer 1978, Gilbert 1986). In the western Gulf of Mexico, it is apparently more common south of the Rio Grande, in Mexico, than in Texas (Hildebrand 1954).

Table 5.29. Relative abundance of Florida pompano in 31 Gulf of Mexico estuaries (Nelson et al. 1992).

| *Estuary* | *Life stage* A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ● | | ◉ | | |
| Ten Thousand Islands | O | | O | | |
| Caloosahatchee River | √ | | √ | | |
| Charlotte Harbor | ◉ | | ◉ | | |
| Tampa Bay | O | | O | | |
| Suwannee River | √ | | √ | | |
| Apalachee Bay | O | | O | | |
| Apalachicola Bay | √ | | √ | | |
| St. Andrew Bay | O | | O | | |
| Choctawhatchee Bay | O | | O | | |
| Pensacola Bay | √ | | O | | |
| Perdido Bay | | | O | | |
| Mobile Bay | O | √ | O | √ | √ |
| Mississippi Sound | √ | O | ◉ | O | O |
| Lake Borgne | | | | | |
| Lake Pontchartrain | | | | | |
| Breton/Chandeleur Sounds | O | O | O | O | O |
| Mississippi River | | | O | | |
| Barataria Bay | | | O | | |
| Terrebonne/Timbalier Bays | √ | | O | | |
| Atchafalaya/Vermilion Bays | | | √ | | |
| Calcasieu Lake | | | O | | |
| Sabine Lake | | | | | |
| Galveston Bay | | | O | | |
| Brazos River | | | | | |
| Matagorda Bay | | | O | | |
| San Antonio Bay | O | | O | | |
| Aransas Bay | √ | | O | | |
| Corpus Christi Bay | √ | | O | | |
| Laguna Madre | O | | ◉ | | |
| Baffin Bay | √ | | √ | | |
| | A | S | J | L | E |

**Relative abundance:**
- ● Highly abundant
- ◉ Abundant
- O Common
- √ Rare
- blank Not present

**Life stage:**
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

**Life Mode**

Pompano are a dominant species of exposed sandy beach habitats. All stages are pelagic and nektonic, with diurnal feeding behavior (Finucane 1969b, Armitage and Alevizon 1980, Modde and Ross 1981, Benson 1982). Juveniles and adults show schooling behavior (Benson 1982, Christmas and Waller 1973, Simmons 1957).

**Habitat**

Type: Eggs and larvae are pelagic in offshore waters. Larvae have been collected in depths of 5.5 m and as far as 24.2 km offshore in marine waters (Fields 1962, Finucane 1969a, Fahay 1975, Johnson 1978). The optimum habitat for juveniles is shallow water, low energy, marine surf zones along open beaches with gradual slopes; however, they are also reported from marshes and bays (Gunter 1945, Gunter 1958, Springer and Woodburn 1960, Gunter and Hall 1965, Hoese 1965, Iversen and Berry 1969, Bellinger and Avault 1971, Swingle 1971, Dahlberg 1972, Armitage and Alevizon 1980, Modde 1980, Modde and Ross 1981). They are collected in salinities ranging from mesohaline to euhaline, but appear to prefer polyhaline and higher salinities (Gunter 1945, Springer and Woodburn 1960, Gunter and Hall 1965, Finucane 1968, Bellinger and Avault 1970, Swingle 1971, Christmas and Waller 1973, Johnson 1978). Adults are abundant around inlets and along sandy beaches of barrier islands, and around oil platforms and artificial reefs. They tend to be more characteristic of marine waters in turbid rather than clear areas, although they are collected occasionally from bay waters. The recorded salinities for sites where adults have been collected range from mesohaline to euhaline, but captive fish have been adapted to fresh water. Adults may be found in shallow waters, but are also found in waters somewhat deeper than juveniles with fish over 200 mm TL being collected from depths of 33 to 40 m (Hildebrand 1954, Parker 1965, Finucane 1969a, Johnson 1978, Benson 1982).

Substrate: The Florida pompano is typically found over sandy bottoms with little or no rooted vegetation. They are also reported from bottoms of broken shell debris, and silt and mud (Bellinger and Avault 1971, Modde 1980, Modde and Ross 1981).

Physical/Chemical Characteristics:

Temperature - Eggs and Larvae: Eggs in laboratory conditions developed up to middle and late gastrulation at temperatures from 23.0 to 25.0° (Finucane 1969b).

Temperature - Juveniles and Adults: Juveniles have been taken from 10.0° to 34.9°C and (Gunter 1945, Springer and Woodburn 1960, Gunter and Hall 1963, Gunter and Hall 1965, Finucane 1969a, Bellinger and

Avault 1970, Perret et al. 1971, Christmas and Waller 1973), and adults from a temperature range of 17.0° to 31.7°C (Finucane 1969a, Johnson 1978). The majority of fish collected are from a temperature range of 28.0 to 31.7°C (Finucane 1969a). Temperature appears to strongly affect the presence and behavior of this species. Experimental work has shown the need for stable temperatures for maximum growth, with the ideal temperature being 25.0°C or above (Finucane 1969b). Feeding is reduced below 18.0°C, and ceases at 13.0°C. Activity is also greatly reduced at this temperature (Finucane 1968). Physiological shock becomes evident at about 12.0°C with partial to complete kills occurring from 10.0° to 15.5°C (Berry and Iversen 1967, Moe et al. 1968). All fish have an upper lethal limit of about 38.0°C, although small juveniles have been observed in tide pools at temperatures above 46.0°C (Moe et al. 1968).

Salinity - Eggs and Larvae: Under laboratory conditions, eggs developed up to middle and late gastrulation at salinities of 31.2 to 37.71‰ (Finucane 1969b).

Salinity - Juveniles: Juveniles have been reported from salinities ranging from 9.3 to 36.7‰, with a preference shown for 20‰ and higher (Gunter 1945, Springer and Woodburn 1960, Gunter and Hall 1963, Gunter and Hall 1965, Finucane 1968, Finucane 1969a, Bellinger and Avault 1970, Perret et al. 1971, Swingle 1971, Christmas and Waller 1973). One collection from Laguna Madre, Texas reported large schools at 45 to 50‰ (Simmons 1967). Fish in laboratory conditions were able to tolerate salinities down to 1.27‰ (Moe et al. 1968).

Salinity - Adults: Adults occur in salinities from 32.1 to 35.6‰. They do not normally enter water less than 32‰, although fish in captivity were acclimated to 1.27‰ (Moe et al. 1968, Johnson 1978).

Dissolved Oxygen: This species has been collected from a dissolved oxygen (DO) range of 3.43 to 5.64 parts per million (ppm), but is adversely affected below 4 ppm with death occurring at about 2.5 ppm (Finucane 1969a, Moe et al. 1968).

pH: Experiments with pH showed physiological shock at 11.9 and 3.9 on either end of the scale, and death occurring at 12.4 and 3.7 (Moe et al. 1968)

**Movements and Migrations**

The Florida pompano apparently undergoes extensive migrations, but patterns of movement are not clearly known. Spawning apparently takes place in offshore waters in early spring to late summer in the Gulf Stream or in locations where transport of eggs and larvae are influenced by current (Fields 1962, Moe 1972). In the Gulf of Mexico, larvae are present May through August (Ditty et al. 1988) as they move with currents. Young pompano arrive in the surf zone as juveniles, at a size of approximately 10 to 15 mm TL (Bellinger and Avault 1970, Bellinger and Avault 1971, Christmas and Waller 1973, Finucane 1969a, Gunter 1945, Hoese 1965, Moe et al. 1968, Perret et al. 1971, Modde 1980, Modde and Ross 1981). Juveniles leave the surf zone when 75 to 150 mm TL for deeper water and move south along the coast, probably in response to colder winter temperatures (Bellinger and Avault 1970, Berry and Iversen 1967, Fields 1962, Gunter 1945, Iversen and Berry 1969, Swingle 1971).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe.

Spawning: Spawning has not been directly observed. Specific spawning areas are unknown, but they are probably offshore (Fields 1962, Berry and Iversen 1967, Finucane 1969a, Sabins and Truesdale 1974, Fahay 1975, Gilbert 1986), and spawning may occur over an extended period of time. It may begin as early as February and peak from April to June followed by lesser spawnings in summer and early fall (July-October). Spawning throughout the year is possible in the tropical Gulf of Mexico and the Caribbean Sea (Gunter 1945, Gunter 1958, Berry and Iversen 1967, Finucane 1969a, Iversen and Berry 1969, Christmas and Waller 1973, Sabins and Truesdale 1974).

Fecundity: Maturity probably occurs after one year with spawning unlikely until the second year (Finucane 1968, Moe et al. 1968). At least four different egg development stages are present in adult females indicating multiple spawning (Finucane 1968) with an average size female containing 4 to 8 hundred thousand eggs (Finucane 1968, Moe et al. 1968, Finucane 1969a).

**Growth and Development**

Egg Size and Embryonic Development: Mature unfertilized eggs are round, symmetrical, and average 0.7 mm in diameter. They possess a large yolk with a narrow perivitelline space occupying 10 to 15% of the egg volume. One oil globule is evident, and the surface of the egg is smooth (Finucane 1968,1969a). Fertilized eggs are spherical with a single, large oil globule, partially segmented yolk mass, narrow perivitelline space, and a sculptured membrane. Average diameter of the oil globule and egg is 0.29 mm, and 0.92 mm respectively. Eggs are almost colorless and have an irregularly segmented light yellow yolk. The oil globule is nearly spherical and is dark yellow in a position at the top of the egg. No chromatophores are present

(Finucane 1969b). Eggs incubated at 23°-25°C under laboratory conditions reached blastula stage 10-12 hours after fertilization; mid to late gastrulation required 20-22 hours. Eggs did not survive past that stage (Finucane 1969b).

Age and Size of Larvae: In the month it takes larvae to reach coastal beaches after being spawned, larvae increase in size from 3 to 12 mm SL or longer (Finucane 1969a).

Juvenile Size Range: The juvenile stage begins when fish reach a standard length (SL) of about 7.0 mm and larger. At 7.0 mm SL dorsal and anal spines are prominent and soft rays evident. At 150 mm SL, all but dentary teeth disappear; and by about 170 mm SL the dentary teeth are not evident (Fields 1962). Daily growth rates range from 0.5 mm/day for fish in the surf zone to 1.3 mm/day for hatchery reared specimens (Bellinger and Avault 1970, Johnson 1978). Rates of 25 to 42 mm for monthly growth under optimal conditions has been noted with 255 to 356 mm TL possible for first year growth (Finucane 1968, 1969a, Moe et al. 1968, Bellinger and Avault 1970). A weight gain of 18 g/month was reported for hatchery reared fish and weights of 454 to 567 g were considered possible as a first year weight for fish in mariculture (Finucane 1968, 1969b).

Age and Size of Adults: Wild fish probably first spawn in their second year, but in hatchery culture it may be possible to spawn them in less than 2 years (Finucane 1968, Moe et al. 1968). Ripe fish taken in Florida were 275 to 380 mm TL and weighed 456 to 1140 g (Finucane 1968). Other Florida studies reported ripe females with fork lengths (FL) of 255 and 356 mm, and females with developing oocytes were 273 to 400 mm FL and weighed 468 to 596 g. Ripe males were collected with a length range of 225 to 230 mm FL (Finucane 1968, 1969a, Moe et al. 1968). The maximum size for this fish is about 450 mm TL (Hoese and Moore 1977). Florida pompano probably live 3 or 4 years under natural conditions (Berry and Iversen 1967).

**Food and Feeding**

Trophic Mode: Florida pompano are a generalized carnivore that feed primarily during the day on infaunal bottom bivalves (Finucane 1969a, Bellinger and Avault 1971, Armitage and Alevizon 1980, Benson 1982). Adults have large, well developed pharyngeal plates which allow them to feed on hard-shelled prey items such as bivalves and crabs (Bellinger and Avault 1971). Smaller pompano are opportunistic feeders, apparently preying on those organisms that are most available at the time and utilizing the surf to help uncover food. As juvenile pompano grow in size, they undergo a shift towards hard-shelled prey items (Bellinger and Avault 1971).

Food Items: Smallest size classes feed primarily on benthic and pelagic invertebrates, frequently eating polychaetes, amphipods, gastropod larvae, insects, and some calanoid copepods. The frequency of these items decrease as the fish grows (Hildebrand and Schroeder 1928, Berry and Iversen 1967, Bellinger and Avault 1971). Fish 10 to 25 mm TL were found to have eaten polychaetes, amphipods, gastropod larvae, mysids, brachuran megalops, and dipteran larvae. When 26 to 50 mm TL they ate fewer polychaetes and amphipods, and ate a wider variety of organisms, but still fed heavily on gastropod larvae, post larval shrimp, clams, and brachuran megalops. Fish 76 to 125 mm TL fed most frequently on small clams especially *Donax variablis* and *Hippa* species. Larger juveniles have also been reported to feed on crab larvae, barnacles, cumacea, and fish eggs and larvae (Springer and Woodburn 1960, Fields 1962, McFarland 1963, Berry and Iversen 1967, Finucane 1969a, Bellinger and Avault 1971, Modde and Ross 1981). Prey of fish 200 to 275 mm SL were primarily bivalves such as *Tellina, Donax variablis*, and *Brachiodon exustus* (Finucane 1968, Armitage and Alevizon 1980). Although not major prey items, larger pompano have been reported to eat shrimp, crabs, and fish (Gunter 1945, Gunter 1958, Miles 1949).

**Biological Interactions**

Predation: No studies have identified Florida pompano as a regular item in the diet of other fishes or higher vertebrates (Gilbert 1986). Juveniles are probably preyed on by larger fish and birds that forage along the beaches.

Factors Influencing Populations: Several parasites have been reported for this species including protozoans, nematodes encysted in the viscera or in the body cavity, cestodes encysted in mesentary and on viscera, trematodes, isopods in the mouth, gill area, and various body parts and fins, and copepods on the skin (Linton 1904, Finucane 1968). However, infestations do not appear to be heavy, and there is no evidence that parasites or diseases are a threat to this species in its natural habitat (Gilbert 1986).

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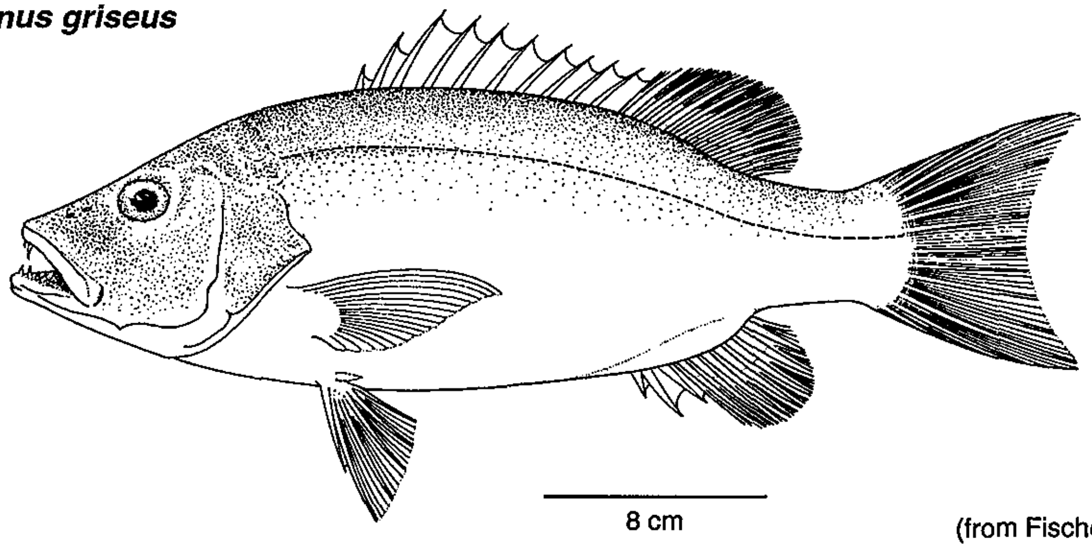
# Gray snapper



(from Fischer 1978)

**Common Name:** gray snapper
**Scientific Name:** *Lutjanus griseus*
**Other Common Names:** mangrove snapper, mango snapper, black snapper (Shipp 1986); Pensacola snapper (Goode 1884); *ivaneau sarde grise* (French), *pargo prieto* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Perciformes |
| Family: | Lutjanidae |

### Value

Commercial: The commercial fishery for gray snapper is used as a seasonal supplement to other fisheries. Hook and line, long line, and fish traps are the main fishing methods, but boat seines and gill nets are also used. The main fishing grounds are continental and island shelf waters, especially in the vicinity of Cuba, south Florida, Laguna Madre, and Venezuela (Starck and Schroeder 1971, Fischer 1978, Bortone and Williams 1986, Grimes 1987). In U.S. federal waters of the Gulf of Mexico, a 12 inch minimum size limit applies (GMFMC 1996a). This species is marketed mostly as a fresh product and is considered an excellent food fish (Fischer 1978).

Recreational: The gray snapper is common in Florida and supports an important sport fishery with 3 and 4 year old fish making up most of the inshore harvest (Rutherford et al. 1989b). The most common angling method is hook and line with cut bait, but in southern Florida they are also caught by fish traps and spear guns (Bortone and Williams 1986). The largest landings occur in Florida where, in 1986, approximately 1,540,000 fish were landed recreationally (Starck and Schroeder 1971, NMFS 1987). Greatest catches occur in late summer. In U.S. federal waters of the Gulf of Mexico, a 12 inch minimum size limit and daily bag limit have been established (GMFMC 1996b).

Indicator of Environmental Stress: This species is not typically used in studies of environmental stress.

Ecological: The gray snapper is a general carnivore. Adults and particularly juveniles are associated with estuarine areas. Along with other snappers, this species is an important component of marine, nearshore reef, or reef-like biotopes (Bortone and Williams 1986).

### Range

Overall: The gray snapper is found in the western Atlantic, tropical and subtropical marine and estuarine waters of Florida, the West Indies, Bermuda, the Bahamas, and the shelf waters of the Gulf of Mexico. Occasionally juveniles are found as far north as Cape Cod, Massachusetts and as far south as Rio de Janeiro, Brazil (Croker 1962, Starck and Schroeder 1971, Fischer 1978, NOAA 1985).

Within Study Area: This species is distributed throughout the Gulf of Mexico. It is common along the entire Florida west coast increasing in abundance southward, and is the most common species of snapper in Florida Bay and adjacent estuaries (Tabb and Manning 1961). It is less common along the central and western Gulf coast (Starck and Schroeder 1971, Hoese and Moore 1977, Shipp 1986). The relative abundance of gray snapper in 31 Gulf of Mexico estuaries is depicted in Table 5.30 (Nelson et al. 1992, Comyns pers. comm., VanHoose pers. comm.).

Table 5.30. Relative abundance of gray snapper in 31 Gulf of Mexico estuaries (*from Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | | | ◉ | | |
| Ten Thousand Islands | | | ○ | | |
| Caloosahatchee River | | | √ | | |
| Charlotte Harbor | ○ | | ○ | | |
| Tampa Bay | | | ○ | | |
| Suwannee River | ○ | | ○ | | |
| Apalachee Bay | ○ | | ○ | | |
| Apalachicola Bay | √ | | √ | | |
| St. Andrew Bay | ○ | | ○ | | |
| Choctawhatchee Bay | ○ | | ○ | | |
| Pensacola Bay | ◉ | | ○ | | |
| Perdido Bay | | | ○ | | |
| Mobile Bay | √ | | ○ | | |
| Mississippi Sound | √ | | ○ | | |
| Lake Borgne | | | | | |
| Lake Pontchartrain | | | | | |
| Breton/Chandeleur Sounds | | | ○ | | |
| Mississippi River | | | | | |
| Barataria Bay | | | ○ | | |
| Terrebonne/Timbalier Bays | | | √ | | |
| Atchafalaya/Vermilion Bays | | | | | |
| Calcasieu Lake | | | √ | | |
| Sabine Lake | | | | | |
| Galveston Bay | | | √ | | |
| Brazos River | | | | | |
| Matagorda Bay | √ | | √ | | |
| San Antonio Bay | | | √ | | |
| Aransas Bay | √ | | √ | | |
| Corpus Christi Bay | √ | | √ | | |
| Laguna Madre | √ | | ○ | | |
| Baffin Bay | √ | | √ | | |
| | A | S | J | L | E |

*Life stage*

| Relative abundance: | | Life stage: |
|---|---|---|
| ● | Highly abundant | A - Adults |
| ◉ | Abundant | S - Spawning |
| ○ | Common | J - Juveniles |
| √ | Rare | L - Larvae |
| blank | Not present | E - Eggs |

**Life Mode**

Eggs can be considered pelagic and non-adhesive, and occur in offshore waters (Thresher 1984, Shaffer pers. comm.). Larvae whose total length (TL) is under 10 mm are planktonic and occur offshore (Bortone and Williams 1986). Juveniles are pelagic and non-schooling in early stages; larger juveniles are weak schoolers (Starck 1971, Hardy 1978). Adults are pelagic and demersal, and are often in schools diurnally, dispersing by night and moving to inshore grass beds (Croker 1962, Starck and Schroeder 1971, Hardy 1978, NMFS 1987, Sogard et al. 1989).

**Habitat**

Type: Eggs are marine, neritic, and demersal (Starck and Schroeder 1971). Larvae are marine, neritic, and planktonic. Their range is not reported, but they are known to occur in offshore shelf waters and near coral reefs. Larvae of *Lutjanus* species are known to be present in the Gulf of Mexico April through November, with an abundance peak June through August (Ditty et al. 1988). Gray snapper pre-juveniles begin to move into estuarine habitats and have been collected in grass beds (Starck and Schroeder 1971, Richards et al. 1984, Hardy 1978). Juveniles are estuarine, riverine and marine, and are found in estuaries, channels, bayous, ponds, coastal marshes, mangrove swamps, and freshwater creeks. Older juveniles may move to offshore habitats with adults and can occur as far out as 14 km. Juveniles occupy inshore grassy areas until they reach lengths of 80 mm (Croker 1962, Starck 1971). They are sometimes associated with areas of swift tidal flow, and, less frequently, will occupy areas around ledges, pilings, jetties, rocks, coral hedges, grass, or gorgonian coral patches (Starck and Schroeder 1971; Hardy 1978). In Florida Bay, they prefer habitats where seagrass density and species diversity is high (Chester and Thayer 1990). Adults are marine, estuarine, and riverine. They occur offshore up to 32 km near coral reefs, rock shelves and similar structures, and inshore near ledges of channels and around artificial structures, and in estuaries, mangrove swamps and lagoons. They have also been reported in coastal plain freshwater drainage canals, creeks and rivers, and even from some coastal freshwater lakes. This species has been reported from depths ranging from 0 to 180 m with smaller snapper generally inhabiting shallower water than larger snapper (Lee et al. 1980, Bortone and Williams 1986, Loftus and Kushlan 1987, Chester and Thayer 1990).

Substrate: Eggs are typically found in proximity to offshore reefs (Starck and Schroeder 1971, Rutherford et al. 1983, Powell et al. 1987). Powell et al. (1987) noted pre-flexion larvae "candidates" over offshore reefs. Lutjanidae larvae have been reported in shelf waters from Florida to Texas. Postflexion larvae and juveniles (15-35 mm) are present in shallow basins with *Thalassia* present adjacent to mud banks, and postlarval juveniles have been found over dense (1000-4000 shoots/m$^2$) seagrass beds of *Halodule wrightii* and *Syringodium filiforme.* Juveniles are recorded from *Thalassia* grass flats; soft marl bottoms, marl sands, fine marl mud with shell and rock outcrops, and detritus; seagrass meadows and mangrove roots; seagrass meadows near jetties and pilings (Tabb and Manning 1961, Rutherford et al. 1983, Rutherford et al. 1989a). Adults typically occur around hard bottoms, natural and artificial, but also soft bottoms; wharves, pilings, rocky areas; sand, rubble, rock with supporting alcyonarians, sponges and *Thalassia*; coral reefs, rock outcrops, shipwrecks; sandy grass beds, coral reefs, sandy, muddy and rocky bottoms (Springer and Woodburn 1960, Starck and Davis 1966, Starck and Schroeder 1971, Manooch and Matheson 1984). It is also suggested that the preferred substrate is mud. They are occasionally found in areas of alcyonarian or algal growths. In one study, specimens between 110 and 275 mm were recorded in areas of mud to shelly-sand bottoms (Lindall et al. 1973).

Physical/Chemical Characteristics:
Temperature: Eggs are found in the marine seawater zone in the vicinity of offshore reefs (Starck and Schroeder 1971). Larvae have been recorded occurring in ranges of 15.6 to 27.2°C (Hardy 1978) and 26 to 28°C *in vitro* (Richards and Saksena 1980). Juveniles are found in temperature ranges of 17.2° to 36.0°C (Hardy 1978); 16 to 31°C (Tabb and Manning 1961); and 12.8° to 31.7°C (Rutherford et al. 1989a). Adults occur in water temperatures from 13.4° to 32.5°C (Springer and Woodburn 1960, Wang and Raney 1971), and their lower lethal limit is 11°-14°C (Starck and Schroeder 1971). Increased mortalities accompany sudden temperature drops (Starck 1971).

Salinity: Eggs have been hatched *in vitro* in a salinity range from 32 to 36‰ (Richards and Saksena 1980). Larvae and juveniles are euryhaline. Juveniles have been observed in salinities ranging from 0 to 66.6‰ (Tabb and Manning 1961, Bortone and Williams 1986, Rutherford et al. 1983, Rutherford et al. 1989a). Adults are euryhaline and have been found in salinities ranging from 0 to 47.7‰ (Hardy 1978, Wang and Raney 1971).

Migrations and Movements: Newly hatched larvae are planktonic, but develop rapidly and make their way to the inshore nursery areas at about 10 mm (Starck and Schroeder 1971, Chester and Thayer 1990). By about 80 mm, early juveniles move to deeper estuarine habitats, but have been observed moving out of an area in response to extreme temperatures (Starck and Schroeder 1971, Chester and Thayer 1990). Adults are considered to be generally non-migratory, and tend to remain in areas in which they have become established. A mark-recapture study in Florida, however, found movement to the southwest as the individuals grew, with a mean travel distance of 18.3 km (Bryant et al. 1989). Some movements are noted in connection with feeding, environmental conditions, and seasonal spawning. Mature fish migrate to offshore reefs during the summer to spawn. Most return to the inshore and estuarine habitats, however, some remain near the reefs (Starck and Schroeder 1971). Adults that inhabit reefs move off into surrounding waters to feed at night (Starck and Davis 1966, Moe 1972).

**Reproduction**
Mode: The gray snapper has separate male and female sexes (gonochoristic), but exhibits no apparent external dimorphism. Sex ratio is reported as equal (Croker 1962, Starck and Schroeder 1971, Rutherford et al. 1983). Eggs and milt are broadcast into the water column, and fertilization is external, with no indication of nest building or egg guarding (Starck and Schroeder 1971, Grimes 1987).

Spawning: The gray snapper is a summer spawner, typically from June through August, but is also reported to spawn in September in the Florida Keys (Starck and Schroeder 1971, Grimes 1987). Spawning occurs offshore in the Gulf of Mexico around reefs or shoals. Evidence indicates batch spawning occurs at night near full moons throughout the reproductive cycle (Starck and Schroeder 1971, Grimes 1987). The spawning season may be protracted over a long period (Druzhinin 1970).

Fecundity: Since gray snapper are multiple spawners, batch fecundity and spawning frequency must be estimated in order to describe overall fecundity. Collins (pers. comm.) has estimated batch fecundity of 20 gray snapper from northwest Florida. These fish were captured in the summer months of 1993-1995, and ranged from 333 to 641 mm TL. Batch fecundity estimates ranged from 29,000 to 1,256,000 hydrated oocytes. Estimates of spawning frequency for gray snapper have not yet been completed (Collins pers. comm.). In other studies, a 315 mm female produced 590,000 eggs (Starck 1971, Hardy 1978), while a 354 mm standard length (SL) fish produced 548,000,000 (Grimes 1987). One gram of ovarian tissue has been reported to contain 125,000 eggs (Starck and Schroeder 1971).

**Growth and Development**
Egg Size and Embryonic Development: Eggs are oviparous, non-adhesive, ranging 0.04-0.06 mm in diameter, and contain a single central oil globule (Starck and Schroeder 1971, Grimes 1987). These demersal eggs

develop rapidly and hatch in about 18 hours in ambient seawater (Grimes 1987). Eggs hatch in the vicinity of offshore reefs.

Age and Size of Larvae: Larval development takes place offshore near spawning sites (Richards et al. 1984, Kelly et al. 1986, Powell et al. 1987). Newly hatched larvae absorb their yolk sac within 45 hours (Grimes 1987). Richards and Saksena (1980) gave growth rates of continually fed larvae as 2.7-2.8 mm notocord length (NL) (4 days), 3.0-3.1 mm NL (5 days), 3.4 mm NL (7 days), 4.1-4.2 mm NL (9 days), 6.2 mm SL (15 days), 9.6-12.5 mm SL (26 days) and 15.4 mm SL (36 days). The flexion stage occurs at about 4.2 mm SL, and post-flexion at 6.2 mm SL. Larvae are sparsely pigmented.

Juvenile Size Range: The juvenile stage begins at 12 mm SL. They are heavily pigmented and can be identified by a full complement of meristic characters (Richards and Saksena 1980). Springer and Woodburn (1960) reported mean lengths of Age Class 0 fish for periods of September, November and December 1957 as 33 mm, 42.6 mm and 51.7 mm respectively. The following year they assigned lengths to Age Class 0 fish for October (18.2 mm), November (25.3 mm) and December (34 mm). Croker (1962) determined mean fork lengths (FL) using back calculations for age classes I through VII as Class I - 81 mm, Class II - 180 mm, Class III - 241 mm, Class IV - 295 mm, Class V - 352 mm, Class VI - 431 mm, and Class VII - 456 mm. Different results were obtained in another study, particularly in the later age classes: Class I - 79 mm, Class II - 143 mm, Class III - 199 mm, Class IV - 255 mm, Class V - 293 mm, Class VI - 334 mm, Class VII - 381 mm, Class VIII - 438 mm, and Class IX - 478 mm (Starck and schroeder 1971). Growth rates of 126 $\pm$ 2 mm for the first year and 48-62 mm/year for fish one to four years of age have been reported (Rutherford et al. 1983).

Age and Size of Adults: Using sectioned otoliths, Manooch and Matheson (1984) calculated TL for fish up to 19 years of age. Their results were similar to those of Croker (1962). A length of 772 mm was determined for 19 year old fish. The oldest specimen they observed was a 775 mm fish, 21 years old. Starck and Schroeder (1971) suggest a maximum weight for the gray snapper at around 8 kg but stated that fish over 3.6 kg were rare. Maturity is reached at about 200 mm TL, probably during the third year (Starck and Schroeder 1971). In one study, the smallest female observed spawning was 195 mm SL and the smallest ripe male was 185 mm SL (Starck and Schroeder 1971, Hardy 1978). Johnson et al. (1994) collected adult gray snapper from Gulf of Mexico commercial and recreational fisheries, with a length range of 236 to 764 mm TL, and an estimated age range of one to 25 years. Von Bertalanffy growth parameters have been derived for this species (Johnson et al. 1994).

**Food and Feeding**

Trophic Mode: The gray snapper is an opportunistic carnivore at all life stages.

Food Items: Richards and Saksena (1980) fed zooplankton in the 73-110 µm range *in vitro* to newly hatched gray snapper larvae. Copepods and amphipods are important food items of fish at 10-20 mm (Starck and Schroeder 1971). Juveniles are diurnal feeders that primarily prey on crustaceans, but they also consume fish, molluscs and polychaetes. Very small juveniles (10-20 mm TL) forage primarily on amphipods. Penaeid shrimp dominate the diet of larger juveniles, but a variety of crabs (blue crab, spider crab, mud crabs, and fiddler crabs) are also eaten (Rutherford et al. 1983). Grassbeds appear to be the most important feeding habitat for juveniles and adults (Starck 1971, Harrigan et al. 1989, Hettler 1989). Adults are typically nocturnal predators, consuming fish, shrimp, and crabs. Fish eaten are largely grunts (*Haemulon* species), but also include killifishes, pipefish (*Syngnathus* species), gulf toadfish (*Opsanus beta*), gobies, seahorses (*Hippocampus* species), and silver jenny (*Eucinostomus gula*). Algae and marine plants are commonly found, possibly consumed incidentally during routine feeding. Proportions of prey species consumed varies within and among habitats (Rivas 1949, Reid 1954, Springer and Woodburn 1960, Tabb and Manning 1961, Starck and Davis 1966, Starck and Schroeder 1971, Rutherford et al. 1983, Harrigan et al. 1989, Hettler 1989).

**Biological Interactions**

Predation: Little information on predation of gray snapper is available, but other carnivorous fishes probably prey on larvae and juveniles.

Factors Influencing Populations: Abundance and distribution of juveniles appears to be influenced by density and species composition of seagrass (Chester and Thayer 1990).

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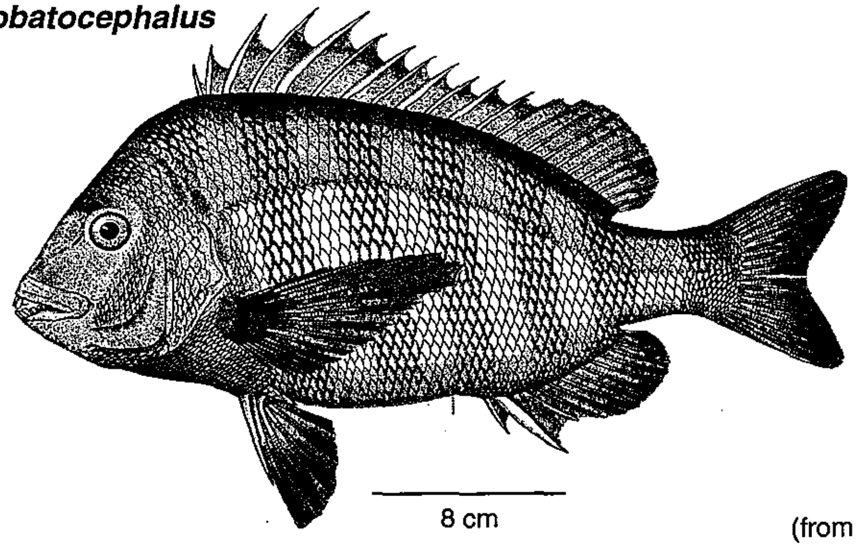
**Archosargus probatocephalus**
**Adult**




(from Goode 1884)

**Common Name:** sheepshead
**Scientific Name:** *Archosargus probatocephalus*
**Other Common Names:** Sheepshead bream, sheepshead porgie, convict fish (Jennings 1985); *rondeau mouton* (French), *sargo chopa* (Spanish) (Fischer 1978).
**Classification** (Robins et al. 1991)

Phylum: Chordata
Class: Osteichthyes
Order: Perciformes
Family: Sparidae

There are three subspecies of sheepshead along the western Atlantic seaboard. *A. p. probatocephalus* is the more northern race ranging from Nova Scotia to Cedar Key, Florida. *A. p. oviceps* limited to the Gulf of Mexico ranging from St. Marks, Florida to Campeche Bank, Mexico. *A. p. aries* is the southern form ranging from Belize to Brazil (Jennings 1985).

**Value**

Commercial: Traditionally, the sheepshead has had some commercial value for food, but its acceptance as a food fish varies among coastal localities (Jennings 1985, Beckman et al. 1991). Commercial interest in this species has, however, increased markedly since 1981 as regulation of fisheries for other more popular food fish has increased (Render and Wilson 1992, GSMFC 1992). It is taken commercially by seines and incidentally by offshore shrimp trawlers, but is sometimes caught intentionally during the spawning season when it is most abundant (Benson 1982, Jennings 1985). It has a low retail value, and most incidental trawl catches are probably discarded.

Recreational: The sheepshead supports a moderate sport fishery in most months (Benson 1982, Beckman et al. 1991). It is a common fish in inshore waters, often caught on fiddler crab or barnacle bait (Hoese and Moore 1977). Fishery information for the Gulf of Mexico showed a total catch of 4,054,000 sheepshead in 1992 (NMFS 1993). It is frequently discarded because the dorsal spines make cleaning difficult.

Indicator of Environmental Stress: The sheepshead is not typically used in studies of environmental stress.

Ecological: Sheepshead juveniles and adults are common demersal predators. Predation by this species may be important in controlling the ecological structure of sessile invertebrate and motile epifauna communities (Sedberry 1987).

**Range**

Overall: Sheepshead range from Nova Scotia to Florida, and the Gulf of Mexico in continental waters. It is found from Honduras to Rio de Janeiro, but is absent from islands of the Caribbean Sea (Fischer 1978, Johnson 1978, Shipp 1988). It is common south of Cape Hatteras.

Within Study Area: *A. probatocephalus* has been divided into three subspecies, with *A. p. oviceps* occurring through the Gulf of Mexico from St. Marks, Florida to Campeche Bank Mexico (Caldwell 1965, Fischer 1978, Lee et al. 1980) (Table 5.31). Greatest abundance in the Gulf of Mexico probably occurs off of southwest Florida (Shipp 1988).

Table 5.31. Relative abundance of sheepshead in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ○ | √ | ○ | ○ | |
| Ten Thousand Islands | ○ | √ | ○ | ○ | |
| Caloosahatchee River | √ | | √ | √ | |
| Charlotte Harbor | √ | | √ | √ | |
| Tampa Bay | ○ | √ | ○ | ○ | √ |
| Suwannee River | ○ | | ○ | ○ | |
| Apalachee Bay | √ | | √ | √ | |
| Apalachicola Bay | ○ | | ○ | ○ | |
| St. Andrew Bay | ○ | √ | ○ | ○ | √ |
| Choctawhatchee Bay | ○ | | ○ | ○ | |
| Pensacola Bay | ○ | | ○ | ○ | |
| Perdido Bay | ◉ | | ○ | ○ | |
| Mobile Bay | ◉ | | ◉ | ○ | |
| Mississippi Sound | ○ | ○ | ○ | ○ | ○ |
| Lake Borgne | ○ | | ◉ | | |
| Lake Pontchartrain | ○ | | ○ | | |
| Breton/Chandeleur Sounds | ○ | | ○ | | |
| Mississippi River | ○ | | ○ | | |
| Barataria Bay | ◉ | | ○ | | |
| Terrebonne/Timbalier Bays | ◉ | | ◉ | | |
| Atchafalaya/Vermilion Bays | ○ | | ○ | | |
| Calcasieu Lake | √ | | ○ | | |
| Sabine Lake | ○ | | ○ | | |
| Galveston Bay | ○ | | ○ | | |
| Brazos River | ○ | | ○ | | |
| Matagorda Bay | ◉ | | ◉ | | |
| San Antonio Bay | ◉ | | ○ | | |
| Aransas Bay | ○ | ○ | ○ | ○ | ○ |
| Corpus Christi Bay | ○ | ○ | ○ | ○ | ○ |
| Laguna Madre | ○ | | ◉ | | |
| Baffin Bay | ○ | √ | ○ | √ | √ |
| | A | S | J | L | E |

Relative abundance:

- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:

- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

**Life Mode**

Eggs are buoyant, and spawning typically occurs over the inner continental shelf. Larvae are pelagic. Juveniles and adults are demersal omnivores, and prefer "live hard-bottomed areas." This fish does not school, but may form feeding aggregations (Johnson 1978, Lee et al. 1980, Sedberry 1987).

**Habitat**

Type: Eggs are typically marine, in coastal waters of the inner continental shelf. Larvae are known to be present in the Gulf of Mexico January through May, with peak abundance February through April (Ditty 1986, Ditty et al. 1988). Larvae are pelagic as they move into estuaries, then become estuarine-dependent and associated with seagrass beds. The pelagic stage probably lasts until larvae are about 30 to 40 days old when metamorphosis into juveniles occurs. After metamorphosis, juveniles "settle out," becoming substrate-oriented, then move to nearshore reefs as they mature (Sedberry 1987, Parsons and Peters 1989). Both juveniles and adults are demersal. Adults occur in nearshore waters over "live bottom" areas.

Substrate: Juveniles are usually associated with grass beds until they are around 50 mm, then they move into the more typical adult habitats (McClane 1964, Dugas 1970, Lee et al. 1980, Juneau and Pollard 1981). Adults occur around oyster beds, shallow muddy bottoms, *Spartina* marshes, piers and rocks, and jetties. They can also be found in some abundance in bare sand surf zones feeding on infaunal bivalves and crustaceans (Shipp 1988).

Physical/Chemical Characteristics:

Temperature: Optimal growth in captivity has been reported at around 25°C (Tucker 1989). Juveniles have been collected in temperatures ranging from 8.0 to 29.6° C (Wang and Raney 1971, Pineda 1975, Jennings 1985). Temperature tolerance in adults ranges from 5° (Christmas and Waller 1973, Perret et al. 1971) to 35.1° C (Roessler 1970).

Salinity: The sheepshead is euryhaline (Gunter 1956) with collection sites ranging in salinities from 0 to 45‰ (Simmons 1957, Kelly 1965, Dugas 1970, Perret et al. 1971, Wang and Raney 1971, Dunham 1972, Perret and Caillouet 1974, Juneau 1975, Tarver and Savoie 1976, Benson 1982). Larvae have been collected from 5.0 to 24.9‰ (Christmas and Waller 1973). Juveniles and adults are found in salinities from nearly fresh (0.26‰) to 43.8‰ (Herald and Strickland 1948, Gunter and Hall 1965, Lee et al. 1980, Loftus and Kushlan 1987).

Dissolved Oxygen:
Minimum dissolved oxygen (DO) tolerances for this species are not well known, but kills have been reported in semi-open and closed canals in coastal Louisiana where severe oxygen depletion occurred (Adkins and Bowman 1976).

Movements and Migrations: This is not considered a true migratory species (Jennings 1985), but one tagging study showed a maximum traveled distance of 109 km prior to the spawning season (Bryant et al. 1989). Adults move to offshore waters in the spring and return to bays after spawning. The sheepshead remains in nearshore waters during warm seasons and moves out of the estuaries during periods of low temperatures (Gunter 1945, Dugas 1970, Jennings 1985, Bryant et al. 1989).

**Reproduction**
Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe into the water column.

Spawning: Spawning probably occurs offshore (Springer and Woodburn 1960), from February through April (Hildebrand and Cable 1938, Springer and Woodburn 1960, Christmas and Waller 1973, Render and Wilson 1993). The reported peak occurs during the months of March and April (Beckman et al. 1991).

Fecundity: Fecundity appears to vary between fish from the inshore area, and older, larger fish that are caught offshore (Render and Wilson 1993). Fish caught offshore had an average fecundity of 87,000 eggs/batch and ranged from 14,000 to 250,000 eggs/batch. The average fecundity of fish from the inshore area was 11,000 eggs/batch, and ranged 1,100 to 40,000 eggs/batch. Frequency of spawning was estimated to be every 1 to 20 days.

**Growth and Development**
Egg Size and Embryonic Development: Eggs are approximately 0.8 mm diameter, and are buoyant. Hatching occurs in about 40 hours at 24-25°C (Johnson 1978, Tucker 1989).

Age and Size of Larvae: Larvae are about 2.0 mm when they hatch, and by 5 mm, they have absorbed the yolk sac. Transition to the juvenile stage begins at about 11 to 12 mm (Mook 1977).

Juvenile Size Range: Juveniles attain adult pigmentation patterns by approximately 25 to 30 mm (Johnson 1978). Growth is rapid up to 6 to 8 years of age, after which it levels off (Beckman et al. 1991).

Age and Size of Adults: Sexual maturity is reported to occur in most individuals by age 2 (Beckman et al. 1991, Render and Wilson 1993). All males are usually mature by age 3, and all females by age 4. The sheepshead is one of the largest members of its family (Shipp 1988). It can grow up to 610 mm (Hoese and Moore 1977), and the record size in Louisiana is 9.6 kg. Females exhibit a faster growth rate and achieve larger maximum sizes than males. This is a long-lived species with a life span of at least 20 years. Von Bertalanffy growth equations have been developed for both sexes (Beckman et al. 1991).

**Food and Feeding**
Trophic Mode: Little information is available regarding the role of sheepshead in the trophic dynamics of estuaries (Jennings 1985). Larvae are carnivorous. Juveniles and adults are omnivores, but adults in offshore environments function more as sessile animal feeders, while juveniles feed primarily on plant material in inshore habitats (Sedberry 1987).

Food Items: Hildebrand and Cable (1938) found that ostracods were the primary food for fishes less than 30 mm. Benson (1982) summarizes the diet of sheepshead as: larvae consuming primarily zooplankton, juveniles consuming zooplankton as well as polychaetes and chironomid larvae; large juveniles and adults eat blue crab, young oysters, clams, crustaceans and small fish. Juveniles and adults are basically omnivorous feeding on plant material as well as crustaceans, molluscs and small fishes (primarily young Atlantic croaker) (Gunter 1945, Darnell 1961, Tabb and Manning 1961, Kelly 1965, Levine 1980, Odum et al. 1982, Overstreet and Heard 1982, Shipp 1988). In one study, smaller adults (<350 mm SL) were found to consume mostly bryozoans, while larger fish (>350 mm SL), that also fed heavily on bryozoans, included more bivalves, echinoderms, and ascidians in their diet. Both size groups consumed barnacles and decapods in lesser amounts. Foraminiferans, cnidarians, polychaetes, gastropods, and small arthropods were also eaten. Algae may be important in the diet of sheepshead in inshore habitats (Ogburn 1984), but plant material becomes less important in the diet of adults as they move offshore (Sedberry 1987).

**Biological Interactions**
Predation: Little information is available regarding predation of sheepshead, but it seems likely that larvae and juveniles could be utilized as a food source by predatory fishes.

Factors Influencing Populations: The sheepshead is host to ciliates, nematodes, trematodes, and isopods, none of which are known to endanger populations of the species (Jennings 1985). Adkins and Bowman (1976) found oxygen depletion in a semi-open and closed canals in Louisiana to result in death of this species. The sheepshead is frequently found associated with black drum (Wang and Raney 1971).

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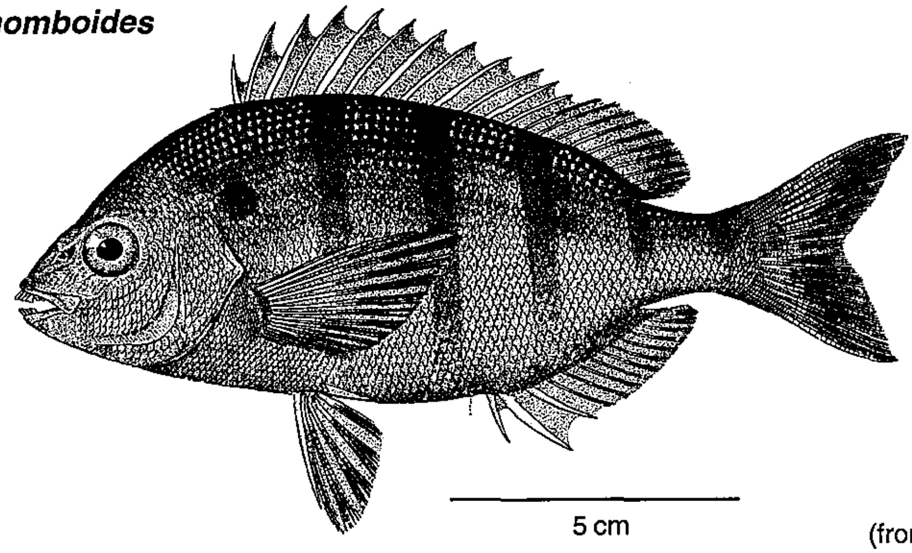
## Pinfish

*Lagodon rhomboides*
**Adult**




(from Goode 1884)

**Common Name:** pinfish
**Scientific Name:** *Lagodon rhomboides*
**Other Common Names:** bream, pin perch, sand perch, sailor's choice, butterfish; *sarselema* (French); *poisson beurre* (Cajun French); *sargo selema, chopa espina* (Spanish) (Fischer 1978, Muncy 1984).
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Perciformes |
| Family: | Sparidae |

### Value

Commercial: The pinfish is included in the unclassified or industrial fish categories in commercial catch statistics (Fischer 1978, Muncy 1984). It is a potential source of fish meal, and has value as a forage fish for many commercial fish species (Muncy 1984). It also contributes a small part to the industrial groundfish fishery of the northern Gulf of Mexico (Roithmayr 1965). Pinfish are caught mainly with trawls, but also with gill nets, trammel nets, beach seines, traps, and on hook and line (Fischer 1978). Commercially caught fish are marketed for food are mostly sold as fresh product.

Recreational: Pinfish are often caught while fishing for other species (Muncy 1984). Although it is excellent eating, the pinfish is not widely consumed due to its relatively small size (Fischer 1978). It is often sought by young anglers (Shipp 1986). Recreational fishery information for the Gulf of Mexico (except Texas) showed an estimated total catch of 8,674,000 pinfish in 1992 (O'Bannon 1994).

Indicator of Environmental Stress: Pinfish have been used extensively in bioassay experiments on the toxicity of hydrocarbons (Finucane 1969, Parrish, et al. 1975, Schimmel et al. 1977) and physiological experiments studying the effects of hydrocarbons and environmental conditions on fish (Cameron 1969b, Cameron 1970, Kloth 1970, Kjelson and Johnson 1976, Lee et al. 1980).

Ecological: The pinfish is an estuarine dependent species. It is often so abundant and predaceous that it is believed to alter the composition of estuarine epifaunal communities (Orth and Heck 1980, Coen et al. 1981, Stoner 1980, Stoner 1982, Muncy 1984). This fish is numerically dominant in the shallow, subtidal seagrass communities in the Gulf of Mexico, and its predation on amphipod communities probably limits amphipod abundance in these areas. In addition, the consumption of plants and detritus by pinfish is important in the export of organic materials in estuaries.

### Range

Overall: The pinfish occurs in coastal waters from as far north as Cape Cod, Massachusetts, through the Gulf of Mexico and the north coast of Cuba, to the Yucatan peninsula. It is rare north of Maryland and most common south of Cape Hatteras, North Carolina through to the northern Gulf of Mexico (Fischer 1978, Lee et al. 1980, Muncy 1984). Fitzsimons and Parker (1985) have demonstrated no karyotypic differences among sampling locations, suggesting a single population for the southeast and Gulf coasts.

Within Study Area: The pinfish is abundant throughout the Gulf of Mexico, except in the very turbid brackish waters of Louisiana west of the mouth of the Mississippi River (Table 5.32) (Hoese and Moore 1977).

Table 5.32. Relative abundance of pinfish in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ● | | ● | √ | |
| Ten Thousand Islands | ● | | ◉ | ◉ | |
| Caloosahatchee River | ○ | | ● | | |
| Charlotte Harbor | ● | | ● | ● | |
| Tampa Bay | ● | | ● | ○ | |
| Suwannee River | ● | | ● | ○ | |
| Apalachee Bay | ◉ | | ◉ | ○ | |
| Apalachicola Bay | ◉ | | ◉ | ○ | |
| St. Andrew Bay | ● | | ● | ◉ | |
| Choctawhatchee Bay | ○ | | ◉ | ● | |
| Pensacola Bay | ◉ | | ● | ◉ | |
| Perdido Bay | ○ | | ◉ | ○ | |
| Mobile Bay | ◉ | | ◉ | ◉ | |
| Mississippi Sound | ● | | ● | ◉ | |
| Lake Borgne | ◉ | | ◉ | | |
| Lake Pontchartrain | ○ | | ◉ | | |
| Breton/Chandeleur Sounds | | | ○ | | |
| Mississippi River | | | ○ | | |
| Barataria Bay | | | ◉ | | |
| Terrebonne/Timbalier Bays | | | ◉ | | |
| Atchafalaya/Vermilion Bays | | | ○ | | |
| Calcasieu Lake | ○ | | ○ | | |
| Sabine Lake | | | ○ | | |
| Galveston Bay | | | ◉ | | |
| Brazos River | | | ◉ | | |
| Matagorda Bay | ◉ | | ● | | |
| San Antonio Bay | ○ | | ◉ | | |
| Aransas Bay | ◉ | | ◉ | | |
| Corpus Christi Bay | ◉ | | ◉ | | |
| Laguna Madre | ◉ | | ● | | |
| Baffin Bay | ○ | | ◉ | | |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

**Life Mode**

Eggs that are fertile are semi-buoyant. Although little is known about spawning areas and egg distributions, they are assumed to be planktonic and offshore, based on indirect evidence of their larval distributions (Sabins and Truesdale 1974, Darcy 1985). The pinfish is typically non-schooling, although compact aggregations have been reported (Kloth 1970). Pinfish have a primarily diurnal pattern of activity, but some nocturnal activity has been observed (Sogard et al. 1989).

**Habitat**

Type: Eggs are marine and neritic. Larvae are marine and estuarine. Larval pinfish are known to occur in the Gulf of Mexico October through April, with peak abundance December through February (Ditty 1986, Ditty et al. 1988). Juveniles are marine, estuarine and riverine. Juveniles are common over areas of seagrass, where activity appears to be associated with high tides (Fischer 1978, Sogard et al. 1989). Adults are marine to riverine, preferring protected waters and depths of 30 to 50 m in the Gulf (Franks et al. 1972, Chittenden and MacEachran 1976), but they have been collected in waters as deep as 92 m (Perry 1970). Adults probably prefer euhaline (marine) salinities (Wang and Raney 1971).

Substrate: The pinfish is most abundant over vegetated shallow flats, preferred mainly by juveniles, but also occurs occasionally in other areas that offer some degree of cover such as rocky bottoms, jetties, pilings, and in mangrove areas (Reid 1954, Gunter and Hall 1965, Hansen 1970, Fischer 1978, Lee et al. 1980, Coen et al. 1981).

Physical/Chemical Characteristics:

Temperature: Pinfish are eurythermal, tolerating temperatures from 3.4° to 37.5° C (Pineda 1975, Roessler 1970, Lee et al. 1980). Water temperature has been suggested as a major factor in the control of emigration to offshore spawning sites. Extremely high and low temperatures cause pinfish to leave shallow areas for nearby deeper waters seasonally, and even daily (Cameron 1969a). Increased water temperatures increase the amount of erythrocytes and hemoglobin of pinfish (Cameron 1970, Houston 1973). Tolerance to cold temperatures is strongly influenced by acclimation temperature, and this has led to ambiguous measures of low lethal temperatures in the past (Bennett and Judd 1992). In a recent study, juveniles were found to have a Critical Thermal Minimum (CTMin) of 3.4° C.

Salinity: Pinfish are euryhaline, tolerating salinities from 0 to 43.8‰ in the Gulf of Mexico (Roessler 1970, Pineda 1975, Lee et al. 1980). Vegetation rather than salinity is thought to have a greater affect on the distribution of pinfish (Weinstein 1979). However, heavy rains reducing salinity to 4‰ have been reported to decrease the abundance of juvenile pinfish in a shallow seagrass bed (Cameron 1969b). In addition, Subrahmanyam and Coultas (1980) positively correlated salinity and pinfish abundance. Adult pinfish apparently prefer higher salinity waters and stay mostly in the Gulf or close to Gulf passes (Wang and Raney 1971).

Dissolved Oxygen (DO): The oxygen-carrying capacity of pinfish blood is related to environmental conditions, increasing with lower dissolved oxygen, higher salinities, and increased activity (Cameron 1970). The incipient lethal level for this species is a DO content of about 1.1 mg/l (Cameron 1969a).

Migrations and Movements: Larvae begin to move into estuaries from the marine environment when they reach a total length (TL) of 11 mm (Johnson 1978). Juveniles migrate up into the estuaries during spring and summer. Juveniles rarely leave the protected areas of vegetated flats except at night when they move into the nearby sand flats (Stoner 1979). In addition, when water temperatures exceed 32°C in the flats they move to the cooler, deeper waters of channels. Juveniles and adults migrate out of the estuaries in the fall to their spawning grounds in the mostly deeper Gulf waters (Gunter 1945, Perry 1970). Here they aggregate in size groups. Gunter (1945) reported that some juveniles remain inshore, while Perry (1970) found a stable adult population remaining offshore in deep (73-91 m) Gulf waters.

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe into the water column (Cody and Bortone 1992).

Spawning: Spawning location is probably related to water depth and temperature (Johnson 1978). Most studies in the northern Gulf of Mexico indicate that spawning takes place in the fall and winter (Gunter 1945, Reid 1954, Caldwell 1957, Christmas and Waller 1973, Sabins and Truesdale 1974, Kjelson and Johnson 1976, Johnson 1978, Lee et al. 1980, Cody and Bortone 1992).

Fecundity: In one study, a 157 mm TL female from Florida collected in November contained an estimated 90,000 eggs (Caldwell 1957). In another study, eight pinfish, with standard lengths (SL) ranging from 111 to 152 mm, spawned an estimated 7,700 to 39,200 (averaging from 21,600) eggs (Hansen 1970). A protracted spawning period is considered likely for this species based on gonadosomatic indices (Cody and Bortone 1992).

**Growth and Development**

Egg Size and Embryonic Development: The diameter of pinfish eggs is reported to range from 0.90 to 0.93 mm (Schimmel 1977) and 0.99 to 1.05 (Cardeilhac 1976).

Age and Size of Larvae: When observed in a laboratory study, larvae hatched after 48 hours when incubated at 18°C, and were 2.3 mm TL (Cardeilhac 1976, Johnson 1978). The yolk sac, visible for 24 hours after hatching, was completely absorbed when the larvae reached 2.7 mm TL. Larval development is complete when individuals reach 12.0 mm SL (Zieske 1989). Zieske (1989) thoroughly describes pinfish larvae and early juveniles.

Juvenile Size Range: Juveniles range in size from 15 mm TL (12 mm SL) to 100 mm TL or more (Hansen 1970, Zieske 1989).

Age and Size of Adults: The majority of pinfish become sexually mature from 80 to 100 mm TL (Hansen 1970, Johnson 1978). This usually occurs during the spawning migration or at the offshore spawning grounds (Hansen 1970). Adults average growth increments of 80 mm SL after the first year, 50 mm SL after the second, and 45 mm SL after the third (Caldwell 1957). Most adults are greater than 110 mm TL in size.

**Food and Feeding**

Trophic Mode: Pinfish are voracious predators as juveniles and subadults (Carr and Adams 1973, Stoner 1979). Adults are reported to be omnivorous (Stoner 1980).

Food Items: Juveniles feed primarily on shrimps, mysids, and amphipods (Carr and Adams 1973, Stoner 1979, Levine 1980, Schmidt 1993). The diet of adults is similar to juveniles, but has a large component of plant material (Stoner 1980). Weinstein et al. (1982) have reported cellulose digestive activity. Other reported food items are: fish eggs, insect larvae, decapod crabs, bivalve molluscs, and polychaetes (Levine 1980, Schmidt 1993).

**Biological Interactions**

Predation: Pinfish are an important forage item for many fish species (Darcy 1985). Known piscine predators include alligator gar (*Lepisosteus spatula*), longnose gar (*Lepisosteus osseus*), ladyfish (*Elops saurus*), spotted seatrout, red drum, bighead searobin (*Prionotus tribulus*), southern flounder, and gulf flounder (Gunter 1945, Kemp 1949, Darnell 1958, Diener et al. 1974, Muncy 1984, Rozas and Hackney 1984). Pinfish are also preyed on by bottle-nosed dolphin (*Tursiops truncatus*) (Kemp 1949).

Factors Influencing Populations: Large numbers of pinfish have died during episodic winter events when water temperatures have dropped to approximately 4°C (Gunter 1941, Muncy 1984).

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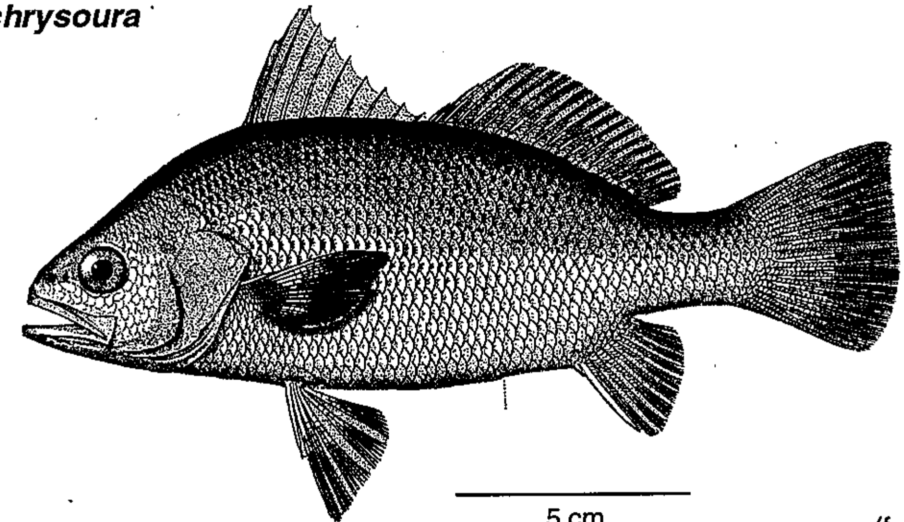
# Silver perch

***Bairdiella chrysoura***
**Adult**




(from Goode 1884)

**Common Name:** silver perch
**Scientific Name:** *Bairdiella chrysoura*
**Other Common Names:** butterfish (Springer and Woodburn 1960); yellowtail (Gunter 1945); silver croaker, *mamselle blanche* (French), and *corvineta blanca* (Spanish) (Fischer 1978).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Perciformes
Family: Sciaenidae

**Value**
Commercial: Catches of silver perch are mostly incidental in fisheries for more important commercial species. The principal gear used is pound nets, seines, and bottom trawls. Separate statistics are not reported for this species. Occasionally, large individuals are marketed fresh for human consumption (Fischer 1978, Manooch 1984).

Recreational: Silver perch are caught on hook and line by anglers, but are not specifically sought. Catches are usually incidental, and often discarded due to small size (Fischer 1978, Manooch 1984, Shipp 1986). Silver perch are sometimes used as bait by recreational fishermen (Fischer 1978, Manooch 1984). Its silvery color makes it an attractive bait, but it is uncommon in large numbers for capture. An estimated 305,000 silver perch were caught in Gulf of Mexico waters (excluding Texas) during 1991 by recreational fishermen (Van Voorhees et al. 1992).

Indicator of Environmental Stress: Hansen and Wilson (1970) recorded concentrations of DDT and its metabolites from 0.02 to 1.26 in 0-class fish from Florida's Pensacola estuary.

Ecological: The silver perch is primarily a benthic carnivore that consumes a diet consisting mostly of crustaceans (Killam et al. 1992). It can be an abundant species in estuaries (Sheridan et al. 1984), and therefore play a key role in the ecology of a system. Because of its abundance, it is likely to be the prey of numerous piscivorous fish species (Killam et al. 1992).

**Range**
Overall: The silver perch occurs in coastal waters of the western Atlantic from the Gulf of Maine off of Massachusetts to southern Florida and through the northern Gulf of Mexico (Lee et al. 1980, Shipp 1986).

Within Study Area: In the Gulf of Mexico, the silver perch ranges from south Florida into Mexico near the Rio Grande River (Lee et al. 1980, Shipp 1986). It is common in northern Gulf of Mexico estuaries, and less so to the south (Shipp 1986) (Table 5.33).

**Life Mode**
Eggs are pelagic and buoyant, larvae are pelagic to demersal, and both juveniles and adults are demersal (Johnson 1978, Ditty and Shaw 1994). Spawning occurs in the evening (Kuntz 1914). Activity is primarily nocturnal, and is affected by tidal cycles (Sogard et al. 1989).

**Habitat**
Type: Silver perch are estuarine-dependent, and the majority of spawning occurs in estuaries (Ditty pers. comm.). Eggs may be estuarine to marine depending on where spawning occurs (Johnson 1978), and larvae are pelagic (Ditty and Shaw 1994). Juveniles are found

Table 5.33. Relative abundance of silver perch in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | O | O | ◉ | O | O |
| Ten Thousand Islands | O | ◉ | ◉ | ◉ | ◉ |
| Caloosahatchee River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Charlotte Harbor | ◉ | ● | ◉ | ● | ● |
| Tampa Bay | ◉ | ● | ◉ | ◉ | ◉ |
| Suwannee River | ◉ | ◉ | O | ◉ | ◉ |
| Apalachee Bay | O | O | O | O | O |
| Apalachicola Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| St. Andrew Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Choctawhatchee Bay | O | O | O | O | O |
| Pensacola Bay | O | O | O | O | O |
| Perdido Bay | O | O | O | O | O |
| Mobile Bay | O | O | O | O | O |
| Mississippi Sound | ● | O | ● | O | O |
| Lake Borgne | ● | O | ● | O | O |
| Lake Pontchartrain | O | | O | | |
| Breton/Chandeleur Sounds | O | | O | | |
| Mississippi River | O | | O | | |
| Barataria Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Terrebonne/Timbalier Bays | O | O | ◉ | O | O |
| Atchafalaya/Vermilion Bays | | | O | | |
| Calcasieu Lake | | | O | | |
| Sabine Lake | O | | √ | | |
| Galveston Bay | O | O | O | O | O |
| Brazos River | O | O | O | O | O |
| Matagorda Bay | O | O | O | O | O |
| San Antonio Bay | O | O | O | O | O |
| Aransas Bay | O | O | O | O | O |
| Corpus Christi Bay | O | O | O | O | O |
| Laguna Madre | O | O | ◉ | O | O |
| Baffin Bay | ◉ | ◉ | ◉ | ◉ | ◉ |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- O Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

mostly in estuaries (Lee et al. 1980). They occur in a wide variety of habitats, including backwater areas, tidal tributaries, and over bare bottom areas but show a preference for shallow vegetated seagrass regions (Killam et al. 1992). They also can be found in abundance around other structured habitats such as rocks and seawalls. Adults, although most common in bays and quiet lagoons (De Sylva 1965), can also occur in sandy unvegetated habitats in shallow nearshore waters of the Gulf of Mexico at depths up to 18 m (Gunter 1945, Miller 1964, Killam et al. 1992). All life stages appear to prefer polyhaline to euhaline salinities (Killam et al. 1992). Hoese and Moore (1977) report that the silver perch is more common in higher salinity bays.

<u>Substrate</u>: Adults are found over mud and sand bottoms (Robins and Tabb 1965). Juveniles are found along shore zone rivers in ditches, in lower portions of marsh creeks over mud and sand bottoms (Thomas 1971), and often over heavy detritus (Hildebrand and Cable 1930). They usually occur in grass beds (Hoese and Moore 1977, Lee et al. 1980).

<u>Physical/Chemical Characteristics</u>:
Temperature: This is a eurythermal species that is very tolerant of the warm water conditions that are typical of estuaries (Killam et al. 1992). Ripe individuals or eggs have been collected at 19.4 to 28°C (Johnson 1978). Larvae have been taken in temperatures from 16.4° to 31.8°C (Jannke 1971). Juveniles are taken in temperatures from 4.8° (Thomas 1971) up to 32.5°C (Springer and Woodburn 1960, Wang and Raney 1971). Adults have been taken at temperatures from 10° to 34.5°C (Roessler 1970, Darovec 1983). Upper lethal limits determined for fish 20 to 200 mm were LD50 at 34° to 37°C after 3 hours, and LD100 at 37° to 40°C after 30 minutes (Killam et al. 1992).

Salinity: The silver perch is a euryhaline species (Killam et al. 1992). Ripe individuals or eggs have been collected at 14.3 to 26‰ (Johnson 1978). Larvae have been taken in salinities from <1 to 37.4‰, although most occurred at salinities >10‰ (Lippson and Moran 1974, Killam et al. 1992). Juveniles are taken in salinities from 0 (Thomas 1971, Wang and Raney 1971, Lee et al. 1980) to 35.5‰ (Springer and Woodburn 1960; Wang and Raney 1971, Wagner 1973). They are most abundant at salinities >20‰ (Killam et al. 1992). Adults have been found in salinities ranging from 0 to 48‰ (Gunter 1945; De Sylva 1965; Wagner 1973, Darovec 1983), but appear to prefer those parts of the estuary characterized by moderate to high salinities (Killam et al. 1992).

<u>Movements and Migrations</u>: Adults move to deeper bay waters and offshore in the winter, and return to

coastal lagoons in the spring to spawn (Gunter 1945, Miller 1964, De Sylva 1965). Juveniles move into the shallow inner bays (Gunter 1945), and then, as they grow, move back to deeper bay and offshore water, especially during winter months (Killam et al. 1992).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe into the water column

Spawning: As with most of the drums, sounds produced by specialized muscles inserted at the swim bladder wall are believed to have a purpose in the spawning activity. Spawning probably occurs in the deeper waters of primary bays and passes (Hildebrand and Cable 1930, Gunter 1945, Springer and Woodburn 1960, Thomas 1971, Sabins and Truesdale 1974, Mok and Gilmore 1983), but may also occur offshore to some extent since eggs have been collected there (Hildebrand and Cable 1930, Wang and Raney 1971, Christmas and Waller 1973). The reported season is May to September in northern Florida (Reid 1954) with similar times in Texas and Louisiana (Gunter 1945, Wagner 1973, Sabins and Truesdale 1974). Some year-round spawning appears to occur in the estuaries of southern Florida (Killam et al. 1992). Spawning peaks may occur in spring and late summer, but may vary with location (Christmas and Waller 1973, Lee et al. 1980). Based on the presence of larval silver perch in the northern Gulf of Mexico, it can be inferred that spawning occurs March through October, with peak from April to August (Ditty et al. 1988).

Fecundity: A Florida study examined 11 females ranging in size and weight from 139.3 to 177.4 mm SL and 55.3 to 123.8 g, respectively, and determined their mean fecundity to be 90,407 eggs (Schmidt 1993).

**Growth and Development**

Egg Size and Embryonic Development: Reported egg sizes range from 0.59 to 0.88 mm total diameter (mean 0.69-0.83 mm). They are buoyant, transparent, and possess one relatively large oil globule (Kuntz 1914, Joseph et al. 1964, Ditty and Shaw 1988). Embryonic development is oviparous.

Age and Size of Larvae: Yolk sac larvae hatch at 1.5-1.9 mm TL (Welsh and Breder 1923). Ditty and Shaw (1994) report incubation times of 18 hours at 27°C, and 40-50 hours at 20°C. Two days after hatching the yolk sac is completely absorbed when larvae measure 2.5 to 2.8 mm TL (Kuntz 1914, Welsh and Breder 1923).

Juvenile Size Range: The juvenile stage is attained at a total length (TL) of about 10 - 12 mm (Kuntz 1914, Ditty and Shaw 1994). By 15 mm, their fin rays are fully developed, and their body is lightly pigmented except in the thoracic region (Wang and Kernehan 1979). By 30 mm SL, juveniles essentially have the form of an adult (Johnson 1978). Juveniles have growth rates around 15 mm/month from May to November (Hildebrand and Cable 1930, Christmas and Waller 1973).

Age and Size of Adults: The silver perch reaches sexual maturity during its first year in the warmer, more southern parts of its range (Schmidt 1993). In northern areas of its range where water temperatures are cooler for longer periods of time, growth is slower and maturity may not occur until the second year (Hildebrand and Cable 1930, Welsh and Breder 1923). A study in south Florida found maturity in both males and females occurred at about 95 mm SL (Schmidt 1993). Maximum size seldom exceeds 240 mm TL (Welsh and Breder 1923). This fish may live up to 6 years (Welsh and Breder 1923, Lee et al. 1980).

**Food and Feeding**

Trophic Mode: The silver perch is primarily a benthic carnivore, feeding mostly on crustaceans, and to a lesser degree, polychaetes and nematodes (Darnell 1958, Springer and Woodburn 1960, Diener et al. 1974, Gosselink 1984, Killam et al. 1992, Schmidt 1993).

Food Items: Diet varies seasonally and with development (Schmidt 1993). Larvae and small juveniles consume mostly zooplankton (copepod and fish larvae) (Hildebrand and Cable 1930, Darnell 1958). Small juveniles (7 to 20 mm TL) consume invertebrates such as copepods, ostracods, cladocera, schizopods, amphipods, mysids, and annelids. At 50 to 80 mm TL, they feed increasingly on annelids, larger crustaceans (such as shrimp), molluscs, chironomidae larvae. Larger juveniles and adults also consume small fishes (pinfish, anchovies, gobies, silver perch) and crabs, in addition to these other food items (Darnell 1958, Springer and Woodburn 1960, Diener et al. 1974, Levine 1980, Gosselink 1984, Killam et al. 1992, Schmidt 1993). Larger fish tend to have a more diverse diet (Schmidt 1993).

**Biological Interactions**

Predation: Little information is available concerning predation on this species, but considering its abundance, it is a likely prey item for numerous species of piscivorous fish (Killam et al. 1992). Reported predators include spotted seatrout and king mackerel (*Scomberomorus cavalla*) (Kemp 1949, Darnell 1958, Killam et al. 1992).

Factors Influencing Populations: Distribution and abundance may be influenced by a variety of water quality and structural habitat parameters (Killam et al. 1992). All life stages appear to be more abundant in moderate to high salinities. High mortalities can occur during extreme low water temperatures induced by seasonal cold fronts. The dietary habits of silver perch are especially similar to juvenile spotted seatrout of comparable size (Darnell 1958), which may result in competition between the two species.

**Personal communications**

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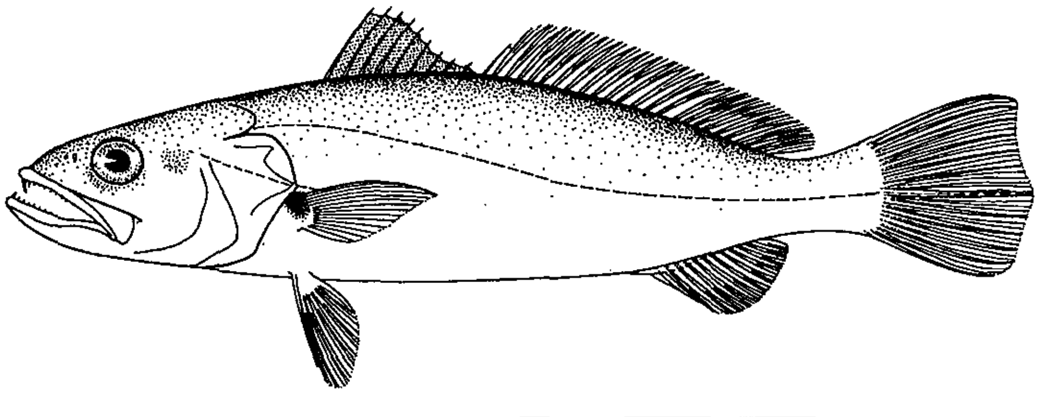
*Cynoscion arenarius*
**Adult**




(from Fischer 1978)

**Common Name:** sand seatrout
**Scientific Name:** *Cynoscion arenarius*
**Other Common Names:** white trout (Benson 1982, Sutter and McIlwain 1987); sand trout (Hoese and Moore 1977); sand weakfish, *acoupa de sable* (French), *corvinata de arena* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Perciformes
Family: Sciaenidae

**Value**
Commercial: The sand seatrout is one of the most abundant fishes in estuarine and nearshore waters of the Gulf of Mexico (Gunter 1945, Christmas and Waller 1973). It is one of the most important species caught in the industrial bottomfish and foodfish fisheries of the northern Gulf of Mexico (Roithmayr 1965, Sheridan et al. 1984, Sutter and McIlwain 1987, Ditty et al. 1991), and is a major component of bycatch in shrimp trawls. It consistently ranks among the top five most abundant species in demersal fish surveys. Sand seatrout (*Cynoscion arenarius*) and silver seatrout (*Cynoscion nothus*) landings are grouped together as "white seatrout" in statistics reported by the National Marine Fisheries Service (NMFS) (NMFS 1993). The two species are difficult to distinguish from one another and they overlap somewhat in distribution. The Gulf region reported landings of 131.5 mt of white seatrout valued at $154,000 in 1992 (NMFS 1993). Alabama and Louisiana Gulf landings in 1992 were 265,000 pounds valued at $146,000. Based on 1992, the Louisiana and Alabama white seatrout fishery contributed almost 95% of the western and central Gulf region's white seatrout landings (Newlin 1993). The majority of these landings are believed to be attributable to silver seatrout (Shipp 1986). The bulk of the groundfish harvest comes from the deeper nearshore waters of the Gulf of Mexico.

Recreational: The sand seatrout is highly prized by recreational fishermen. The National Marine Fisheries Service (NMFS) estimates that the recreational catch was 3,243,000 sand seatrout in the Gulf of Mexico during 1992 (NMFS 1993). The Gulf recreational catch accounted for about 99% of the U.S. sand seatrout recreational landings (NMFS 1993). NMFS estimated the following catches by fishing method in 1992: charter boats-44,000; private/rental boats-2,214,000; shore fisherman-986,000 (NMFS 1993). Shrimp are the preferred bait for this fish. Sand seatrout are also taken in recreational shrimp trawls.

Indicator: Sand seatrout are not typically used in studies of environmental stress.

Ecological: The sand seatrout serves as an important link between estuarine and marine food webs. It provides a direct link in the food chain between the primary consumers and the top predators. The sand seatrout feeds mostly on shrimp (penaeids), bay anchovies (*Anchoa mitchilli*), and Gulf menhaden (*Brevoortia patronus*) (Moffet et al. 1979, Overstreet and Heard 1982). Juvenile sand seatrout may be an important food item in the diets of piscivorous sport and food fish. However, the larger sand seatrouts' piscivorous, predacious habits possibly place them in competition with other predators that target similar prey species.

Table 5.34. Relative abundance of sand seatrout in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | | | √ | | |
| Ten Thousand Islands | ○ | | ◉ | ◉ | |
| Caloosahatchee River | √ | √ | ● | √ | √ |
| Charlotte Harbor | ● | ◉ | ● | ◉ | ◉ |
| Tampa Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Suwannee River | ◉ | ○ | ● | ○ | ○ |
| Apalachee Bay | ◉ | ○ | ● | ○ | ○ |
| Apalachicola Bay | ◉ | | ● | ◉ | |
| St. Andrew Bay | ○ | ○ | ◉ | ○ | ○ |
| Choctawhatchee Bay | ◉ | ● | ◉ | ● | ● |
| Pensacola Bay | ○ | ○ | ○ | ○ | ○ |
| Perdido Bay | ○ | ○ | ○ | ○ | ○ |
| Mobile Bay | ● | ● | ◉ | ● | ● |
| Mississippi Sound | ● | ○ | ● | ● | ○ |
| Lake Borgne | ● | ○ | ◉ | ○ | ○ |
| Lake Pontchartrain | ○ | | ◉ | | |
| Breton/Chandeleur Sounds | ○ | | ○ | | |
| Mississippi River | | | ● | | |
| Barataria Bay | ○ | | ◉ | | |
| Terrebonne/Timbalier Bays | ○ | | ◉ | | |
| Atchafalaya/Vermilion Bays | ○ | | ◉ | | |
| Calcasieu Lake | ○ | | ◉ | | |
| Sabine Lake | | | √ | | |
| Galveston Bay | ◉ | | ○ | | |
| Brazos River | | | ○ | | |
| Matagorda Bay | ○ | | ○ | | |
| San Antonio Bay | | | ○ | | |
| Aransas Bay | ○ | ○ | ○ | ○ | ○ |
| Corpus Christi Bay | ◉ | ○ | ◉ | ○ | ○ |
| Laguna Madre | √ | | √ | | |
| Baffin Bay | ○ | | ○ | | |

*Life stage*: A S J L E

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

**Range**

Overall: The range of the sand seatrout is limited to the coastal and shelf waters of the Gulf of Mexico, extending from Florida Bay to the Bay of Campeche. It is considered rare in the Bay of Campeche reef areas, and in the lower mangrove areas of the lower west coast of Florida (Fischer 1978, NOAA 1985, Shipp 1986).

Within Study Area: The sand seatrout is common in estuarine and nearshore waters of the Gulf of Mexico, with the exception of the lower mangrove areas of the lower west coast of Florida (Shipp 1986) (Table 5.34).

**Life Mode**

The sand seatrout is estuarine-dependent, and spends most of its life in the estuaries and nearshore waters of the Gulf of Mexico. Eggs are pelagic and buoyant (Johnson 1978). Larvae are pelagic. Juveniles and adults are estuarine and demersal (Benson 1982, Ditty and Shaw 1994). This is a schooling fish, often forming groups with spotted seatrout (*Cynoscion nebulosus*). Its activity patterns tend to be diurnal (Vetter 1977).

**Habitat**

Type: The sand seatrout is truly estuarine dependent, but can be found in environments ranging from marine to estuarine. Larvae have been collected in inshore to midshelf waters in depths ranging from 5 to 70 m, with most occurring between 10-25 m (Cowan 1985, Cowan and Shaw 1988, Cowan et al. 1989). Shlossman and Chittenden (1981) report spring spawned larvae use estuarine marsh habitat, while late summer spawned larvae utilize the inshore gulf waters as nurseries. Larvae appear to have some surface orientation (Cowan 1985, Cowan and Shaw 1988), but become increasingly demersal with size (Ditty et al. 1991). Adults and juveniles prefer nearshore and inshore areas and are rarely taken in waters deeper than 55 m (Miller 1964, Kelley 1965. Warren and Sutter 1982), but adults have been caught offshore as deep as 110 m. According to Shipp (1986) "this fine food fish abounds in areas around passes and channels." Aggregations of 0.5 to 1.0 kg sand seatrout are known to occur in deep holes and over oyster reefs during the summer in estuaries. Gallaway and Strawn (1974) stated that oyster reefs and water depths greater than 1 m were preferred by adults. Larger sand seatrout (1.5 kg) are known to aggregate around offshore oil rigs (Shipp 1986).

Substrate: Juveniles prefer muddy bottoms, while adults are found over most bottom types in estuaries and nearshore Gulf areas. Larvae and juveniles prefer grass beds and marsh areas, with soft organic bottoms (Conner and Truesdale 1972, Benson 1982).

Physical/Chemical Characteristics:
Temperature: The sand seatrout is apparently sensitive to temperature extremes, and temperature appears to affect distribution more than does salinity (Trent et al. 1969, Vetter 1982).

Temperature - Eggs: Eggs have been collected in water temperatures from 24.5° to 29°C (Holt et al. 1988).

Temperature - Larvae and Juveniles: Spawning occurs only above 20°C, and larvae are only found at these temperatures (Ditty pers. comm.). Most juveniles are found at temperatures above 10°C; however, they have been reported from 5° to 36.9°C (Gunter 1945, Wang and Raney 1971, Christmas and Waller 1973, Warren and Sutter 1982, Cowan and Shaw 1988, Cowan et al. 1989). Copeland and Bechtel (1974) reported optimum catches in temperatures of 20° to 35°C. Some have been caught in temperatures as high as 40°C (Gallaway and Strawn 1974).

Temperature - Adults: Adults prefer temperatures of 12° to 36°C (Miller 1964, Vetter 1977, Benson 1982) (Simmons 1957).

Salinity - Eggs: Eggs have been collected in salinities from 27 to 37‰ (Holt et al. 1988).

Salinity - Larvae and Juveniles: Larvae mostly occur from 14° to 21°C in water salinities of 15 to 36‰ (Cowan 1985, Cowan and Shaw 1988, Cowan et al. 1989). Small sand seatrout have been reported in salinities from 0 to 34.5‰ (Wang and Raney 1971, Christmas and Waller 1973, Wagner 1973, Warren and Sutter 1982). In Mississippi Sound, best catches for fish with total lengths (TL) of 20 to 90 mm were reported in salinities <15‰; fish of 90 to 220 mm TL were caught in salinities >15‰ at 25 to 30° C (Warren and Sutter 1982).

Salinity - Adults: Adults have been caught in salinities as high as 45‰ (Simmons 1957).

Dissolved Oxygen: Sand seatrout avoid water with dissolved oxygen (DO) less than 4.6 to 5.0 mg/l (Benson 1982).

Movements and Migrations: Shlossman and Chittenden (1981) noted that the inshore movement of young sand seatrout coincided with periods of rising sea level in the northern Gulf of Mexico due to surface currents and prevailing onshore winds. Larvae spawned in the northwestern Gulf of Mexico appear to be carried inshore from spawning grounds by longshore currents (Cowan and Shaw 1988). Larvae migrate into shallow areas of the upper estuaries and apparently prefer small bayous, shallow marshes, and channels during their early development (Ditty et al. 1991). Larvae and early juveniles (<30 mm SL) first appear in estuaries in April and occur throughout the summer and early fall, but with distinct peaks during April-May and September-October (Swingle 1971, Franks et al. 1972, Warren and Sutter 1982, Ditty et al. 1991). Catch data indicates that they move into the low salinity waters (less than 15‰). A migration from bay waters to offshore breeding grounds usually occurs in late fall or winter (Springer and Woodburn 1960, Warren and Sutter 1982) or with a decrease in temperature (Gunter 1938, 1945, Kelley 1965, Perry 1970, Wagner 1973, Vetter 1977, Warren and Sutter 1982, Vetter 1982, Ditty et al. 1991). Most have left the estuaries by December, but some remain all winter. The sand seatrout will also move to deeper water to avoid extremes in temperature (Vetter 1982). Adults move back into higher salinity (>15‰) areas of estuaries after spawning (Benson 1982). Recruitment of juveniles into estuaries occurs from spring through the fall (Gunter 1945, Christmas and Waller 1973, Warren and Sutter 1981).

**Reproduction**
Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe into the water column.

Spawning: Sand seatrout adults first spawn at age 12 months (Ditty et al. 1991). Spawning has been reported from March through September (Wagner 1973, Shlossman and Chittenden 1981, Warren and Sutter 1982) with limited spawning possible as early as December (Cowan et al. 1989) or January (Cowan 1985, Cowan and Shaw 1988, Ditty et al. 1991). Based on the presence of larval sand seatrout in the northern Gulf of Mexico, it can be inferred that spawning occurs February through October, with peaks in March-April and July-August (Ditty 1986, Ditty et al. 1988). Shlossman and Chittenden (1981) identified two spawning peaks for sand seatrout in Texas Gulf waters. The first peak occurred from early March to May (spring) and the second occurred during August to September (late summer). Other studies indicate a broad period of spawning during spring and late summer (Franks et al. 1972, Gallaway and Strawn 1974, Moffett et al. 1979). Spawning usually occurs during the early evening hours (Shipp 1986, Ditty et al. 1991). Perry (1970) suggests sand seatrout spawn throughout the winter in deep water (73-91 m) based on catches of females in February and March with roe leaking from their anal pore. Sand seatrout spawn in the higher salinity estuarine and nearshore Gulf waters (Sutter and McIlwain 1987). Most spawning appears to occur in the shallow Gulf primarily in waters between 7 to 15 m in depth (Cowan 1985), but can occur in depths up to 91 m and as far as 175 km from shore (Perry 1970, Sheridan et al. 1984, Cowan and Shaw 1988); Shlossman (1980) suggested spawning occurs in 14 to 40 m depths. Sheridan et al. (1984) collected the following percentages of ripe and mature sand seatrout in the northern Gulf: 9-17 m deep (14%); 18-36 m (15%); 37-55m (24%); 56-73 m (38%); 79-91m (21%). Shlossman and Chittenden (1981) used length-frequencies gradients to identify Texas spawning areas/depths to be from 7 to 22 m. Sheridan et al. (1984) speculates that the difference between Texas and the northern Gulf may be due to variations in the depths of the spawning grounds. Spawning appears to take place initially in midshelf to offshore waters and move shoreward as the season progresses (Ditty et al. 1991). Spawning location is probably determined by salinity and intensity of spawning by water temperature.

Fecundity: Sheridan et al. (1984) estimated the mean fecundity for sand seatrout (140 mm-278 mm SL) to be 100,990 ova with a range from 28,000 to 423,000 ova. They also developed equations to estimate individual fecundity.

**Growth and Development**

Egg Size and Embryonic Development: Sand seatrout eggs are 0.67-0.90 mm in diameter (Holt et al. 1988, Ditty and Shaw 1994). They develop oviparously and hatch within one day of being fertilized (Shipp 1986). At 25° to 27°C eggs begin to hatch 16 to 22 hours after spawning (Holt et al. 1988). Other characteristics of sand seatrout eggs have not been fully described (Powles 1981).

Age and Size of Larvae: Geographical location and time of the year appear to have an influence on the rate of larval growth (Ditty et al. 1991). Larvae spawned early in the season have faster growth than those spawned in the late summer.

Juvenile Size Range: Transformation to the juvenile stage occurs at a length of 10 - 12 mm (Ditty and Shaw 1994). Recruitment of juveniles into estuaries occurs from spring through the fall (Gunter 1945, Christmas and Waller 1973, Warren and Sutter 1981). Their estimated growth rate is 5.8 mm/week (Warren 1981). Fish spawned in the spring reach 160 to 190 mm TL after six months and 220 to 280 mm after one year. Those spawned in late summer range from 120 to 150 mm TL after 6 months, and 210 to 250 mm TL after one year (Shlossman and Chittenden 1981). Monthly increases in total length of sand seatrout are greatest during the warm water temperatures from May to October (35 mm TL/month) and slowest in winter (5-10 mm TL/month) when waters are cooler (Shlossman and Chittenden 1981). Growth rates in the central and eastern Gulf range from 9.3 to 27.7 mm SL/month, and 5-10 to 35 mm TL/month in the western Gulf.

Age and Size of Adults: In one study, the smallest maturing male was 129 mm SL and the smallest maturing female was 140 mm SL (Sheridan et al. 1984). Sand seatrout generally mature at 140-180 mm total length (TL) as they approach age I in the Gulf waters of Texas (Shlossman and Chittenden 1981). Maximum life span for this species is estimated to be 3 years, with maximum lengths of 590 mm TL reported by Trent and Pristas (1977). Few sand seatrout exceed a maximum of 300 mm TL although trawl-caught fish up to about 500 mm TL have been reported (Ditty et al. 1991).

**Food and Feeding**

Trophic Mode: The sand seatrout is a generalized predator that feeds primarily in daylight hours on live and dead organisms (Vetter 1977). Its food habits show that it is an opportunistic carnivore whose diet changes with age (Ditty et al. 1991).

Food Items: Age, habitat, abundance of suitable prey and its availability in different geographic locations influences the diet of the sand seatrout (Ditty et al. 1991). Mysids and calanoid copepods are the main diet items of sand seatrout less than 40 mm SL (Sheridan 1979, Sheridan and Livingston 1979, Levine 1980). Fish are the predominant food item of all larger sand seatrout, with the bay anchovy being the most frequently consumed prey (Moffet et al. 1979, Levine 1980, Overstreet and Heard 1982, Sheridan et al. 1984). Mysidaceans were eaten more often in lower salinity areas, whereas fish were heavily consumed near passes of the estuaries. Sand seatrout from 45 to 159 mm SL in Texas were found to have stomach contents of 38% crustaceans, and 30% fish (Moffett et al. 1979). Sand seatrout from 160 to 375 mm SL in Texas contained 46% fish (mostly bay anchovies), 10% crustaceans, and 1% polychaetes. Sand seatrout from Mississippi Sound had 3% stomatopods, 53% penaeid shrimp, 7% caridean shrimp, and 55% fish (mostly bay anchovies and Gulf menhaden) (Overstreet and Heard 1982) Fish from Lake Pontchartrain, Louisiana had 95% crustaceans, 4.7% fish, and a small percentage of molluscs (Levine 1980). Other studies have found intraspecific cannibalism and a seasonal shift in food habits with more crustaceans consumed during the fall and winter than during other months (Ditty et al. 1991). In addition, piscine prey is more abundant in the diet of sand seatrout inshore than those offshore (Ditty et al. 1991).

**Biological Interactions**

Predation: Although predator information on this species is unavailable, it seems likely that larvae and juveniles may serve as minor prey items for other fishes.

Factors Influencing Populations: "Ecological separation" among life stages has been suggested by Springer and Woodburn (1960), with juveniles occurring in the bays and adults staying primarily offshore. The sand seatrout forms a major segment of the finfish bycatch discarded by the U.S. shrimp fleet (Ditty et al. 1991). Fishery pressure will also continue to increase as a result of management of the more popular and exploited species (Cowan et al. 1989, Ditty et al. 1991). The comparison of length-weight relationships suggests that distinct populations off Texas and the Louisiana-Mississippi coasts might exist.

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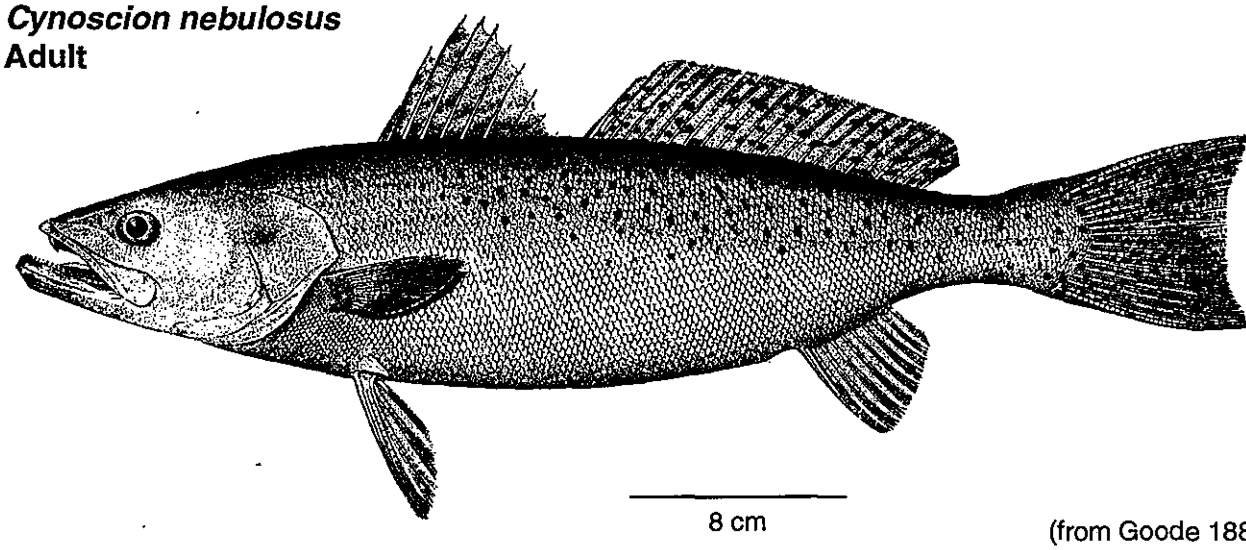
*Cynoscion nebulosus*
**Adult**




(from Goode 1884)

**Common Name:** spotted seatrout
**Scientific Name:** *Cynoscion nebulosus*
**Other Common Names:** spotted weakfish, spotted squeteague, speckles, speckled trout, salmon trout, simon trout (Hildebrand and Schroeder 1972); *acoupa pintade* (French), *corvinata pintada* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Perciformes |
| Family: | Sciaenidae |

### Value

Commercial: Commercial landings of spotted seatrout occur throughout the year along the Gulf of Mexico. Fresh catch is sold in local markets. During 1992, 703.1 mt of spotted seatrout were landed in the Gulf (Newlin 1993). Louisiana harvested over 61% (431.4 mt) of the total landings followed by Florida (257.2 mt) and Mississippi (14.5 mt). A decline in landings has been reported for Gulf coast states in recent years, possibly due to over-fishing and habitat destruction (Heffernan and Kemp 1982). These reported declines resulted in closure of the Alabama and Texas commercial fishery, and an annual harvest quota of 454 mt (GSMFC 1993). Runaround gill nets, trammel nets, pound nets, seines, and longlines are the common gear used, and occasionally bottom trawls are used. However, the commercial fishery in Florida is now strictly hook-and-line because of a recent net ban (DeVries pers. comm.). Many spotted seatrout are caught incidentally while fishing for other inshore fishes (Fischer 1978, Lassuy 1983, Perret et al. 1980).

Recreational: The spotted seatrout is one of the species most often sought by anglers, and the sport catch is substantially greater than the commercial harvest (Tabb and Manning 1961, Van Voorhees et al. 1992, NMFS 1993). Fishery information for the Gulf of Mexico (except Texas) showed a total catch of 18,188,000 spotted seatrout in 1992 (NMFS 1993). Seatrout are taken on light to heavy spinning tackle from shorelines, piers and boats in beach Gulf waters, inshore estuarine bays, sounds, bayous, and tidal streams (Lassuy 1983, Perret et al. 1980). Regulations for recreational fishing of this species vary among the Gulf states (GSMFC 1993).

Indicator of Environmental Stress: Bryan (1971) found levels of DDT in the ovaries and eggs to be 4.77 and 2.93 parts per million, respectively, and considered these concentrations to affect the reproductive capacity of spotted seatrout in the lower Laguna Madre. However, Butler (1969) indicates that successful spawning can occur with concentrations as high as 8 parts per million in the ovaries. The presence of PCB levels below the maximum permissible level in food fish has been verified in spotted seatrout from the Gulf of Mexico (Killam et al. 1992). Experiments with sublethal concentrations of fuel oil (0.00-1.00 ppm) found an increase in the occurrence of larvae with unpigmented eyes, and a decrease in total body length and distance needed to initiate avoidance responses (Johnson et al. 1979). The effect of chlorine concentrations in seawater has been tested on eggs and larvae and found to cause increased mortality (Johnson et al. 1977).

Ecological: The spotted seatrout is a top trophic level carnivore within coastal and estuarine ecosystems, and probably plays a significant role as a predator in

Table 5.35. Relative abundance of spotted seatrout in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| | *Life stage* | | | | |
| Florida Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Ten Thousand Islands | ○ | ○ | ○ | ○ | ○ |
| Caloosahatchee River | ○ | ○ | ○ | ○ | ○ |
| Charlotte Harbor | ◉ | ◉ | ◉ | ◉ | ◉ |
| Tampa Bay | ○ | ○ | ○ | ○ | ○ |
| Suwannee River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Apalachee Bay | ○ | ○ | ○ | ○ | ○ |
| Apalachicola Bay | ○ | ○ | ○ | ○ | ○ |
| St. Andrew Bay | ◉ | ○ | ○ | ○ | ○ |
| Choctawhatchee Bay | ◉ | √ | ◉ | ◉ | √ |
| Pensacola Bay | ○ | ○ | ○ | ○ | ○ |
| Perdido Bay | ○ | √ | ○ | ○ | √ |
| Mobile Bay | ◉ | √ | ◉ | ◉ | √ |
| Mississippi Sound | ◉ | ◉ | ◉ | ◉ | ◉ |
| Lake Borgne | ◉ | ◉ | ◉ | ◉ | ◉ |
| Lake Pontchartrain | ○ | ○ | ○ | ○ | ○ |
| Breton/Chandeleur Sounds | ◉ | ○ | ○ | ○ | ○ |
| Mississippi River | ◉ | | ◉ | | |
| Barataria Bay | ○ | ○ | ○ | ○ | ○ |
| Terrebonne/Timbalier Bays | ◉ | ○ | ◉ | ○ | ○ |
| Atchafalaya/Vermilion Bays | ◉ | ○ | ○ | ○ | ○ |
| Calcasieu Lake | ○ | ○ | ○ | ○ | ○ |
| Sabine Lake | √ | √ | ○ | ○ | √ |
| Galveston Bay | ○ | ○ | ○ | ○ | ○ |
| Brazos River | ○ | ○ | ○ | ○ | ○ |
| Matagorda Bay | ○ | ○ | ○ | ○ | ○ |
| San Antonio Bay | ○ | ○ | ○ | ○ | ○ |
| Aransas Bay | ○ | ○ | ○ | ○ | ○ |
| Corpus Christi Bay | ○ | ○ | ○ | ○ | ○ |
| Laguna Madre | ○ | ○ | ○ | ○ | ○ |
| Baffin Bay | ○ | ○ | ○ | ○ | ○ |
| | A | S | J | L | E |

| Relative abundance: | | Life stage: |
|---|---|---|
| ● | Highly abundant | A - Adults |
| ◉ | Abundant | S - Spawning |
| ○ | Common | J - Juveniles |
| √ | Rare | L - Larvae |
| blank | Not present | E - Eggs |

the structure of estuarine communities (Lassuy 1983, Killam et al. 1992).

**Range**

Overall: The spotted seatrout is found in coastal waters from Cape Cod, Massachusetts to Carmen Island in the Bay of Campeche, Mexico. It is most abundant from Florida to Texas (Fischer 1978, Lee et al. 1980, Lassuy 1983, Mercer 1984, NOAA 1985).

Within Study Area: The spotted seatrout is found from Key West, Florida to the Rio Grande, Texas. Areas of abundance occur around eastern Louisiana, south Texas, Mississippi, Alabama, and along the west coast of southern Florida (Tabb and Manning 1961, Hoese and Moore 1977, Lee et al. 1980, Lassuy 1983, Johnson and Seaman 1986) (Table 5.35).

**Life Mode**

Eggs are pelagic (>30‰) or demersal (25‰) depending on salinity; initially, larvae are pelagic and become demersal after 4 to 7 days. Juveniles and adults are demersal, completing their entire life cycle in inshore waters (Ditty and Shaw 1994). Large juveniles and adults form small schools. This species possesses a definite diel pattern of metabolic activity, with increased activity occurring at night (Pearson 1929, Wagner 1973, Vetter 1977),

**Habitat**

Type: This species is estuarine-dependent, and it completes its entire life cycle in inshore waters (Wagner 1973). Seasonal abundance appears to be associated with estuarine zones, with different estuarine habitats utilized by different life history stages (Helser et al. 1993). Eggs are found from marine to estuarine environments, are buoyant or demersal depending on salinity, and are generally associated with grass beds at or near barrier island passes. They are also found in areas with fine to medium texture detritus devoid of vegetation (Sabins and Truesdale 1974). Larvae are demersal in deep channels with shell rubble, or in bottom vegetation (Tabb 1966). Juveniles in Florida have been reported from a water depth range of 0.5 to 2.2 m (Rutherford et al. 1989a). Seagrass appears to be a critical habitat for juveniles and adults, but backwaters (bayous, tidal creeks, slow flowing rivers), marshes, and other areas without extensive seagrass beds can contain substantial numbers of juveniles as well (Van Hoose 1987, McMichael and Peters 1989, Killam et al. 1992). Juveniles and adults have been found in the seagrasses *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*, and abundance and distribution of juveniles may be influenced by biomass, shoot density, and species composition of seagrass beds (Hettler 1989, Killam et al. 1992). The preferred habitat in Louisiana is along relatively shallow marsh edges of small, saline water bodies in *Spartina alterniflora* dominated areas (Peterson 1986, McMichael and Peters 1989, Chester and Thayer 1990). Individuals have also been found around oil drilling platforms in the nearshore area (Stanley and Wilson 1990). Juveniles and adults can occur in a variety of estuarine habitats including seagrass beds, mangrove-lined depressions, and in relatively deep basins, tidal river mouths, channels and canals (Mok and Gilmore 1983, Van Hoose 1987, Thayer et al. 1988, Chester and Thayer 1990, Killam et al. 1992). Juveniles remain in submerged vegetation during summer, but may move to deeper water during the winter months when water temperatures drop. Adults also occur in the surf zones of barrier islands, particularly in fall months (Perry 1970).

Substrate: The substrate for larvae is highly variable. Vetter (1977) states larvae are dependent on grass beds, while Benson (1982) indicates that the deep channels near grass beds may serve as their initial habitat rather than algae and muddy sand (Tabb 1961), prior to movement into the grass bed as juveniles. In Louisiana, where inshore salinities can be fairly low due to the influence of the Mississippi River, nursery habitat is probably higher salinity lower bays and the nearshore Gulf of Mexico (Herke et al. 1984). Juveniles and adults are generally associated with seagrasses, particularly *Halodule* and *Thalassia*, but they are also common over sand, sand-mud, or medium to soft, mud-detritus substrates, shallow muddy areas, oil platforms and shell reefs (Benson 1982, Peterson 1986, Rutherford et al. 1989a, McMichael and Peters 1989, Chester and Thayer 1990, Killam et al. 1992).

Physical/Chemical Characteristics:
Temperature: Spotted seatrout appear to have a high capacity for metabolic compensation for dealing with the wide extremes in temperature that occur in the estuarine habitats that they exploit on a year-round basis (Vetter 1982).

Temperature - Eggs: Eggs and yolk sac larvae have an optimal temperature of 28°C, but have been hatched experimentally at 32°C (Taniguchi 1980, Gray and Colura 1988). However, complete survival is expected between 23.1° and 32.7°. Eggs incubated at 20°C had a lower mean hatch rate (Gray and Colura 1988).

Temperature - Larvae and Juveniles: Larvae and juveniles have been collected in temperatures of 5° to 36°C (Wang and Raney 1971, Perret et al. 1980, Benson 1982, Rutherford et al. 1989a, Killam et al. 1992); their preferred temperatures range from 20° to 30°C (Arnold et al. 1976).

Temperature - Adults: Adults prefer temperatures from 15° to 27°C, and may move seaward if estuarine temperatures become extreme (Mahood 1974). Simmons (1957) reported active feeding and movement between 4° to 33°C with gradual acclimation; however, sudden drops in temperature can result in mass mortality (Gunter 1941, Moore 1976). Temperatures for spawning range from 20° to 30°C (Benson 1982).

Salinity - Eggs: The highest hatch rates for experimentally incubated eggs have been reported to occur at 15 to 25‰ and 19 to 38‰ at 28°C (Shepard 1986, Gray and Colura 1988), and it is suspected that in lower salinities in the wild, survival may be reduced (Tabb 1966). The optimum salinity for eggs has been reported to be 28.1‰ (Killam et al. 1992). These eggs had a significantly lower hatch rate at 5‰ and all eggs died at any temperature when the salinity was 45‰. Eggs at 5‰ would also sink to the bottom, which would probably increase mortality in the wild. A critical minimum (0‰) and a critical maximum (50‰) has been determined that corresponds to 0% embryo survival at 28°C (Shepard 1986). Salinity acclimation of parents may also affect salinity tolerance of eggs (Gray and Colura 1988).

Salinity - Larvae: Spotted seatrout larvae are considered the most euryhaline of all sciaenid larvae (Killam et al. 1992). They have been collected in Florida from 8.0 to 40.0‰ (Rutherford et al. 1989a, Killam et al. 1992) and optimal salinity has been reported to range from 20 to 35‰ in hatchery conditions (Arnold et al. 1976, Killam et al. 1992).

Salinity - Juveniles: Juveniles seem to prefer mesohaline and polyhaline waters where salinities range from 8 to 25‰ (Peterson 1986). They have been collected in waters with salinities ranging from 0 to 48‰ (Gunter 1945, Wang and Raney 1971, Wagner 1973, Peterson 1986, Rutherford et al. 1989a, Killam et al. 1992).

Salinity - Adults: Adults are considered euryhaline and have been collected over a salinity range of 0.2 to 75‰ (Simmons 1957, Perret et al. 1971, Mercer 1984, Killam et al. 1992). Juveniles and adults appear to prefer moderate salinities (Wagner 1973). Optimum salinities, as judged by swimming performance, occurred at salinities of 20 to 25‰ (for fish with a total length (TL) of 174-438 mm), but were reduced above and below these salinities (Wakeman and Wohlschlag 1977). They are rarely collected below 10‰ or above 45‰ in south Texas waters.

Dissolved Oxygen: Fish kills of spotted seatrout that were due to low dissolved oxygen (DO) concentrations have been reported in Mississippi (Etzold and Christmas 1979).

Turbidity: Spotted seatrout appear to prefer areas of low turbidity (Pearson 1929). Increased mortality due to hurricane-induced high turbidity levels has been reported from Louisiana (Perret et al. 1980).

Movements and Migrations: In Alabama, early juveniles move into tidal rivers in late fall to overwinter (Van Hoose 1987). Adult seatrout migrate very little with most movements occurring seasonally in association with thermal and salinity tolerances, and with spawning activities (Tabb 1966, Bryant et al. 1989, Helser et al. 1993). Large individuals often seek cooler deeper water during the summer, and deeper, warmer waters of bays or the nearshore Gulf of Mexico during the winter (Pearson 1929, Gunter 1945). Several studies indicate that spotted seatrout are estuary-specific, particularly in Florida, with very little movement occurring between estuaries (Killam et al. 1992). This is further substantiated by the existence of independent populations of this species in different estuaries (Iversen and Tabb 1962, Weinstein and Yerger 1976). In Texas, although evidence suggests that sub-populations in bay systems mingle very little, mixing of different groups may occur during the spawning season which may be the reason for the low degree of variability between major bays in this state (King and Pate 1992, Baker and Matlock 1993).

**Reproduction**

Mode: Spotted seatrout have separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe into the water column, and development is oviparous.

Spawning: Sound produced by specialized muscles inserted at the swim bladder wall may have a purpose in spawning activities (Mok and Gilmore 1983). The spawning season is protracted and varies throughout the Gulf of Mexico. It can begin as early as February and continue until October (Pearson 1929, Gunter 1945, Herke et al. 1984, Van Hoose 1987, McMichael and Peters 1989), but generally runs from March to October (Hein and Shepard 1980). Saucier and Baltz (1993) reported that spotted seatrout form "drumming" aggregations in estuarine waters of Louisiana from late May to early October, at salinities from 7to 27‰, and temperatures from 24.5 to 33.5°C, from 6pm to midnight, and that spawning sites were primarily located in deep, moving water in passes between barrier islands. Based on the presence of larval spotted seatrout in the northern Gulf of Mexico, it can be inferred that spawning occurs February through October, with a peak from April through August (Ditty et al. 1988). Spawning may occur throughout the year in southern Florida and Mexican waters (Tabb 1961, Tabb and Manning 1961, NOAA 1985). Spawning occurs at dusk with the peak activity periods usually in late April-June and August-September, and is probably related to water temperature and increasing or decreasing photoperiods (Tabb and Manning 1961, Hein and Shepard 1980, Perret et al. 1980, Wade 1981, Van Hoose 1987, Brown-Peterson et al. 1988, McMichael and Peters 1989, Chester and Thayer 1990). The recorded temperature range for spawning is 24 to 30°C, with 23°C suggested as the minimum temperature for successful spawning (Brown-Peterson et al. 1988). A Florida study recorded surface water temperatures of 15.5 to 31°C during spawning months (McMichael and Peters 1989). In Florida, spawning is essentially completed by the time temperatures rise to 28.3°C (Tabb 1966, Johnson 1978). Spawning probably occurs in moderate to high salinities (Powell et al. 1989). The surface salinity during spawning months can range from 18.5 to 36‰ (McMichael and Peters 1989), and peak spawning occurs between 30 and 35‰ (Tabb 1966). No spawning has been observed above 45‰ (Simmons 1957). Spawning occurs primarily within coastal bays, estuaries, and lagoons, usually in shallow grassy areas, or near passes, and in deeper holes or channels with the eggs drifting into the grassy areas (Welsh and Breder 1923, Pearson 1929, Guest and Gunter 1958, Tabb 1966, Etzold and Christmas 1979, Mok and Gilmore 1983, McMichael and Peters 1989, Powell et al. 1989, Chester and Thayer 1990). Spawning probably occurs in water that is 3 to 4.6 m deep. Spawning may also occur in tidal passes, areas of little or no vegetation, and, in Louisiana, the higher salinity waters of lower bays and the nearshore Gulf of Mexico (Sabins and Truesdale 1974, Allshouse 1983, Herke et al. 1984, Helser et al. 1993).

Fecundity: Spotted seatrout are multiple spawners and their fecundity is difficult to estimate (Brown-Peterson et al. 1988). Estimates of fecundity range from a mean of 14,000 from 283 mm TL I-year class females to 1.1 million eggs for IV-year class averaging 504 mm TL (Sundararaj and Suttkus 1962). Recent evidence suggests that these fecundity estimates may be low and that actual annual fecundity may average greater than 10 million eggs. Spawning frequency appears to be high and is estimated to occur every 3.6 days, but this frequency is probably not sustained throughout the entire spawning season (Brown-Peterson et al. 1988).

**Growth and Development**

Egg Size and Embryonic Development: Eggs are spherical, usually with one oil droplet. Their diameter ranges from 0.7 to 0.85 mm, and hatching occurs 16 to 20 hours after fertilization at 25°C (Fable et al. 1978). Incubation times of 21 hours at 23°C and 15 hours at 27°C have also been reported (Ditty and Shaw 1994).

Age and Size of Larvae: In one laboratory study, larvae grew from a standard length (SL) of 1.5 mm at hatching to 4.5 mm SL in 15 days at about 25°C (Fable et al. 1978). Peebles and Tolley (1988) report growth rates for larval spotted seatrout in south Florida to be approximately 0.4 mm/day. Larval stage sizes range from about 1.8 to 10-12 mm TL (Johnson 1978).

Juvenile Size Range: Transformation to the juvenile stage occurs at a length of 10 - 12 mm (Ditty and Shaw 1994). Juveniles range from 10-12 to 180-200 mm TL (Johnson 1978). Juvenile growth rates during the fall are about 13 to 18 mm/month (McMichael and Peters 1989). Along the Gulf coast of Florida, spotted seatrout have been reported to reach 301-337 mm TL at the end of their first year, but growth slows after age I (Murphy and Taylor 1994). Hatchery-reared juveniles have been reported to reach 160 mm TL in 100 days (Van Hoose 1987). Size at maturity varies among estuaries (Mercer 1984). Spotted seatrout mature between one and three years of age with males tending to mature at smaller sizes than females.

Age and Size of Adults: Maturity and spawning may first occur at 2 years of age (Pearson 1929), but they can occur at the end of their first year (Lassuy 1983). Males mature as early as their first year and females by the end of the second year (Klima and Tabb 1959). Some females mature as early as 271 mm SL in Texas, and they are generally all mature by 300 mm SL (Brown-Peterson et al. 1988). Males are much smaller than females at maturity with all fish 200 mm SL and longer being mature. In a northwest Florida study, 50% of females 200-220 mm FL and 90% of females 220-240 mm FL were mature, all of which were age I (DeVries et al. 1995). Seventy of 73 males, all age I, were found to be mature. There is some variation in growth rate of spotted seatrout throughout its range (Benson 1982), and this variation may be due to ecological rather than genetic factors (Murphy and Taylor 1994). In Florida, estimated maximum ages are 6 to 8 years for females and 5 to 9 years for males (Murphy and Taylor 1994). Adults up to 15 years old have also been reported (Mercer 1984).

**Food and Feeding**

Trophic Mode: The spotted seatrout is an opportunistic, visual carnivore that feeds near the surface and in mid-water depths. It feeds mainly in seagrass areas, and relies almost solely on free swimming organisms for food (Darnell 1958, Stewart 1961, Vetter 1977).

Food Items: The diet of the spotted seatrout changes as it grows and with the seasonal abundance of food items (Pearson 1929, Gunter 1945). Larvae feed primarily on zooplankton, especially copepods, and switch to mostly benthic invertebrates as small juveniles. Juveniles have been found to consume: planktonic schizopods, mysids, copepods, isopods, amphipods, gastropods, bivalves, caridean and penaeid shrimp, and fish (Stewart 1961, Hettler 1989, McMichael and Peters 1989). Juveniles <30 mm SL consume amphipods, mysids and carideans in equal proportions (Hettler 1989). The single most important food for juveniles >30 mm SL was shrimp. Fish increase in dietary occurrence as juveniles reach 50 mm SL and larger, and can comprise almost 90% of the volume in individuals 105-120 mm SL. Fish species consumed include: bay anchovy, gulf menhaden, shad (*Dorosoma* sp.), silversides (*Menidia* sp.), striped mullet, sheepshead minnow, rainwater killifish (*Lucania parva*), gulf toadfish (*Opsanus beta*), inshore lizardfish(*Synodus foetens*), pipefish (*Syngnathus* sp.), pinfish, pigfish (*Orthopristes chrysopterus*), silver jenny (*Eucinostomus gula*), gray snapper, unidentified snappers (*Lutjanus* sp.), hardhead silverside (*Atherinomorus stipes*), goldspotted killifish (*Floridichthys carpio*), code goby (*Gobiosoma robustum*), naked goby (*G. bosci*), clown goby (*Microgobius gulosus*), Atlantic croaker, and spotted seatrout. Young adults prey on a variety of invertebrates and fish, changing almost exclusively to fish as large adults (Gunter 1945, Darnell 1958, Seagle 1969, Danker 1979, Levine 1980, Hettler 1989, McMichael and Peters 1989). Some marine vegetation and shell fragments have been noted that were probably picked up while capturing prey (Tabb and Manning 1961). The diets of larger juveniles and adults are skewed to the consumption of shrimp in the warmer months and fish in the cooler months when shrimp are not as available (Pearson 1929, Gunter 1945). Variations in food habits indicates that geographical location and type of estuary influences available prey, and that spotted seatrout stomach contents reflect this availability (Hettler 1989).

**Biological Interactions**

Predation: Known predators of juvenile spotted seatrout include alligator gar (*Lepisosteus spatula*), striped bass (*Morone saxatilis*), ladyfish (*Elops saurus*), tarpon, bluefish, silver perch, Atlantic croaker, snook, yellow bass (*Morone mississippiensis*), spotted seatrout, barracuda (*Sphyraena barracuda*), Spanish mackerel, and king mackerel (*Scomberomorus cavalla*) (Miles 1949, Darnell 1958, Benson 1982, Killam et al. 1992).

Factors Influencing Populations: Species that may possibly compete with spotted seatrout for habitat and food include hardhead catfish, grouper (*Mycteroperca* sp.), silver perch, red drum, spot, and Atlantic croaker (Killam et al. 1992). Distribution and abundance of juvenile spotted seatrout in Florida Bay appears to be influenced by the biomass, shoot density, and species composition of the seagrass community (Shipp 1986, Chester and Thayer 1990, Killam et al. 1992). Losses in seagrass beds and other key habitat areas have been linked with declining seatrout populations. Overfishing may also be contributing to this decline (Shipp 1986). Periods of low rainfall and high salinity may lower recruitment of young fish into the population (Rutherford et al. 1989b). Catastrophic mortalities have been attributed to severe cold, hurricanes, high turbidity, excessive fresh water, red tide, and supersaturated dissolved oxygen conditions (Gunter 1941, Gunter and Hildebrand 1951, Springer and Woodburn 1960, Renfro 1963, Perret et al. 1980, Killam et al. 1992). In Louisiana, the use of weirs in canals may impede migration of young-of-the-year fish into the marsh areas of impounded water bodies or the movement of fish trying to escape environmental extremes (Herke et al. 1984). Larger adults are frequently infected with pleurocerci of the tapeworm *Poecilancistrium robustrum* (spaghetti worm) (Lorio and Perret 1978). Fish with these worms are frequently discarded although they do not affect the taste of the fish, nor are they infectious to humans.

**Personal communications**

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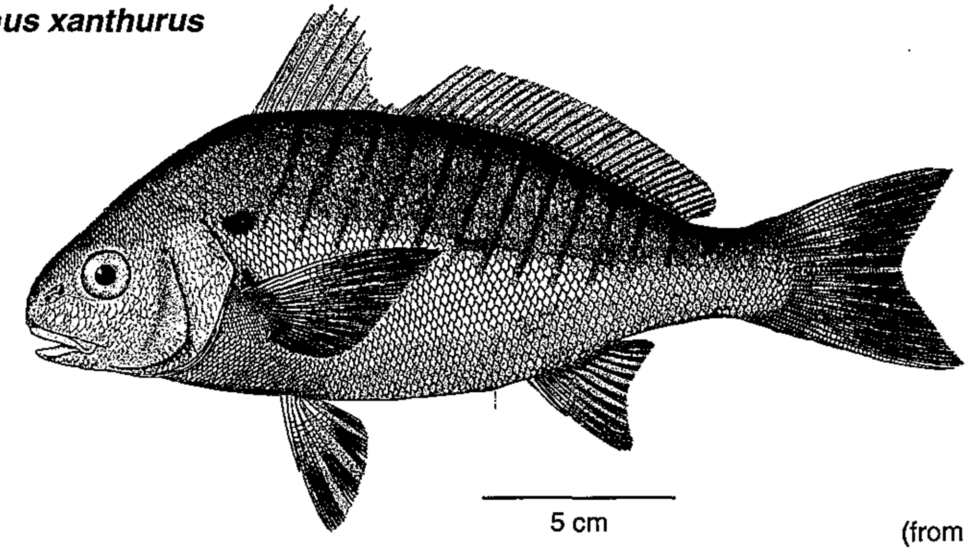
# Spot

***Leiostomus xanthurus***
**Adult**




(from Goode 1884)

**Common Name:** spot
**Scientific Name:** *Leiostomus xanthurus*
**Other Common Names:** Flat croaker, yellowtail; golden croaker during spawning season (Hoese and Moore 1977); goody, roach, and post croaker (Benson 1982), spot croaker, *tambour croca* (French), and *verrugata croca* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Perciformes
Family: Sciaenidae

**Value**

Commercial: Most of the commercial foodfish harvest of spot comes from the Chesapeake Bay and southeast U.S. Atlantic coast. Larger fish are marketed mainly as fresh product, but due to the small size of this species it is more frequently used by pet food processors. In the Gulf of Mexico, it contributes to the commercial bottomfish industry of Louisiana and Mississippi which uses it for fish meal and oil as well as pet food (Fischer 1978, Shipp 1986, Hales and Van Den Avyle 1989). Approximately 1 to 2 mt are harvested each year in the Gulf of Mexico, mostly for this purpose. It is taken primarily by otter trawl, but also by gill nets, haul seines, and pound nets (Mercer 1989).

Recreational: This species is less likely than other sciaenids to be taken by hook and line due to its dietary habits; however, some recreational fishing for spot does occur on the Atlantic coast (Hales and Van Den Avyle 1989). It readily takes the proper bait and can be caught near bridges, piers, and wharves, and is also caught frequently in the smaller trawls used by sportnetters in lower bay and nearshore areas (Shipp 1986, Hales and Van Den Avyle 1989). Fishery information for the Gulf of Mexico (excluding Texas) showed a total recreational catch of 825,000 spot in 1993 (O'Bannon 1994).

Indicator of Environmental Stress: This species is a bottom feeder which often accumulates contaminants and is a target species for NOAA's National Status and Trends Program and other environmental monitoring studies (NOAA 1987a, NOAA 1987b, Killam et al. 1992). It is used for monitoring many pesticides, herbicides, heavy metals, chlorinated hydrocarbons, and chlorination byproducts (Hales and Van Den Avyle 1989, Heitmuller and Clark 1989, Mercer 1989, Killam et al. 1992). The spot can be a common inhabitant in environmentally stressed estuaries due to its tolerance of a wide range of environmental conditions (Killam et al. 1992).

Ecological: The spot is a dominant species in bottom habitats of nearshore and inshore areas of the northern Gulf of Mexico (Shipp 1986, Killam et al. 1992). It is considered to be a major regulator of benthic invertebrate species and important in the structure and function of estuarine ecosystems (Phillips et al. 1989, Killam et al. 1992).

**Range**

Overall: The spot is found along the coasts of the western Atlantic Ocean and the Gulf of Mexico, ranging from the Gulf of Maine to the Bay of Campeche, Mexico in coastal shelf waters in depths up to 205 m (Bigelow and Schroeder 1953, Springer and Bullis 1956, NOAA 1985). It is most abundant from Chesapeake Bay to the Carolinas, and is uncommon in the Florida Keys (Fischer 1978, Wang and Kernehan 1979).

Table 5.36. Relative abundance of spot in 31 Gulf of Mexico estuaries (Nelson et al. 1992, VanHoose pers. comm.).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | | | ○ | | |
| Ten Thousand Islands | | | ○ | ◉ | |
| Caloosahatchee River | √ | | ○ | | |
| Charlotte Harbor | √ | | ○ | √ | |
| Tampa Bay | ◉ | | ● | ● | |
| Suwannee River | ○ | | ◉ | ○ | |
| Apalachee Bay | ◉ | | ● | ○ | |
| Apalachicola Bay | ◉ | | ◉ | ○ | |
| St. Andrew Bay | ◉ | | ◉ | ○ | |
| Choctawhatchee Bay | ◉ | | ● | ● | |
| Pensacola Bay | √ | | ● | ● | |
| Perdido Bay | ◉ | | ◉ | ◉ | |
| Mobile Bay | ◉ | | ● | ○ | |
| Mississippi Sound | ● | ◉ | ● | ● | ● |
| Lake Borgne | ○ | | ● | ● | |
| Lake Pontchartrain | ○ | | ○ | ○ | |
| Breton/Chandeleur Sounds | ○ | | ◉ | | |
| Mississippi River | ◉ | | ◉ | | |
| Barataria Bay | | | ● | ◉ | |
| Terrebonne/Timbalier Bays | ○ | | ◉ | | |
| Atchafalaya/Vermilion Bays | | | ◉ | | |
| Calcasieu Lake | | | ○ | | |
| Sabine Lake | ◉ | | ○ | | |
| Galveston Bay | ○ | | ◉ | | |
| Brazos River | na | | ◉ | | |
| Matagorda Bay | ○ | | ◉ | | |
| San Antonio Bay | ○ | | ◉ | | |
| Aransas Bay | ◉ | | ◉ | | |
| Corpus Christi Bay | ◉ | | ◉ | | |
| Laguna Madre | ◉ | | ● | | |
| Baffin Bay | ○ | | ● | | |

*Life stage* columns: A S J L E

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present
- na No data available

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

Within Study Area: The spot is found throughout coastal shelf areas of the U.S. Gulf of Mexico from Florida Bay to the Rio Grande River. It is common in both bays and open Gulf areas except at the extremities of its range (Hoese and Moore 1977, Shipp 1986) (Table 5.36).

**Life Mode**

Eggs and early larvae are planktonic and pelagic. Juveniles and adults are demersal in estuarine and coastal waters (Ditty and Shaw 1994).

**Habitat**

Type: The spot utilizes several habitat types throughout its life cycle. Larvae are found in the marine environment, and have been collected in the northern Gulf of Mexico on the continental shelf up to the 40 m isobath, or 130 km offshore. They occur at all depths, but are found primarily in the upper 30 m of the water column (Sogard et al. 1987, Cowan and Shaw 1988). Larvae are transported inshore into estuarine nursery areas where postlarval and juvenile spot are found. Younger juveniles are often found in the shallow head waters of tidal creeks, and sometimes in seagrass beds, while older juveniles move to deeper, more saline areas of estuaries (Wang and Kernehan 1979, Mercer 1989, Hales and Van Den Avyle 1989). Adults migrate seasonally between estuarine and coastal waters, with movement offshore occurring in the fall (Hales and Van Den Avyle 1989).

Substrate: Adults are taken most frequently over mud and sand bottoms in inside waters and offshore waters to at least 132 m (Dawson 1958, Music 1974, Huish and Geaghan 1987). They are also found over mud, sand, and sandy shell bottom. Juveniles are found primarily in nursery areas with mud and detritus bottoms (Mercer 1989).

Physical/Chemical Characteristics:

Temperature - Eggs and Larvae: Lab-spawned eggs successfully developed at 20°C (Powell and Gordy 1980). In waters in or near the Gulf Stream, larvae less than 15 days old have been collected only in water above 19.3°C (Warlen and Chester 1985). Spot below 20.0 mm SL have been found below 20°C in Mississippi Sound with the majority taken at temperatures from 7° to 15°C (Warren and Sutter 1982). Larvae have been collected at 5° to 19.3°C, and juveniles at 4° to 35°C and (Wang and Raney 1971, Wagner 1973, Pineda 1975, Cowan and Shaw 1988, Hales and Van Den Avyle 1989). The upper incipient lethal temperature for post larval and small juvenile spot has been estimated at 35.2°C (Mercer 1989), and the critical thermal maximum for juvenile spot acclimated at 15°C was 31.0°C.

Temperature - Juveniles and Adults: Spot tolerate temperatures from 1.2° to 36.7°C; however, extended periods of low temperatures have resulted in dead or stunned fish. Death due to temperature is a function of size, acclimation and rate of temperature drop (Benson 1982). Juvenile spot are reportedly more tolerant of cold than adults. Large numbers of adults are found between 25° to 30°C (Warren and Sutter 1982).

Salinity - Eggs and Larvae: Laboratory spawned eggs have developed at 30 to 35‰ (Powell and Gordy 1980). Larvae have been collected in the field from 6 to 36‰, and appear capable of tolerating a wide range of estuarine salinities (Warlen and Chester 1985, Cowan and Shaw 1988, Killam et al. 1992). They have been reared successfully in the laboratory at 30 to 35‰.

Salinity - Juveniles and Adults: Spot is a euryhaline species. Juveniles have been found from 0 to 36.2‰ (Kelley 1965, Wang and Raney 1971, Wagner 1973, Pineda 1975, Lee et al. 1980, Benson 1982). They occur in greater numbers at salinities above 10‰, and are less abundant in freshwater areas (Killam et al. 1992). Adults seem to prefer a more polyhaline environment than juveniles. Although they have been found from 0 to 60‰ (Hildebrand and Cable 1930, Thomas 1971, Powell and Gordy 1980), large numbers occur most often from 15‰ to 30‰ (Warren and Sutter 1982).

Dissolved Oxygen: This species is very tolerant of low dissolved oxygen (DO) conditions and has been found in waters with DO less than 2 parts per million (ppm) (Killam et al. 1992). It is most common in waters where the DO exceeds 4 ppm. For juvenile spot acclimated to 28° C, 1 and 96 hour LC50s were determined to be 0.43 and 0.60 ppm respectively.

Migrations and Movements: Adults migrate seasonally between estuarine and coastal waters. They enter bays and sounds in spring and move offshore in fall and winter to spawn (Hildebrand and Schroeder 1928, Pearson 1929, Hildebrand and Cable 1930, Gunter 1945, Dawson 1958, Kelley 1965, Perry 1970, Franks et al. 1972, LeBlanc et al. 1991) and avoid cold temperatures (Christmas and Waller 1973, Huish and Geaghan 1987). Post-spawning fish have been collected in nearshore waters, and it is possible that adults remain offshore after spawning although few are taken in these areas by bottom trawling (Gunter 1945, Dawson 1958, Hales and Van Den Avyle 1989). Larvae are probably carried by longshore currents or by direct across-shelf transport into nearshore waters, and into estuarine areas by tidal flow (Cowan and Shaw 1988, Mercer 1989). Immigration into estuaries of postlarvae begins in December and continues through May (Joseph 1972, Warren and Sutter 1982, Cowan and Shaw 1988, Mercer 1989). A pattern of recruitment along the sandy shorelines and seagrass beds of Tampa Bay have been observed for postlarvae less than 20 mm SL (Killam et al. 1992). These protected regions appear extremely beneficial in promoting the rapid growth of postlarvae. Juveniles move up into low salinity headwater areas and may ascend brackish water to fresh water during the spring and summer (Hildebrand and Cable 1930). Older fish tend to seek out deep, higher salinity waters in bays, and begin to emigrate from estuaries in May or June, becoming absent by late fall (Nelson 1967, Parker 1971, Warren and Sutter 1982). Emigration occurs when they reach total lengths (TL) of about 60 (Townsend 1956) to 88 mm, or after about 8-9 months (Kilby 1955, Wagner 1973, Killam et al. 1992), and may be a response to seasonal temperature declines (Sheridan 1979). Some adults may not migrate back to inshore waters, but remain in deep waters (50-91 m) in the Gulf (Perry 1970).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe into the water column, and the degree of fertilization is determined by the density of spawning individuals (Killam et al. 1992). Egg development is oviparous.

Spawning: Spawning occurs from late fall to early spring offshore in moderately deep water over the continental shelf (Townsend 1956, Dawson 1958, Nelson 1967, Wang and Raney 1971, Sabins and Truesdale 1974, Allshouse 1983, Mercer 1989, Killam et al. 1992) with possibly some activity near beaches and passes (Pearson 1929, Music 1974). Spawning in the Gulf waters off Louisiana occurs from near midshelf (about 65 km) out to 175 km from the coast (Cowan and Shaw 1988), although spawning activity appears to decrease in the offshore direction (Sogard et al. 1987). Spawning seasons in the Gulf of Mexico are: from October through March or April in the Tampa Bay region of Florida (Killam et al. 1992); in the northern Gulf off Alabama, probably from December to at least late February (Nelson 1967); in Louisiana waters from November through March (Cowan and Shaw 1988); off Texas late November to April, with peaks from December to February (Pearson 1929, Allshouse 1983). Based on the presence of larval spot in the northern Gulf of Mexico, it can be inferred that spawning occurs October through April, with a peak from December through January (Ditty 1986, Ditty et al. 1988). Sheridan et al. (1984) suggested a late fall peak for fish in the northern Gulf, but no winter samples were taken. Spot held in a laboratory only spawned at temperatures between 17.5 to 25.0° C.

Fecundity: Fecundity ranges from 20,900 eggs in a female with a standard length (SL) of 136 mm to 514,400 eggs in a 178 mm SL female (Sheridan et al. 1984). The spot appears to be a fractional spawner capable of several spawning events during a single season (Killam et al. 1992).

**Growth and Development**

Egg Size and Embryonic Development: Egg sizes range from 0.72 to 0.87 mm (Lippson and Moran 1974, Johnson 1978, Ditty and Shaw 1994).

Age and Size of Larvae: Larvae hatch in about 48 hours at 20°C at a size of 1.6 to 1.7 mm SL (Ditty and Shaw 1994). Fruge and Truesdale (1978) collected 86 larval spot in coastal waters of Louisiana, ranging in size from 1.6 to 10.7 mm SL. Larvae can grow from 1.6 mm SL to 17-19 mm in 90 days (Warlen and Chester 1985). In North Carolina's Cape Fear River estuary, daily growth rates for larvae are 0.14 to 0.16 mm/day (Weinstein and Walters 1981). Increases in the rate of daily growth have been demonstrated when high densities of microzooplankton are present, particularly when larvae and food are concentrated in waters that are hydrographically discontinuous (Govoni et al. 1985).

Juvenile Size Range: Transformation to the juvenile stage occurs at about 15 mm TL (Ditty and Shaw 1994). Growth rate varies with location, environmental factors (Johnson 1978), and possibly age (Warren 1981). Juveniles from the Gulf of Mexico grow at about 7-18.6 mm/month (Parker 1971, Ruebsamen 1972, Warren 1981, Warren and Sutter 1982). Spot grow rapidly in their first year growing as much as 90 to 140 mm TL. Growth is slower during the second year, proceeding at only 5.5 mm/month.

Age and Size of Adults: Maturation occurs at the end of the second year or early in the third year on the Atlantic coast. In the Gulf of Mexico, some spot mature at age I; males at 123 mm SL and females at 127 mm SL (Sheridan et al. 1984). Spot are one of the smallest members of the drum family (Shipp 1986). In the Gulf of Mexico it can grow up to 250 mm TL (Hoese and Moore 1977), although it can reach up to 340 mm SL in the northern parts of its range (Johnson 1978). There is a pronounced sexual dimorphism in growth rate with females growing more rapidly. Females also become proportionally more abundant in the population at a later age, and live longer than males. Overall, this is a short-lived species that rarely attains a maximum age of 5 years, but usually only lives 2 to 3 years (Hales and Van Den Avyle 1989, Mercer 1989).

**Food and Feeding**

Trophic Mode: The spot can be both an opportunistic generalist or a selective predator depending on its developmental stage and food availability (Hales and Van Den Avyle 1989, Killam et al. 1992). Larval and postlarval spot are size-selective planktivores (Livingston 1984, Mercer 1989, Govoni and Chester 1990). Juveniles and adults are nocturnal, opportunistic bottom feeders utilizing infaunal and epibenthic invertebrates (Hales and Van Den Avyle 1989, Killam et al. 1992). Feeding by juveniles appears to tidally influenced, with most feeding occuring in marsh intertidal zones during high tide when they can presumably take advantage of the greater concentration of prey items that occur there (Archambault and Feller 1991, Killam et al. 1992). Prey items within 2 to 3 mm of the substrate surface are most susceptible to feeding activities by juvenile spot. Adults feed on benthic fauna by scooping and straining sediments through their gill rakers to remove prey items and spitting out unwanted material (Killam et al. 1992).

Food Items: Food habits of the spot change with its growth and development (Currin et al. 1984). Larvae feed on zooplankton such as tintinnids, fish and invertebrate eggs, bivalve veligers, copepod nauplii, and postlarvae feed predominantly on copepods (Livingston 1984, Mercer 1989, Govoni and Chester 1990). Feeding appears to be influenced by visibility, size, and motility of potential prey items (Govoni et al. 1985, Govoni and Chester 1990). Juveniles feed primarily on crustaceans (especially copepods), molluscs, nematodes, and polychaete worms (Ruebsamen 1972, Sheridan 1979, Levine 1980, Livingston 1984). In a portion of Florida's Apalachicola Bay complex, the diet of spot fell into two feeding patterns (Sheridan 1979). Food items from shallow, low salinity, nearshore areas consisted mostly of insect larvae, bivalves, and detritus, while in deeper, higher salinity areas, it was primarily polychaetes and harpacticoid copepods. Adults most frequently consume polychaetes, amphipods, bivalve and gastropod molluscs, cumaceans, nematodes, mysids, and copepods (Hales and Van Den Avyle 1989). Although some studies show that spot will forage regardless of substrate type, evidence suggests that muddy substrates are preferred over sandy ones (Killam et al. 1992). The ability of spot to sieve coarser sediment through their gill rakers may be a limiting factor.

**Biological Interactions**

Predation: A study in the Cape Fear River estuary in North Carolina found that silversides (*Menidia* sp.) and killifish (*Fundulus* sp.) prey on larval and early juvenile stage spot (Weinstein and Walters 1981). Other reported piscine predators of spot from the U.S. Atlantic coast include sand bar shark, silky shark, longnose gar, striped bass, bluefish, different species of seatrout, king mackerel, and flounders (Dawson 1958, DeVane 1978, Medved and Marshall 1981, Rozas and Hackney

1984, Hales and Van Den Avyle 1989, Mercer 1989, Killam et al. 1992). Wading birds such as the clapper rail also utilize this species as food (Heard 1982).

Factors Influencing Populations: Results in a study from the Mississippi Sound area suggest that inshore shrimping activities have a pronounced effect on the abundance of this and other species of groundfish (Warren 1981). The principal causes of mortality in juvenile spot include predation and low winter temperatures during early recruitment events (Killam et al. 1992). Predation in higher salinity waters may also be a limiting factor in juvenile spot production (Currin et al. 1984). Although spot may be able to survive in waters of low DO, many of the prey items are not able to tolerate such conditons (Killam et al. 1992). Low DO may therefore indirectly influence the distribution patterns of spot, that will move to areas with abundant food resources. Spot and Atlantic croaker may compete for the same food resources, but it is not known to what extent this competition affects their abundance and distribution.

**Personal communications**

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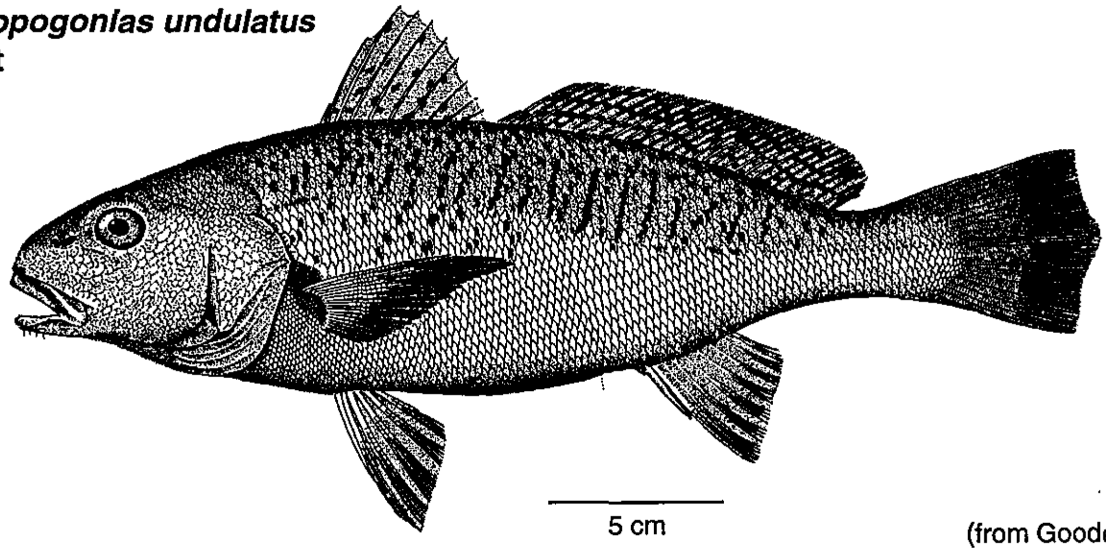
# Atlantic croaker

***Micropogonias undulatus***
**Adult**



5 cm

(from Goode 1884)

**Common Name**: Atlantic croaker
**Scientific Name**: *Micropogonias undulatus*
**Other Common Names**: Croaker, crocus, hardhead, king billy; *tambour bresilien* (French); *la corbina, corvinon brasilieno*, and *gorrubata* (Spanish) (Fischer 1978, Lassuy 1983, NOAA 1985).
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Perciformes |
| Family: | Sciaenidae |

**Value**

Commercial: A commercial fishery for this species has existed in the Atlantic Ocean since the late 1880's (NOAA 1993). In the Gulf of Mexico, the Atlantic croaker is the most important species of industrial bottomfish, representing about 76% of the total landings (Warren and Sutter 1982, NOAA 1985, NOAA 1993). The major harvesting areas are located between Mobile Bay, Alabama and Calcasieu Lake, Louisiana. The Gulf fishery for croaker began expanding in 1967 with the decline in landings from the Chesapeake Bay and the discovery of large stocks around the mouth of the Mississippi River. About 44 mt of croaker estimated at $48 thousand were taken by commercial fishermen in the Gulf (Newlin 1993). More than 43 mt were caught within 5 km of the coast. Landings by state for 1992 were: Florida - 6.8 mt; Alabama - 8.6 mt; Louisiana - 25.4 mt; and Texas - 3.18 mt (Newlin 1993). Major methods of harvest include pound nets, haul seines, otter trawls, and gill nets with some additional catches made by trammel and fyke nets (Mercer 1989). It is considered an excellent foodfish, and is exported to foreign countries where it is a preferred species (Fischer 1977, Shipp 1986). It occasionally appears in domestic markets where it is usually marketed fresh (Fischer 1978).

Recreational: Atlantic croaker also contributes significantly to the sportfish fishery in the eastern Gulf of Mexico (Warren and Sutter 1982). While not a particularly popular game fish, it is still caught by many fishermen. Large "bull croakers" are particularly sought for around oil rigs west of the Mississippi delta in Louisiana waters (NOAA 1985). The United States marine recreational catch was about 3,293 million croakers in 1993 for the Gulf of Mexico (except Texas), the majority being caught in nearshore waters (O'Bannon 1994).

Indicator of Environmental Stress: This species is a bottom feeder which often accumulates contaminants and is a target species for NOAA's National Status and Trends Program (NOAA 1987). The effects of heavy metals and PCB's on Atlantic croaker reproduction (Thomas 1989, Thomas 1990), the effects of sublethal copper exposure (Scarfe et al. 1982), and of lead on glutathione levels (Juedes 1985) have also been studied.

Ecological: Because of its high abundance, Atlantic croaker is an important predator of benthic invertebrates (Lassuy 1983).

**Range**

Overall: The Atlantic croaker occurs in coastal waters of the western Atlantic, from the Gulf of Maine to southern Florida and along the Greater Antilles. It is rare around the Florida Keys. In the Gulf of Mexico, it is found from southern Florida to central Mexico. It may also occur in the southern Gulf and the lesser Antilles

Table 5.37. Relative abundance of Atlantic croaker in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | | | √ | | |
| Ten Thousand Islands | | | √ | | |
| Caloosahatchee River | | | √ | | |
| Charlotte Harbor | | | ○ | | |
| Tampa Bay | | | √ | | |
| Suwannee River | ○ | | ○ | ○ | |
| Apalachee Bay | ○ | | ○ | ○ | |
| Apalachicola Bay | ◉ | | ● | ◉ | |
| St. Andrew Bay | ◉ | | ◉ | ○ | |
| Choctawhatchee Bay | ◉ | | ◉ | ◉ | |
| Pensacola Bay | ◉ | | ● | ● | |
| Perdido Bay | ○ | | ○ | ○ | |
| Mobile Bay | ◉ | | ● | ◉ | |
| Mississippi Sound | ● | ◉ | ● | ● | ◉ |
| Lake Borgne | ○ | | ● | ◉ | |
| Lake Pontchartrain | ○ | | ● | | |
| Breton/Chandeleur Sounds | ○ | | ◉ | | |
| Mississippi River | | | ● | | |
| Barataria Bay | | | ● | ◉ | |
| Terrebonne/Timbalier Bays | | | ● | ◉ | |
| Atchafalaya/Vermilion Bays | | | ● | ○ | |
| Calcasieu Lake | | | ● | | |
| Sabine Lake | ◉ | | ◉ | | |
| Galveston Bay | ○ | | ● | | |
| Brazos River | na | | ● | | |
| Matagorda Bay | ◉ | | ● | | |
| San Antonio Bay | ◉ | | ● | | |
| Aransas Bay | ◉ | | ◉ | ◉ | |
| Corpus Christi Bay | ◉ | | ◉ | ◉ | |
| Laguna Madre | ◉ | | ◉ | ◉ | |
| Baffin Bay | ◉ | | ◉ | | |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present
- na No data available

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

down to Argentina, but is may be confused with a similar species, *Micropogonias furnieri* (Chao and Musick 1977, Hoese and Moore 1977, Fischer 1978).

Within Study Area: The Atlantic croaker occurs from Florida Bay to the Rio Grande River in Texas. It is considered one of the most common bottom-dwelling, estuarine fish in the northern Gulf of Mexico (Table 5.37) (White and Chittenden 1976, Hoese and Moore 1977).

**Life Mode**

Atlantic croaker are estuarine-dependent. Eggs are pelagic and buoyant (Ditty and Shaw 1994), and early larvae are pelagic and planktonic. Early larvae are found on the mid- to outer continental shelf, but become generally uniform throughout the shelf. Later stages become more demersal and occur in more inshore to estuarine areas. Juveniles become still more demersal and move into tidal creeks. Adults are demersal and move between estuarine and oceanic waters (Lassuy 1983, Cowan 1985, Cowan and Shaw 1988).

**Habitat**

Type: Adults are estuarine to marine, and have been collected from depths of 1 to 90 m. They appear to be most abundant in mesohaline and polyhaline salinities, and are rare below 10‰ (Christmas and Waller 1973, Wagner 1973). Juveniles are estuarine to riverine and prefer fresh to mesohaline salinities (Parker 1971). Eggs and early larvae are marine, and later larvae are marine to estuarine. Recently spawned larvae have been collected at depths ranging from 15 to 115 m, although most occur in the upper 30 m, about 20 to 200 km from shore (Cowan 1985, Sogard et al. 1987, Cowan and Shaw 1988). Most small larvae were collected near midshelf about 65-125 km from shore in euhaline salinities. Fish three years old tend to dominate estuaries in North Carolina while those >3 years old are found mostly offshore (Ross 1988).

Substrate: Practically all sizes of croaker beyond the larval stage are associated with soft bottoms (Lassuy 1983). Juveniles occur over mud-sand in shallow estuarine and tidal creek areas, i.e., fine unconsolidated substrates. Adults are associated with mud-sand, oyster reefs, shell and live bottoms in deeper waters.

Physical/Chemical Characteristics:

Temperature - Eggs and Larvae: While eggs and newly hatched larvae are found at 18-25°C, larger and older larvae can be found at progressively decreasing temperatures. Larvae have been found in temperatures as low as 10°C in the Gulf of Mexico (Cowan 1985, Cowan and Shaw 1988), but in the Chesapeake Bay area, they are found from 0° to 24° C (Ward and Armstrong 1980).

Temperature - Juveniles and Adults: The Atlantic croaker has been collected from 0.4° to 35.5°C in the Gulf of Mexico (Miller 1964, Parker 1971, Warren and Sutter 1982). Juveniles are generally more tolerant of low temperatures (0.4°-38°C) than adults (5°-35.5°C) (Parker 1971, Wagner 1973, Pineda 1975, Rogers 1979, Ward and Armstrong 1980, Benson 1982). Preferred temperatures for juveniles range from 6° to 20° C, and they grow well between 12.8° and 28.4° C. In Mississippi waters, adults were found in highest numbers at <30° C (Christmas and Waller 1973). They are rarely found below 10° C in Texas waters (Parker 1971). Lethal minimum and maximum temperatures are 0.6° and 38° C for juveniles and 3.3° and 36° C for adults (Parker 1971, Ward and Armstrong 1980).

Salinity - Eggs and Larvae: Eggs and larvae are found in euhaline waters. In the Gulf of Mexico, larvae have been found in salinities ranging from 15 to 36‰ (Cowan 1985, Cowan and Shaw 1988), but in the Chesapeake Bay area, they are found from <1 to 21‰ (Ward and Armstrong 1980).

Salinity - Juveniles and Adults: Atlantic croaker are euryhaline, having been collected from 0 to 40‰ and rarely at 75‰ (Simmons 1957, Parker 1971, Wang and Raney 1971, Warren and Sutter 1982, Darovec 1983, Lassuy 1983). Juvenile croaker have been taken in salinities of 0.0 to 36.7‰ (Miller 1964, Parker 1971, Wagner 1973, Rogers 1979). In Texas and Louisiana bays, they have been found to be most abundant at <15‰ (Gunter 1945, Wang and Raney 1971, Wagner 1973, Ward and Armstrong 1980), but they appear to be relatively abundant from 10‰ to 20‰ in Alabama and Mississippi (Swingle 1971, Etzold and Christmas 1979). Juveniles are reportedly more tolerant of low salinities than adults (Gunter 1975). Adults are collected in waters with salinities that range from 0 to 70‰ (Simmons 1957, Ward and Armstrong 1980). In Mississippi, adults were most abundant in waters with salinities of 15 to 19.9‰ (Christmas and Waller 1973, Ward and Armstrong 1980).

Dissolved Oxygen (DO): Dissolved oxygen (DO) requirements are not well known, but the presence of this species in poorly oxygenated canals indicates a tolerance for low DO (Lassuy 1983). Juveniles are found in waters with a dissolved oxygen content of 5.7 to 8.6 parts per million (ppm) (Hoese et al. 1968). Captures at DO concentrations from 1 through 13 ppm have been reported with most occurring between 8 and 13 ppm (Marotz 1984).

Turbidity: Densities of Atlantic croaker have been noted as more abundant in areas of high water turbidity possibly as the result of increased food availability and predator protection due to lower visibility (Lassuy 1983).

Migrations and Movements: Adults have seasonal inshore and offshore migrations, although some appear to remain in offshore waters (55 to 118 m) all year (Perry 1970). Adults move up bays and estuaries in spring, randomly in summer, and seaward and southerly in fall. Larvae are carried by longshore currents into nearshore areas where tidal flow transports them into estuarine areas (Cowan and Shaw 1988). Larval recruitment into estuaries occurs from October to May, peaking between November and February (Wagner 1973, Marotz 1984). As they mature into juveniles, they move up into headwater areas. After spending 6-8 months in the estuary, offshore emigration begins in late March or early April at about 50 mm standard length (SL) or larger and continues until November (Kelley 1965, Perry 1970, Wagner 1973, Yakupzack et al. 1977, Rogers 1979, Marotz 1984). Emigration is probably governed by cues from fluctuations in environmental conditions in the nursery area (e.g. tides, temperature, salinity, day length, etc.), and is not just a function of fish size (Clairain 1974, Yakupzack et al. 1977).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe into the water column, and development is oviparous.

Spawning: Spawning in the Gulf of Mexico has been reported from September through May, with a peak in October, specifically around mid-October, and possibly November (Sabins and Truesdale 1974, White and Chittenden 1976, Allshouse 1983, Marotz 1984). Based on the presence of larval croaker in the northern Gulf of Mexico, it can be inferred that spawning occurs September through April, with a peak from October through January (Ditty 1986, Ditty et al. 1988). Based on larval growth information, the spawning season off western Louisiana is probably limited to November-January, with very little spawning occurring after January (Cowan 1988). Most spawning probably takes place in the nearshore Gulf of Mexico near island passes (Sabins and Truesdale 1974, Lassuy 1983, Sogard et al. 1987).

Fecundity: Sheridan et al. (1984) found fecundities for Gulf of Mexico fish ranged from 27,000 eggs for 136 mm SL to 1,075,000 for a 318 mm SL specimen. Fish collected from Cape Hatteras, North Carolina northward were reported to have a fecundity range of 100,800 to 1,742,000 for fish 196 to 390 mm total length (TL) (Morse 1980).

**Growth and Development**

Egg Size and Embryonic Development: Eggs are spherical, and sizes range from 0.49 to 0.58 mm (Wang and

Kernehan 1979).

Age and Size of Larvae: Larvae upon hatching are 1.3 to 2.0 mm TL (Wang and Kernehan 1979). Incubation time is 29-32 hours at 23°C and 26-30 hours at 25°C. Fruge and Truesdale (1978) collected 103 larval croaker in coastal waters of Louisiana, ranging in size from 1.7 to 10.5 mm SL. Cowan (1988) determined growth for 40-80 day larvae to be approximately 0.19 mm/day. In Texas, young-of-the-year appear from November to January at 10-50 mm TL. Larval stage is complete by approximately 10 mm TL when the full complement of spines and soft rays in the dorsal and anal fins are reached (Johnson 1978).

Juvenile Size of Larvae: Transformation to the juvenile stage occurs at a length of approximately 12 mm (Ditty and Shaw 1994). Juveniles may range in size from 11 to 140 mm TL (Johnson 1978, White and Chittenden 1976). One study from western Louisiana estimates juvenile growth rate at 0.47 mm/day or 14.2 mm/month (Arnoldi et al. 1973), while other estimates from the Mississippi Sound area are 3.1 mm/week (Warren 1981) and 13.0 mm/month (Warren and Sutter 1982).

Age and Size of Adults: Maturity in fish sampled from Texas and Louisiana areas was reached after the first year of growth when individuals reached 140 to 170 mm TL (White and Chittenden 1976). Most adults live up to 3 years with some living 4 to 5 years, but rarely longer (Etzold and Christmas 1979, Lassuy 1983). In North Carolina, fish older than 3 years were found offshore, but were rare in estuaries (Ross 1988). The oldest fish recovered there were estimated to be 7 years old. The predicted TLs for year classes are: 176.6 mm for age 1; 261.5 mm at age 2; 331.0 mm at age 3; 388.0 mm at age 4; 434.5 mm at age 5; and 472.7 mm at age 6 (Ross 1988). The largest reported specimen was 668 mm TL (Rivas and Roithmayr 1970). Ross (1988) has derived Van Bertalanffy growth models for this species.

**Food and Feeding**

Trophic mode: Larvae and early juveniles are carnivores, feeding on zooplankton in the water column (Lassuy 1983). Older juveniles and adults are opportunistic bottom feeding carnivores that prey on polychaetes, molluscs, crustaceans, and fish. Juveniles feed by forcefully diving into the substrate, digging as they feed. Adults feed similarly to juveniles, but are capable of taking larger invertebrates and some fishes. Atlantic croaker can, therefore, feed on a secondary or higher trophic level. Feeding is by sight, olfaction, and touch (Mercer 1989).

Food Items: Young of the year fish are reported to consume polychaete worms, copepods, and mysids, while older fish principally feed on crustaceans (stomatopods, shrimps and crabs), molluscs (gastropods and bivalves), and fish (Levine 1980, Darovec 1983, Sheridan et al. 1984, Mercer 1989). Early juveniles (15-30 mm) feed on zooplankton, switching to benthic mode as they become older and begin consuming infaunal and epifaunal organisms sorted from bottom debris (Mercer 1989). Food items include molluscs (common rangia, *Macoma mitchilli*, *Congeria leucophaeta*, *Probythinella protera*, *Texadina sphinctosoma*), isopods, amphipods, insects, fish (mostly bay anchovy), and detritus (Levine 1980).

**Biological Interactions**

Predation: Predators of Atlantic croaker are larger piscivorous species such as striped bass, southern flounder, bull shark, blue catfish, yellow bass, spotted seatrout, Atlantic croaker, red drum, sheepshead, bluefish, and weakfish (Levine 1980, Mercer 1989).

Factors Influencing Populations: White and Chittenden (1976) show some habitat segregation by life stage, with smaller (<200 mm TL), younger individuals (age 0) occupying the bays and muddy bottoms, while the larger (>200 mm TL), older individuals (age I+) are more localized around oyster reefs. Hoese et al. (1968) noted that faster growing individuals tend to leave Texas bays before the slower growing individuals, resulting in a bay population of smaller than average sized fish. Warren and Sutter (1983) noted that abundance in Mississippi Sound drops dramatically in July and that these drops may be due to shrimping which begins in June. Shrimping activities may be having an effect on the population of this species. Atlantic croaker comprise an estimated 50% of the fish discarded as bycatch and destroyed during the brown shrimp season, and 18% of those during the white shrimp season (Rogers 1979). The average bycatch from 1972 to 1989 was estimated as 7.5 billion croaker (NOAA 1993). This species is considered overexploited in the southeastern U.S.

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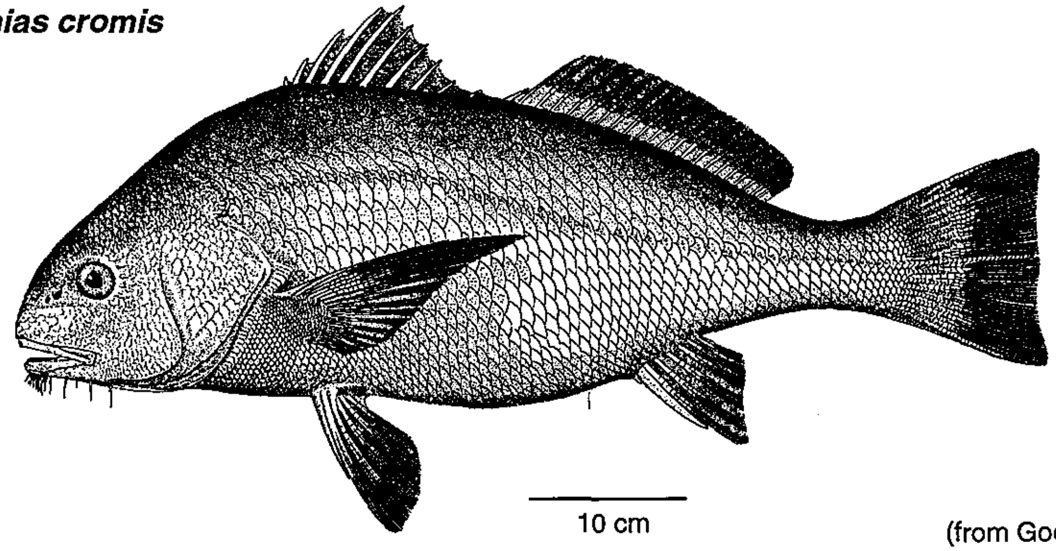
## Black drum

***Pogonias cromis***
**Adult**




(from Goode 1884)

**Common Name:** black drum
**Scientific Name:** *Pogonias cromis*
**Other Common Names:** sea drum, gray drum, oyster cracker, drum fish, striped drum, puppy drum, butterfly drum (Sutter et al. 1986); *grand tambour* (French), *tambor, corvinon negro* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Perciformes
Family: Sciaenidae

### Value

Commercial: Black drum are commercially harvested primarily in inshore state territorial waters, using a wide variety of gear and vessels between states and regions (NOAA 1985, Sutter et al. 1986, Geaghan and Garson 1993, Leard et al. 1993). Fishing effort occurs throughout the year, but is especially high during the spring and summer. Gear used includes trammel nets, gill nets, purse seines, haul seines, trot lines, hand lines, and trawls (trawled fish are usually bycatch). The majority of commercial catch in the U.S. occurs in the Gulf of Mexico. In estuarine waters, most of the fish caught are relatively young (< 4 yrs.), while older fish (>4 yrs.) are harvested mainly in nearshore waters of the Gulf. Landings in the states along the Gulf from 1950 to 1976 comprised 84% of the total harvest in the U.S., with Texas providing as much as 71% of this total (Silverman 1979, Leard et al. 1993). Black drum in the Gulf were relatively underutilized prior to the late 1970's because their flesh was considered to be poor quality, particularly in the larger fish (bull drum). In addition, a marine cestode (the pleurocercoid stage), commonly called the "spaghetti worm" infects the flesh in larger fish making it less marketable, although it poses no human health threat (Simmons and Breuer 1962). Smaller fish (0.5-1.5 kg) called "butterfly drum" were therefore considered to be more valuable in the fishery. It sold mostly as fresh product in local fish markets (Fischer 1978). The increased market for large red drum for the Cajun dish "blackened redfish" in the late 1970's and early 1980's led to expansion of the black drum fishery (Leard et al. 1993, Geaghan and Garson 1993). Overfishing caused restrictions or bans on the red drum commercial fishery in the Gulf coast states and in federal waters (1986), but the high market demand made black drum a suitable substitute, resulting in greater fishing effort for this species. Commercial landings for the Gulf of Mexico reached a peak of 4,800 mt in 1987, and were 964 mt in 1991 (Fitzhugh et al. 1993, Leard et al. 1993).

Recreational: The recreational fishery is very seasonal with most effort occurring during the spring and summer (Hostettler 1982, NOAA 1985). The recreational catch for black drum was much greater than the commercial landing until the previously mentioned expansion of the commercial fishery (Sutter et al. 1986). However, this is not a preferred recreational species, and therefore, receives little directed effort by anglers (Leard et al. 1993). Texas probably has the largest directed recreational fishery for this species in the U.S. Gulf of Mexico, although its popularity is still low when compared to other species. An estimated 583,000 black drum were caught in 1991 for the central and eastern Gulf of Mexico region by recreational fisherman, making up over 64% of the reported catch for the combined Atlantic and Gulf regions (Van Voorhees et al. 1992). Over 93 percent of this was from Louisiana and Florida. Fishing gear, methods, and seasons vary

Table 5.38. Relative abundance of black drum in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ○ | √ | √ | ○ | √ |
| Ten Thousand Islands | ○ | √ | √ | ○ | √ |
| Caloosahatchee River | ○ | | ○ | ○ | |
| Charlotte Harbor | ○ | | ○ | ○ | |
| Tampa Bay | ○ | ○ | ○ | ○ | √ |
| Suwannee River | ○ | | ○ | ○ | |
| Apalachee Bay | ○ | | ○ | ○ | |
| Apalachicola Bay | ○ | | ○ | ○ | |
| St. Andrew Bay | ○ | ○ | ○ | ○ | √ |
| Choctawhatchee Bay | ○ | | ○ | ○ | |
| Pensacola Bay | ○ | | ○ | ○ | |
| Perdido Bay | ○ | | ○ | ○ | |
| Mobile Bay | ○ | | ○ | ○ | |
| Mississippi Sound | ○ | ○ | ○ | ○ | ○ |
| Lake Borgne | ○ | | ○ | √ | |
| Lake Pontchartrain | ○ | | ○ | | |
| Breton/Chandeleur Sounds | ◉ | | ◉ | | |
| Mississippi River | ○ | | ○ | | |
| Barataria Bay | ◉ | | ○ | | |
| Terrebonne/Timbalier Bays | ◉ | ○ | ○ | ○ | ○ |
| Atchafalaya/Vermilion Bays | ○ | | ○ | | |
| Calcasieu Lake | ○ | | ○ | | |
| Sabine Lake | √ | | ○ | | |
| Galveston Bay | ○ | ○ | ○ | ○ | ○ |
| Brazos River | ○ | | ○ | | |
| Matagorda Bay | ○ | ○ | ○ | ○ | ○ |
| San Antonio Bay | ○ | | ○ | | |
| Aransas Bay | ○ | ○ | ○ | ○ | ○ |
| Corpus Christi Bay | ○ | ○ | ○ | ○ | ○ |
| Laguna Madre | ○ | ○ | ○ | ○ | ○ |
| Baffin Bay | ◉ | ◉ | ◉ | ◉ | ◉ |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

from state to state (Leard et al. 1993). In Texas, the most successful baits used by anglers are crabs (*Callinectes* sp.), shrimp (*Penaeus* sp.), and sea lice (*Squilla empusa*) (Hostettler 1982), but cut fish are also used (Simmons and Breurer 1962. Most catches are made with rod and reels equipped with bottom rigs. Angling regulations vary among the Gulf states (GSMFC 1993). Black drum have been experimentally hybridized with red drum to develop a potential hybrid gamefish (NMFS 1983).

Indicator of Environmental Stress: The black drum is not typically used in studies of environmental stress.

Ecological: This is a demersal species that feeds mainly on benthic organisms, primarily bivalve molluscs (Sutter et al. 1986). This species is known to consume large numbers of oysters on seed reefs and oyster "grow-out" leases in Louisiana and Mississippi (Benson 1982, Dugas 1986).

**Range**

Overall: The black drum ranges from Massachusetts to Argentina. It is common from Chesapeake Bay to Florida, and in the Gulf of Mexico. It occurs along the southern coasts of the Greater Antilles and all of the Lesser Antilles, but is rare, and the South American shelf from Guyana to Brazil. It is apparently absent in the southern Gulf, and mainland Central America (Hoese and Moore 1977, Fischer 1978, Shipp 1986, Sutter et al. 1986).

Within Study Area: The black drum is common in the northern portion of the Gulf of Mexico from Florida Bay, Florida to the Rio Grande, Texas. It is relatively abundant along the coasts of Louisiana, near the Mississippi River delta, and Texas (Table 5.38) (Benson 1982, Shipp 1986, Sutter et al. 1986, Nieland and Wilson 1993).

**Life Mode**

The black drum is an estuarine-dependent species (Benson 1982). Spawning occurs primarily in nearshore waters and estuarine passes (Ditty pers. comm.). Eggs are pelagic and buoyant (Joseph et al. 1964, Ditty and Shaw 1994). Larvae are pelagic, and are transported by tidal currents through passes to estuarine waters. Juveniles prefer shallow, nutrient rich, turbid waters, such as tidal creeks and channels, but they have also been found in fresh water habitats (Gunter 1942, Gunter 1956, Sutter 1986). Adults are demersal throughout the estuaries and bays of the northern Gulf (Simmons and Breuer 1962, Cornelius 1984). At maturity there is constant movement in search of food, and feeding fish will typically travel in large schools (Richards 1973, Bryant et al. 1989).

## Habitat

Type: Eggs are marine to estuarine. Larvae are marine, occurring over the inner continental shelf (Cowan 1985, Peters and McMichael 1990), to estuarine. Juveniles are marine to riverine. Adults are marine to estuarine occurring primarily in inshore neretic waters just outside the ocean littoral zone and in estuaries (Richards 1973). Juveniles and young adults prefer estuarine habitats, but older adults (>4 yrs.) move to nearshore Gulf waters (Sutter et al.1986, Leard et al. 1993).

Substrate: Black drum juveniles prefer unvegetated muddy bottoms in marsh habitats. Adults are found over unvegetated sand, mud and oyster/worm reefs (Pearson 1929, Mok and Gilmore 1983, Cornelius 1984, Peters and McMichael 1990). Adult black drum have been collected over heavily vegetated seagrass beds during summer fish kill events in Florida Bay (Schmidt 1993).

Physical/Chemical Characteristics:
Temperature - Eggs and Larvae: Eggs and larvae successfully develop at 18° to 20°C (Garza et al. 1978, Johnson 1978). Larvae have been collected at over a temperature range of 11° to 22°C (Cowan 1985, Peters and McMichael 1990).

Temperature - Juveniles and Adults: Adults and juveniles are eurythermal. They have been found in water temperatures ranging from 3° to 35°C (Wang and Raney 1971, McIlwain 1978). Sharp decreases in water temperature cause movements to deeper water, and mass mortalities result when conditions remain adverse for long periods of time (Cowan 1985).

Salinity - Eggs and Larvae: Laboratory spawned eggs hatched successfully at 8.8 to 34.0‰, with highest survival occurring at 23 to 34‰ (Garza et al. 1978). Larvae have been collected at 0 to 36‰ (Cowan 1985, Peters and McMichael 1990).

Salinity - Juveniles and Adults: Adults and juveniles are euryhaline (Gunter 1942, Gunter 1956). They are found from 0 to 80‰ and are common at 9 to 26‰ (Simmons and Breuer 1962, McIlwain 1978). In hypersaline waters at the upper end of this salinity range, fish can be blinded and have body lesions (Simmons and Breurer 1962). In Florida, juveniles 16 to 90 mm SL occur most often in low to moderate salinities while large juveniles are mainly found in moderate to high salinities (Peters and McMichael 1990).

## Migrations and Movements

Larvae and small young move into upper estuarine areas and tidal creeks to low salinity nursery areas during flood tides (Wang and Kernehan 1979). Juveniles move out of creeks and secondary bays at about 100 mm SL (Peters and McMichael 1990). As they reach 150-200 mm SL they move into the open waters of river mouths, bays, passes, and the nearshore Gulf. Mature individuals often remain in bays until nearly ripe before migrating to passes to spawn. After spawning, they quickly return to their preferred bay habitat (Simmons and Breuer 1962). In fish less than 4 years old, there is little interbay and bay-Gulf movement throughout the year (Osburn and Matlock 1984). There is little intra-bay movement except for the spawning migration, and during adverse conditions such as temperature extremes and/or insufficient food. Black drum move constantly in their search for food, and these movements within a bay system can be considerable if food is not abundant (Simmons and Breuer 1962, Osburn and Matlock 1984, Bryant et al. 1989).

## Reproduction

Mode: This species has separate male and female sexes (gonochoristic). Mature adults are known to form spawning aggregations. Fertilization is external, by broadcast of milt and roe into the water column. Development is oviparous.

Spawning: Black drum exhibit group-synchronous maturation of oocytes and multiple, or batch spawning (Peters and McMichael 1990, Nieland and Wilson 1993). Mature fish spawn near passes, in open bays and channels, and nearshore waters of the northern Gulf of Mexico (Simmons and Breuer 1962, Mok and Gilmore 1983, Peters and McMichael 1990, Fitzhugh et al. 1993, Ditty pers. comm.). Depth of spawning appears to be around 20 to 27 m (Ross et al. 1983, Cody et al. 1985). Ripe individuals are usually present from November until May. Peak spawning occurs from January to mid-April with a secondary peak sometimes reported in Texas during early fall (Pearson 1929, Simmons and Breuer 1962, Allshouse 1983, Cornelius 1984, Murphy and Taylor 1989, Peters and McMichael 1990, Nieland and Wilson 1993). Saucier and Baltz (1993) reported that black drum form "drumming" aggregations in estuarine waters of Louisiana from January to April, at salinities from 10 to 27‰, and temperatures from 15 to 24°C, from 6pm to 10pm, and that spawning sites were primarily located in deep, moving water in passes between barrier islands. Based on the presence of larval black drum in the northern Gulf of Mexico, it can be inferred that spawning occurs December through May, with a peak from February through April (Ditty et al. 1988). Spawning peaks occur during the period of rising water temperatures in the spring (Peters and McMichael 1990). Tides may also influence the amount of spawning activity or successful recruitment. Laboratory spawning has been achieved at 21°C and 28-31‰ (Garza et al. 1977).

Fecundity: In one study, average fecundity of 451 females was 1,090,000 eggs (Cornelius 1984). In Louisiana, the estimated mean annual egg production during three breeding seasons ranged from 31.05 to 41.69 million eggs (Nieland and Wilson 1993). Estimated annual egg production by a 6.1 kg female could be as high as 32 million eggs (Fitzhugh et al. 1993), and the maximum observed was 67.33 million in an 11.51 kg female (age 19, 855 mm FL) (Nieland and Wilson 1993). Spawning may occur as often as every 3 or 4 days during the breeding season, with an average clutch size of 1.6 million eggs over 20 spawns (Fitzhugh et al. 1993, Nieland and Wilson 1993). Batch fecundity increases with age and size, and no evidence of spawning senescence has been observed.

**Growth and Development**

Egg Size and Embryonic Development: Reported egg sizes are from 0.8 to 1.1 mm in diameter, with a mean of 0.9 mm (Ditty and Shaw 1994). Eggs have been reported to hatch in 24 hours at 20°C (Joseph et al. 1964, Johnson 1978, Wang and Kernehan 1979).

Age and Size of Larvae: Larvae are 1.9 to 2.4 mm TL at hatching (Joseph et al. 1964, Johnson 1978) and are as large as 9.2 mm SL before becoming juveniles (Peters and McMichael 1990). Larval growth rates range from 0.2 mm/day to 0.9 mm/day.

Juvenile Size Range: Transformation to the juvenile stage occurs at a total length of approximately 12 mm (Ditty and Shaw 1994). By 15 mm TL, juveniles attain a general adult body shape (Johnson 1978). Juveniles growing from 35 to 150 mm SL average 0.9 mm/day, and reach 140-180 mm standard length (SL) at the end of the first year; 210-250 mm SL at 1.5 years; and 290-330 mm SL in two years (Simmons and Breuer 1962, Peters and McMichael 1990). Ages and sizes at maturity are similar for most U.S. locations with the exception of Texas (Leard et al. 1993). In Texas, studies indicate females reach maturity at 275-320 mm total length (TL) when at the end of their second year (Pearson 1929, Simmons and Breuer 1962). Florida studies found males mature at sizes beginning at 450-499 mm TL at age 4 or 5 years (Murphy and Taylor 1989). Florida females mature when older and slightly longer during their fifth or sixth year and between 650-699 mm TL (Murphy and Taylor 1989). In Louisiana, males and females are first mature at 600-640 mm FL and most are age 5 or older (Fitzhugh et al. 1993, Nieland and Wilson 1993). All males and females studied whose lengths were greater than 640 mm FL and 690 mm respectively were mature. The minimum lengths for mature males and females were 552 mm FL (age 3) and 628 mm FL (age 5), respectively.

Age and Size of Adults: In Texas waters, Simmons and Breuer (1962) reported adults growing to 400-430 mm SL by the end of the third year; beyond that tag returns indicate a growth of 25 to 50 mm/year (Simmons and Breuer 1962, Matlock 1990). There is a sharp decrease in growth rate at 4-5 years that may reflect a reallocation of energy from growth to reproduction, because black drum mature at approximately this age (Beckman et al. 1990). This is a relatively long-lived species. Based on size, some individuals may live as long as 35 years (Benson 1982), while otolith studies indicate some individuals may live up to 43 years in Louisiana (Beckman et al. 1990) and 58 years in Florida (Murphy and Taylor 1989). Black drum are the largest sciaenids in the southeastern United States (Peters and McMichael 1990), and they grow to be the largest members of the family Sciaenidae (Fitzhugh et al. 1993). The average maximum total length typically reached in Texas appears to be approximately 1000 to 1200 mm (Matlock 1990). The largest recorded adult weighed 66.3 kg (Cave 1974). The average maximum TL for black drum in the Gulf of Mexico appears to be smaller than that occurring in the colder waters north of Cape Hatteras. This may be due to zoogeographic variation in black drum population dynamics (Beckman et al. 1990, Matlock 1990). Beckman et al. (1990) have developed Von Bertalanffy growth equations for this species.

**Foods and Feeding**

Trophic Mode: All free swimming life stages are carnivorous. Larvae feed on zooplankton in the water column, while juveniles and adults are benthic feeders. In shallow depths, their tails will stick out of the water at times (flagging) while they feed in a vertical position (Pearson 1929, Leard et al. 1993). Bottom feeding is aided by the presence of a sensitive chin barbel for finding food, and powerful pharyngeal teeth for crushing molluscs and crabs (Simmons and Breuer 1962).

Food Items: The major food organism groups in order of importance are molluscs (mostly bivalves), arthropods (mostly decapod crustaceans), annelids, and fish (Dugas 1986, Leard et al. 1993). Some sand and plant material have also been found that were probably ingested incidentally while feeding. Larvae feed on zooplankton with copepods being the primary prey item found in stomachs (Peters and McMichael 1990). The numeric and volumetric importance of copepods declines with increasing fish size. They are rarely found in 30-60 mm black drum and are not evident in any fish >60 mm SL. Juveniles and adults feed on benthic organisms. Small juveniles eat soft foods such as small fish, polychaetes, bivalve siphon tops, and crustaceans (Pearson 1929, Simmons and Breuer 1962, Martin 1979, Peters and McMichael 1990). In larger juveniles, bivalve and gastropod molluscs are the predominant food items (Peters and McMichael 1990). The consumption of soft food decreases as size increases, shifting to the main adult diet of molluscs and crabs (Dugas 1986, Peters and McMichael 1990). This change in feeding habits occurs as the pharyngeal teeth become developed and the black drum can start consuming hard-bodied prey (Peters and McMichael 1990). Large juveniles (>200 mm SL) with well-developed pharyngeal teeth have diets similar to adults. Martin (1979) reported that black drum >300 mm TL favored bivalve molluscs, with *Mulinia lateralis* most frequently encountered. Dugas (1986) found black drum >700 mm SL prey on oysters approximately 75 mm in length. Another study observed that drum <900 mm TL consumed oysters 25-75 mm in length while drum >900 mm TL consumed oysters 25-115 in length (Cave 1978). Other prey items include: common rangia, hard clam, *Ensis minor,* tellin clams, xanthid crabs, insects, mysids, amphipods, barnacles, isopods, penaeid shrimp, mud shrimp, hermit crabs, blue crab, polychaetes, bay anchovy, Atlantic spadefish, gobies, and Atlantic croaker (Cave 1978, Benson 1982, Dugas 1986, Peters and McMichael 1990).

**Biological Interactions**

Predation: Little information is available that describes specific predators of black drum; however, it is likely that larvae and juveniles are utilized as a food source by larger predator species during their life cycle (Leard et al. 1993). Potential predators include various drums (Sciaenidae), jacks (Carangidae), and mackerels (Scombridae) as well as sharks. Filter feeding fish such as anchovies are potential predators of black drum eggs and larvae.

Factors Influencing Populations: Rapid and extreme fluctuations in temperature may cause mortalities; however, the most limiting habitat requirements appear to be amount of estuarine habitat and the accompanying availability of food (Leard et al. 1993). Interaction with other species have not been well studied (Sutter et al. 1986). Some competition may exist with red drum and other bottom feeders for benthic resources. Fishing pressure on the black drum has increased since the mid-1980s in the northern Gulf of Mexico, with the reductions of harvest of the red drum (Beckman et al. 1990). The long life span of this species implies an extremely low natural mortality rate which probably means little surplus production is available for commercial fishery yield (Murphy and Taylor 1989). This would tend to make this species a poor candidate for an intensive or even moderate fishery. The normal feeding habits of this species may have a detrimental effect on the spawning and nursery grounds of spotted seatrout, red drum, and juvenile penaeid shrimp by the destruction of seagrass beds (Cave 1978).

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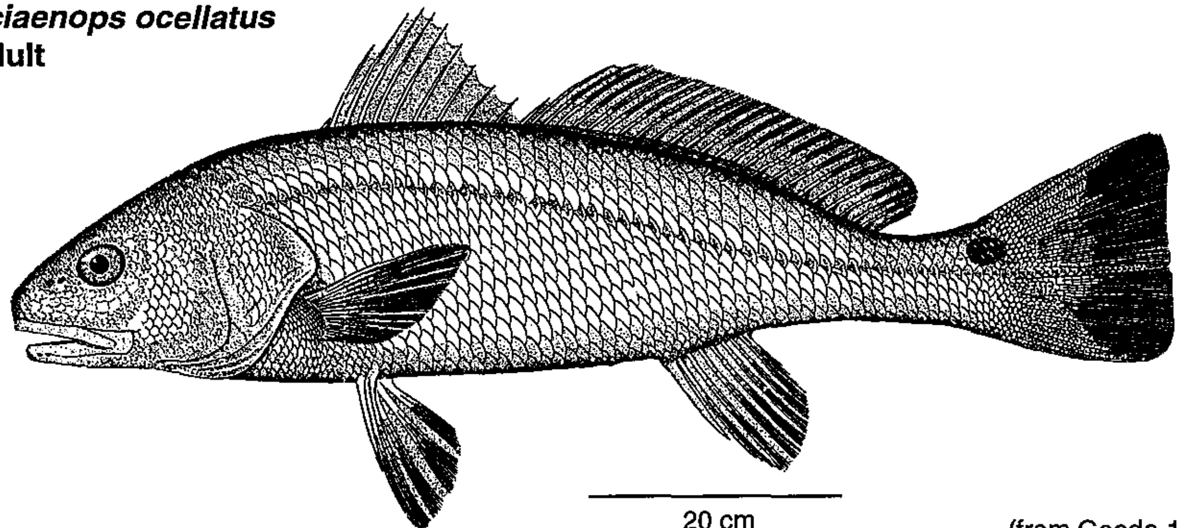
# Red drum

***Sciaenops ocellatus***
**Adult**




(from Goode 1884)

**Common Name**: red drum
**Scientific Name**: *Sciaenops ocellatus*
**Other Common Names**: red fish, red bass, channel bass, drum, branded drum, school drum, spotted bass, spottail (Welsh and Breder 1924, Pearson 1928, Yokel 1966, Bryan 1971, Hoese and Moore 1977, Overstreet and Heard 1978, Benson 1982, Daniels and Robinson 1986, WRGF 1991); *tambour rouge* (French), *corvinon ocelado* (Spanish), *corvina* (Spanish) (Fischer 1978, NOAA 1985). Smaller fish (<2.27 kg) are called rat reds or puppy drum while larger fish (>2.27 kg) are referred to as bull reds (Welsh and Breder 1924, Breuer 1957, Yokel 1966, Christmas and Waller 1973).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Perciformes
Family: Sciaenidae

**Value**
Commercial: The red drum is highly prized as a food fish throughout its range and was probably the most important sciaenid commercially before harvest was virtually banned. Although some commercial fishery exists on the Atlantic coast, the main industry existed along the northern Gulf of Mexico in Texas, Louisiana, and Florida (Boothby and Avault 1971, Bass and Avault 1975, Hoese and Moore 1977, Matlock et al. 1977, Perret et al. 1980, Benson 1982, Vetter et al. 1983). Commercially harvested fish are mainly captured by netting using both gill and trammel nets, and also by trotlines (Matlock et al. 1977, Adkins et al. 1979, Heffernan and Kemp 1980, Matlock 1980). Fish in the Gulf of Mexico are also caught by hand lines, beach seines in the surf, and shrimp trawls in the intertidal zone. Harvest occurs mainly during fall (October through December) and spring (March through June), and usually in estuaries (Matlock 1980). Landings declined for Gulf coast states during the 1970's and 1980's probably due to over-fishing and habitat destruction (Heffernan and Kemp 1982, Swingle et al. 1984). These reported declines resulted in closure of the Texas commercial fishery in 1981, closure of the Alabama commercial fisheries, and restriction of the harvest in Louisiana, Mississippi, and Florida. Commercial landings for 1985 were: Alabama 1,292 mt; Mississippi 12 mt; and Louisiana 1,334 mt (NMFS 1986). A fishery management plan developed under emergency rule by the National Marine Fisheries Service (NMFS) was implemented for federal waters in 1986 (Swingle pers. comm., NMFS 1986, Shipp 1986). Regulation was needed due to uncontrolled harvest by the purse seine industry off the Louisiana coast that was supplying red drum to the market for the popular Cajun dish "blackened redfish." Harvest was prohibited in federal waters off of Texas and Florida, and in 1990, this ban was extended to include the entire Gulf of Mexico (GMFMC 1996a). Surveys indicate that spawning stocks in these waters should be restored in the future, depending on the effectiveness of escapement measures enacted to protect age classes I through IV.

Recreational: Anglers revere this species as both a game and food fish. Its fighting ability on light tackle and delectable flavor has probably made this fish the most important recreational species of sciaenid in the Gulf of Mexico. It is especially esteemed for the table in the south, but in the northern part of its range its principal interest to sportsmen is as a game fish for surf fishing (Welsh and Breder 1924, Arnold et al. 1960, Boothby and Avault 1971, Bass and Avault 1975,

Table 5.39. Relative abundance of red drum in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | *Life stage* A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | √ | | ○ | √ | |
| Ten Thousand Islands | √ | | √ | √ | |
| Caloosahatchee River | √ | | ◉ | ○ | |
| Charlotte Harbor | ○ | √ | ◉ | ○ | √ |
| Tampa Bay | ○ | √ | ● | ◉ | √ |
| Suwannee River | ○ | √ | ○ | ○ | √ |
| Apalachee Bay | ○ | √ | ○ | ○ | √ |
| Apalachicola Bay | ○ | √ | ○ | ○ | √ |
| St. Andrew Bay | ◉ | | ○ | ○ | √ |
| Choctawhatchee Bay | ○ | √ | ○ | ○ | √ |
| Pensacola Bay | ○ | | ○ | ○ | √ |
| Perdido Bay | √ | √ | ○ | √ | √ |
| Mobile Bay | ○ | | ○ | ○ | √ |
| Mississippi Sound | ○ | ○ | ○ | ○ | ○ |
| Lake Borgne | ○ | | ◉ | | |
| Lake Pontchartrain | | | ○ | | |
| Breton/Chandeleur Sounds | ◉ | | ◉ | | |
| Mississippi River | | | ○ | | |
| Barataria Bay | ○ | √ | ○ | ○ | √ |
| Terrebonne/Timbalier Bays | √ | | ○ | | |
| Atchafalaya/Vermilion Bays | √ | | ○ | | |
| Calcasieu Lake | | | ◉ | | |
| Sabine Lake | √ | | ○ | | |
| Galveston Bay | ○ | | ○ | ○ | |
| Brazos River | na | | ○ | | |
| Matagorda Bay | ○ | ○ | ○ | ○ | ○ |
| San Antonio Bay | √ | | ○ | | |
| Aransas Bay | √ | | ○ | | |
| Corpus Christi Bay | √ | | ○ | | |
| Laguna Madre | √ | | ○ | | |
| Baffin Bay | √ | | ○ | | |
| | A | S | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present
- na No data available

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

Hoese and Moore 1977, Adkins et al. 1979, Matlock 1980, Perret et al. 1980, Overstreet 1983). All of these characteristics make this species one of the seven most sought gamefish in the Gulf of Mexico (Van Voorhees et al. 1992). Fishery information for the Gulf of Mexico during 1991 showed a total recreational catch of over 5,549,000 fish weighing a total of 729.4 mt, with the majority caught in nearshore or inshore waters (Van Voorhees et al. 1992). The most sought after fish are those less than 2.2 kg. Larger fish are unpopular due to presence of parasites in the flesh and the belief that they have a poor flavor (Boothby and Avault 1971, Adkins et al. 1979, Benson 1982). The primary angling method is by hook and line in surf, island passes, and estuaries especially during seasonal runs in the spring and fall (Franks 1970, Boothby and Avault 1971, Matlock 1980, Benson 1982). Other fishing methods include drift fishing, jigging, casting, or slow trolling (WRGF 1991). Angling regulations vary among the Gulf states (GSMFC 1993). Increased recreational harvest in federal waters of the U.S. Exclusive Economic Zone (EEZ) has made careful management necessary throughout the range of red drum. As a result, no sport harvest is now allowed in federal waters of the Gulf of Mexico, and any red drum caught must be released unharmed (GMFMC 1996b). Red drum have been experimentally hybridized with black drum to develop a potential hybrid gamefish (NMFS 1983).

Indicator of Environmental Stress: This species is not typically used as an indicator organism, but a case of metal poisoning has been reported among large (7-18 kg) red drum in Florida (Cardeilhac et al. 1981).

Ecological: This is a marine, littoral, crepuscular predator that indiscriminately feeds either on the bottom or in the water column usually in shallow water (Pearson 1928, Gunter 1945, Simmons and Breuer 1962, Zimmerman 1969, Boothby and Avault 1971, Ward and Armstrong 1980, Benson 1982, Holt et al. 1983).

## Range

Overall: The red drum occurs in the western Atlantic from the Gulf of Maine off Massachusetts to Key West, Florida, and in the Gulf of Mexico from Florida to Tuxpan, Mexico (Welsh and Breder 1924, Simmons and Breuer 1962, Yokel 1966, Lux 1969, Boothby and Avault 1971, Hoese and Moore 1977, Lee et al. 1980, Matlock 1980, Ward and Armstrong 1980, Holt et al. 1983, Overstreet 1983, Matlock 1987). Since 1950, populations of red drum have virtually disappeared in waters north of Chesapeake Bay, and New Jersey is now probably the northern limit of this species. Centers of abundance exist in the waters of North Carolina, and the Gulf of Mexico (Yokel 1966, Matlock 1980, Ward and Armstrong 1980).

Within Study Area: Within U.S. Gulf of Mexico estuaries, the red drum occurs from the Rio Grande, Texas, to Florida Bay, Florida (Table 5.39) (Welsh and Breder 1924, Simmons and Breuer 1962, Yokel 1966, Boothby and Avault 1971, Hoese and Moore 1977, Matlock 1980, Ward and Armstrong 1980, Holt et al. 1983, Overstreet 1983, NOAA 1985, Matlock 1987). The species is most abundant in waters of Texas and Louisiana (Ward and Armstrong 1980). It is also abundant in Mississippi, but this may be due to the benefits of the extensive estuaries present in nearby Louisiana (Yokel 1966).

**Life Mode**

Red drum are estuarine-dependent. Eggs, larvae, and early juveniles are planktonic and pelagic (Breuer 1957, Ward and Armstrong 1980, Peters and McMichael 1987). Juveniles and adults are pelagic and nektonic (Gunter 1945, Breuer 1957, Ward and Armstrong 1980, Holt et al. 1981a, Osburn et al. 1982, Benson 1982, Peters and McMichael 1987). Juveniles are often found in schools, but adults are largely solitary when living in shallow water (Pearson 1928, Breuer 1957, Simmons and Breuer 1962, Christmas and Waller 1973, Adkins et al. 1979, Benson 1982, Osburn et al. 1982, Overstreet 1983, Peters and McMichael 1987). Some schools in the Gulf of Mexico are associated with schools of black drum, tarpon, blue runner, little tunny (*Euthynnus alletteratus*), and Florida pompano, at least when near shore, although the red drum does not randomly mix with schools of other species. Large schools can contain 150,000 to 200,000 individuals and first appear about April and disappear offshore from September to October. Schools are often more dispersed during summer than in spring or autumn (Perret et al. 1980, Overstreet 1983). Activity seems to be equally divided between night and day (Zimmerman 1969, Benson 1982, Minello and Zimmerman 1983, Peters and McMichael 1987).

**Habitat**

Type:

Eggs: Eggs are spawned in nearshore and inshore waters close to barrier island passes and channels. After hatching, larvae and post-larvae are carried by tidal currents into the shallow inside waters of bays and estuaries (Pearson 1928, Yokel 1966, Heffernan 1973, Holt et al. 1981a, Benson 1982, Peters and McMichael 1987, Johnson and Funicelli 1991). Eggs from hatchery spawns develop best in polyhaline to euhaline waters (Arnold et al. 1979, Holt et al. 1983).

Larvae: Larvae move through the passes and tend to seek shallow, slack water along the sides of the channels to avoid being carried offshore during periods of ebb tide (King 1971). As larvae enter estuarine waters, they seek grassy quiet coves, tidal flats, and lagoons where the vegetation protects them from predators and currents, and where they can avoid rough waters until they are strong enough to swim actively (Pearson 1928, Simmons and Breuer 1962, Yokel 1966, Perret et al. 1980, Ward and Armstrong 1980, Holt et al. 1983, Overstreet 1983). Early larvae are found in mesohaline to euhaline waters, and older larvae and post larvae are euryhaline (Yokel 1966, Perret et al. 1980, Ward and Armstrong 1980, Crocker et al. 1981, Holt et al. 1981a, Overstreet 1983, Vetter et al. 1983, Peters and McMichael 1987).

Juveniles: Juveniles are euryhaline (Gunter 1942, Gunter 1956, Simmons 1957, Simmons and Breuer 1962, Yokel 1966, Perret et al. 1980, Crocker et al. 1981, Holt et al. 1981a, Benson 1982, Crocker et al. 1983, Daniels and Robinson 1986, Peters and McMichael 1987). They are found in a wide variety of habitats perhaps due to their movements from bay shores to quiet backwater areas as they grow and begin to disperse through the bay (Peters and McMichael 1987). They prefer shallow, protected, open waters of estuaries, coves, and secondary bays with depths up to 3.05 m, but may also be found near the mouths of tidal passes. Juveniles have also been reported from shallow shorelines, tidal pools, marsh habitats, depressions in marshy areas, boat basins, bayous, flats, channels, reefs, back bays, around islands, in rivers and near their mouths, and occasionally the surf along the Gulf of Mexico in the spring following hatching. Older juveniles tend to move into slightly deeper, more open waters and into primary bays (Pearson 1928, Reid 1955, Simmons 1957, Breuer 1957, Simmons and Breuer 1962, Yokel 1966, Zimmerman 1969, Swingle 1971, Christmas and Waller 1973, Perret et al. 1980, Ward and Armstrong 1980, Crocker et al. 1981, Holt et al. 1981a, Pafford 1981, Benson 1982, Osburn et al. 1982, Overstreet 1983, Peterson 1986, Loftus and Kushlan 1987, Peters and McMichael 1987, Van Hoose 1987).

Adults: Adults are also euryhaline (Gunter 1942, Gunter 1956, Simmons and Breuer 1962, Holt et al. 1981a, Crocker et al. 1981, Benson 1982, Daniels and Robinson 1986). They are occasionally found in shallow bays, but tend to spend more time in marine habitats after their first spawning. They are typically found in the Gulf of Mexico in littoral and shallow nearshore waters off beaches (Perret et al. 1980, Ward and Armstrong 1980, Pafford 1981, Benson 1982, Overstreet 1983, Ross et al. 1983). Adults are often caught in more offshore waters as far as 25 km from shore in depths up to 40 m, and are commonly reported from depths of 40 to 70 m. They are occasionally caught on Gulf reefs (Lux 1969, Heffernan 1973, Benson 1982, Overstreet 1983, Ross et al. 1983).

Substrate: Newly hatched larvae are found in the Gulf surf over pure sand bottoms. After entering bays and estuaries, they occur over substrates of mud, sand, or sandy mud bottoms as well as in and among patchy sea grass meadows, but prefer muddy bottoms. Small juveniles seem to prefer medium soft mud to firm sandy substrates (Peterson 1986). Small fish are probably more successful at capturing prey in the less dense vegetation areas, while living in areas of greater sea grass density probably helps them to avoid predation (Pearson 1928, Simmons and Breuer 1962, Yokel 1966, Perret et al. 1980, Ward and Armstrong 1980, Benson 1982, Holt et al. 1983, Overstreet 1983). They are normally associated with such sea grasses as *Halodule beaudettes, Ruppia maritima*, and *Thalassia testudinum* (Zimmerman 1969, Perret et al. 1980). Large juveniles and adults are common over muddy, sandy, or oyster reef bottoms with little or no sea grass (Yokel 1966, Lee et al. 1980, Perret et al. 1980).

Physical/Chemical Characteristics:
Temperature: Tolerance of environmental conditions changes with age, life history stage, season, and geography (Crocker et al. 1981). No major difference between thermal tolerances appears to exist between populations of red drum from the Gulf of Mexico and mid-Atlantic coast (Ward et al. 1993).

Temperature - Eggs and Larvae: Eggs and newly hatched larvae tend to be stenothermal while 10 day and older larvae are more eurythermal (Crocker et al. 1981). Eggs and larvae from captive spawns have developed over a temperature range of 20° to 30°C with optimal survival at 25°C. Higher temperatures (30 and 35°C) are associated with poor survival of yolk sac larvae (Holt et al. 1981a, Overstreet 1983, Lee et al. 1984). Larvae and post-larvae have been collected in the wild from 18.3° to 31.0°C (Yokel 1966, Perret et al. 1980, Peters and McMichael 1987, Van Hoose 1987).

Temperature - Juveniles: Juveniles are eurythermal, and are found in waters ranging in temperature from 2.0° to 34.9°C (Gunter 1945, Simmons and Breuer 1962, Yokel 1966, Franks 1970, Perret et al. 1971, Wang and Raney 1971, Christmas and Waller 1973, Pineda 1975, Tarver and Savoie 1976, Bonin 1977, Barret et al. 1978, Adkins et al. 1979, Perret et al. 1980, Holt et al. 1981a, Daniels and Robinson 1986, Peters and McMichael 1987). They appear to prefer temperatures ranging from 10° to 30° (Ward and Armstrong 1980). Juveniles in heated discharge waters have survived up to 35°C, but at 39°C some died, apparently from handling stress (Overstreet 1983). Large numbers have been killed in sudden severe cold spells, but normally fish will move into deeper waters during periods of extreme temperatures (Simmons and Breuer 1962, Adkins et al. 1979). In a laboratory study, fish ceased feeding between 7° to 9°C and death generally occurred when temperatures fell to 4°C or lower for several days (Miranda and Sonski 1985).

Temperature - Adults: Adults are also eurythermal, and have been collected over a temperature range from 2.0° to 33°C (Simmons and Breuer 1962, Yokel 1966, Juneau 1975, Perret et al. 1980, Ward and Armstrong 1980, Daniels and Robinson 1986). Adults are considered more susceptible to the effects of winter cold waves than smaller fish (Yokel 1966), and they normally move into deeper waters for refuge (Simmons and Breuer 1962).

Salinity: All life stages are sensitive to high salinities when combined with high temperatures, but susceptibility is influenced by the size of the fish (Simmons 1957).

Salinity - Eggs and Larvae: Eggs and larvae in particular are sensitive to environmental conditions (Overstreet 1983). Eggs from hatchery spawns develop successfully into feeding larvae at salinities of 10 to 40‰ in a temperature of 25°C. Below 10‰ the hatch rate is poor, and below 25‰ eggs sink resulting in losses from fungal infection, crowding, and low oxygen (Vetter et al. 1983). High salinities coupled with high temperatures were associated with poor yolk sac larvae survival (Holt et al. 1981a). The best salinities reported for 24 hour survival and hatch are 30‰ at 25°C and 34 to 36.5‰ at 23° to 26°C (Neff et al. 1982, Overstreet 1983, Lee et al. 1984). Eggs have been collected in the field from 21°C to 23°C in a salinity range of 29 to 32‰ (Johnson and Funicelli 1991). Larvae from hatchery spawns were more stenohaline than older life stages, particularly during the first two weeks after hatching with best survival at about 30‰ (Crocker et al. 1981, Holt et al. 1981a, Overstreet 1983). One article reports tolerance from <1 to 50‰ and a preference of 20 to 40‰ salinity (Ward and Armstrong 1980). Larvae and post-larvae collected in the wild were found over a salinity range of 8 to 36.4‰ (Yokel 1966, Peters and McMichael 1987, Van Hoose 1987). One study reports spawning occurring during a salinity range of 14.7 to 18.5‰ (Hein and Shepard 1986a).

Salinity - Juveniles and Adults: Both juveniles and adults are euryhaline (Gunter 1942, Gunter 1956, Simmons and Breuer 1962, Yokel 1966, Perret et al. 1980, Crocker et al. 1981, Holt et al. 1981a, Benson 1982, Daniels and Robinson 1986). They are very efficient osmoregulators with the ability to tolerate abrupt changes in salinity which is especially important to juveniles in the estuarine environment. Juveniles appear more tolerant to low salinity, whereas adults which are less dependent on estuarine areas and spend more time at sea are more tolerant of high salinity (Yokel 1966, Crocker et al. 1983). Both groups have been collected from salinities ranging from 0 to 45‰, but only rarely at 50‰ or above (Gunter 1945, Simmons 1957, Simmons and Breuer 1962, Yokel 1966, Franks 1970, Perret et al. 1971, Christmas and Waller 1973, Juneau 1975, Tarver and Savoie 1976, Bonin 1977, Swift et al. 1977, Barret et al. 1978, Ward and Armstrong 1980, Perret et al. 1980, Crocker et al. 1981, Holt et al. 1981a, Daniels and Robinson 1986, Loftus and Kushlan 1987, Peters and McMichael 1987). Juveniles and adults appear to prefer salinities from 20 to 40‰ with maximum growth for juveniles occurring at 35‰ (Bonin 1977, Perret et al. 1980, Ward and Armstrong 1980, Crocker et al. 1981, Holt et al. 1981a, Benson 1982, Peterson 1986). One report found the greatest abundance of small juveniles (17-58 mm total length (TL)) in salinities below 15‰ (Gunter 1945). Captive juveniles survived best at salinities of 1.3‰ or greater (Miranda and Sonski 1985).

Dissolved Oxygen: Fry can not survive low dissolved oxygen (DO) concentrations of 0.6 to 1.8 parts per million (ppm) (Overstreet 1983). Large juveniles have been reported in waters with oxygen concentrations of 5.2 and 8.4 ppm (Barret et al. 1978).

Other: The maximum ammonia ($NH_3$) concentration allowing normal growth of larvae is 0.11 mg/l, but older fish are able to tolerate higher concentrations (Holt and Arnold 1983).

Movements and Migrations: The red drum is relatively non-migratory with no major coastwise movements, but does have broad random movements, loosely coordinated temperature induced migrations, and strong offshore or deep water spawning migrations (Simmons and Breuer 1962, Moe 1972, Adkins et al. 1979, Perret et al. 1980, Ward and Armstrong 1980, Osburn et al. 1982). Larger fish (>750 mm) appear to move greater distances than smaller fish (Bryant et al. 1989). Tagging studies have shown little intra-bay movement or bay-Gulf travel except, perhaps, for short periods, and a few infrequent individuals with some extensive movement (Simmons and Breuer 1962, Beaumariage 1969, Pafford 1981, Osburn et al. 1982, Bryant et al. 1989). These studies also indicated that fish tagged in the Gulf of Mexico tended to stay there (Simmons and Hoese 1959, Simmons and Breuer 1962). Eggs, larvae, and early juveniles are carried by tides and currents in late fall into the shallow estuaries and bays with peaks occurring in October. Larvae tend to move through barrier island passes in mid-channel surface waters with the tidal current (King 1971, Bass and Avault 1975, Holt et al. 1981a, Benson 1982). Fish move from bay shores farther into the estuary to quiet back water areas as they grow, eventually occupying secondary bays considerable distances from their original point of entry (Yokel 1966, Perret et al. 1980, Peters and McMichael 1987). Young drum will leave these shallow areas when about 40 to 120 mm TL and move into primary bays and somewhat deeper waters (>1.8 m). This movement may be accelerated by cold temperatures (Pearson 1928, Yokel 1966, Osburn et al. 1982, Peters and McMichael 1987). Movement of sub-adults (<3 years) in bays appears limited with schools remaining in a single locale for several months (Osburn et al. 1982). Most of their movements apparently consist of responses to temperature and salinity, and foraging which can be considerable even if these fish remain within a small general area (Pafford 1981, Overstreet 1983). As juveniles approach 200 mm TL during their first spring, they may remain in deep water areas of bays or congregate near passes usually in large aggregations (Simmons and Hoese 1959, Peters and McMichael 1987). Sub-adults may remain in the bays throughout the year, but older fish (≥2) move into the open Gulf in fall and winter, and possibly during late summer (Perry 1970, Perret et al. 1980, Hein and Shepard 1986a, Matlock 1987, Beckman et al. 1988). This seasonal movement is a general, gradual one with fish disappearing offshore presumably to spawn (Pearson 1928, Benson 1982). Class I juveniles leaving bay systems in the fall probably reenter with older juveniles the following spring in a more contracted migration (Pearson 1928, Ward and Armstrong 1980, Benson 1982). Migrating fish may use salinity gradients as predictive cues for directed movements from estuarine to oceanic habitats and back (Owens et al. 1982). Results from recent studies suggest large fish in offshore waters may have a more extensive migration over time than was previously thought. These movements may be due to the abundance of specific food items, causing the red drum to continually migrate in a relatively consistent pattern in order to optimize feeding in specific rich and different areas on a seasonal basis (Overstreet and Heard 1978, Pafford 1981, Overstreet 1983).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe into the water column, and egg development is oviparous. Mature adults probably form spawning aggregations (Johnson and Funicelli 1991). Red drum are multiple batch spawnwers, with group-synchronous oocyte maturation (Wilson and Nieland 1994).

Spawning: The spawning season typically lasts from summer through early winter, but its onset and duration vary with photoperiod, water temperature, and possibly other factors (Holt et al. 1981a, Overstreet 1983). Spawning can start as early as August in some parts of the study area, but it usually begins in September and ends in early January with peaks occurring in mid-September through October, and then declining (Welsh and Breder 1924, Gunter 1945, Yokel 1966, Boothby and Avault 1971, Christmas and Waller 1973, Heffernan 1973, Sabins and Truesdale 1974, Perret et al. 1980, Holt et al. 1981a, Benson 1982, Overstreet 1983, Lee et al. 1984, Hein and Shepard 1986a, Peterson 1986, Matlock 1987, Van Hoose 1987, Murphy and Taylor 1990). Gonadosomatic index (GSI) studies in the northern Gulf of Mexico suggest an 8 to 9 week spawning season, mid-August to early October (Wilson and Nieland 1994). Based on the presence of larval red drum in the northern Gulf of Mexico, it can be inferred that spawning occurs August through November, with a peak from September through October (Ditty 1986, Ditty et al. 1988). Spawning principally occurs in nearshore coastal waters on the Gulf side of barrier islands, usually in or near the passes and channels between islands where currents can carry the eggs to shallow inside waters (Higgins and Lord 1926, Pearson 1928, Gunter 1945, Breuer 1957, Yokel 1966, Sabins and Truesdale 1974, Perret et al. 1980, Holt et al. 1981a, Benson 1982, Lee et al. 1984, Hein and Shepard 1986a, Matlock 1987, Peters and McMichael 1987, Murphy and Taylor 1990). Freshly spawned eggs were recovered during one investigation in water depths ranging from 1.5 to 2.1 m (Johnson and Funicelli 1991). One study estimated spawning occurring 7.3 to 21.9 m offshore of a natural pass in Texas (Heffernan 1973). In Florida, ripe adults have been collected 4.8 km offshore in the Gulf of Mexico suggesting that some offshore spawning may also occur (Murphy and Taylor 1990). Some spawning can also occur inside large estuaries. Spawning activities are initiated in early evening or night (Guest 1978, Holt et al. 1981b, Overstreet 1983, Johnson and Funicelli 1991), in an average salinity of 28‰ and in temperatures of 21° to 24°C (Hopkins et al. 1986, Johnson and Funicelli 1991).

Fecundity: Captive fish spawn repeatedly and produce large numbers (about 1 million per spawn) of small buoyant eggs (Vetter et al. 1983). The estimated number of oocytes from a female with a standard length (SL) of 758 mm was 61,998,776 when calculated by volumetric means or 94,513,172 using the gravimetric method (Overstreet 1983). In one experiment, 10 to 12 spawns per fish over 90 to 100 days were typical with one captive fish spawning 31 times over 90 days, while another reported 3 females spawning 52 times in 76 days producing an estimated total of 60 million eggs. Captive fish spawned about 1 million eggs per spawn during the first 45 days, dropping to 10 to 100 thousand thereafter. The maximum recorded spawn was 2,058,000 per fish during one night (Arnold et al. 1979, Overstreet 1983), and a maximum individual annual fecundity is estimated as 30,000,000 for 9 to 14 kg fish (Overstreet 1983). In the northern Gulf of Mexico, Wilson and Nieland (1994) reported a typical batch spawning frequency of 3 days, and a batch fecundity range of 160,000 to 3.27 million eggs for females 3 to 33 years old.

**Growth and Development**

Egg Size and Embryonic Development: Eggs develop oviparously. They are buoyant, and their shape is spherical with a mean diameter of 0.95 mm and a range of 0.86 to 0.98 mm diameter (Ditty and Shaw 1994). Usually one and up to six clear oil globules averaging 0.27 mm (0.24-0.31 mm) are present. The perivitelline space varies in size, but is generally less than 2% of the egg diameter (Holt et al. 1981b, Vetter et al. 1983). Eggs spawned at 24°C and 28‰ hatch in 19 to 20 hours (Arnold et al. 1979), 22 hours when spawned at 23°C and 36‰ (Vetter et al. 1983), and 28 to 29 hours at 22 to 23°C (Holt et al. 1981b). Live eggs float with the oil globule on top, and animal pole downward. Holt et al. (1981b) has thoroughly described the embryonic development of this species. Hatching usually occurs in late summer to early winter, peaking in September and October (Matlock 1987).

Age and Size of Larvae: Larvae are less than 8.0 mm SL, and those 8 to 15 mm SL are considered transitional juveniles (Peters and McMichael 1987). Larvae are either transparent with no pigment patterns at hatching, or have a compressed band of dendritic melanophores on the ventral surface of the body in the yolk sac region (Holt et al. 1981b). Newly hatched larvae are negatively buoyant with a SL range of 1.71 to 1.79 mm (mean 1.74). Three days after hatching, at 25°C, the mouth forms, eyes are pigmented, and more time is spent swimming to stay near the surface. The swim bladder is well developed by day 4 and larvae remain in a horizontal position in the water column with little effort (Holt et al. 1981b). The yolk sac is present in larvae 3 to 5 mm TL, but has disappeared at 7 mm TL. Temperature has a pronounced effect on larval growth (Holt et al. 1981b, Lee et al 1984, Comyns et al. 1984). In laboratory raised fish, the yolk sac stage can range from 40 hours at 30°C to 85 hours at 20°C (Holt et al. 1981a, Holt et al. 1981b), and larval weight increase can average 17.74 µg/day at 24° and 30.25 µg/day at 28°C. Larvae in the field grow at faster rates than similar aged laboratory spawned larvae (Comyns et al. 1989). Wild larvae have an average weight gain of 141 µg/day at 27.8° to 29.0°C. The growth rate for wild larvae smaller than 4 mm is about 0.3 mm/day, but growth increases rapidly in sizes greater than 4 mm (0.42 mm/day for 4 to 6 mm larvae). Two distinct growth periods are evident in early larval development. One extends from hatching through depletion of the yolk sac, while the other begins with the onset of active feeding. Growth rate in terms of SL was low in the first stage, averaging less than 0.06 mm/day or more (Lee et al. 1984).

Juvenile Size Range: Transformation to the juvenile stage occurs at a total length (TL) of approximately 12 mm (Ditty and Shaw 1994). The size range for the juvenile stage is from 8.0 mm SL until about 40 mm TL (Gunter 1945, Peters and McMichael 1987). Above 10 mm TL, pigment rapidly appears with distinctive color patterns at about 25 mm TL. Twenty to 50 dark distinct blotches are present at this point from the lateral line to the dorsal fin on each side of the trunk. At 36 mm TL, a pronounced chromatophore enlargement at the base of the upper part of the caudal fin appears that results in the characteristic black ocelli. Juveniles are morphologically identical to adults by 42 mm TL except for a slightly more pointed caudal fin and lack of distinct ocelli. Ocelli are faintly visible at 50 mm TL and are very apparent at 75 mm TL. Brown lateral blotches enlarge with the fish until it reaches 150 mm TL, and then tend to fade and finally disappear (Pearson 1928, Simmons and Breuer 1962). Growth tends to be sporadic in juveniles, averaging 18.8 mm TL/month or 20.4 mm SL/month for the first 7.5 months of life (Bass and Avault 1975). Other estimates based on Texas red drum report sizes of 320 to 360 mm SL for the first year, 500 mm SL for the second year, 550 to 600 for the third year, 875 mm SL for the sixth year, 925 mm SL for the seventh year, and 975 to 1000 mm SL for the eighth (Miles 1950). Growth has been expressed modally in year class lengths of: 340 mm SL first year, 540 mm SL second year, 640 mm third year, 750 mm SL fourth year, 840 mm SL fifth year; 330 to 356 mm first year, 484 to 559 second year, 660 to 762 mm third year, 890 to 965 fourth or fifth year (Johnson 1978). Growth is rapid until age 4 or 5 years and then slows markedly (Murphy and Taylor 1990). Sexual maturity occurs at the end of the third, fourth, or fifth year with 5 year old fish constituting the bulk of the spawning population. Males mature at smaller sizes than females with most mature at age 1 or 2, and all mature by age 3 years. Some females are mature by age 3, and all are mature by age 6 years (Pearson 1928, Simmons and Breuer 1962, Johnson 1978, Benson 1982, Murphy and Taylor 1990). Red drum generally mature at approximately 700 to 800 mm TL (Miles 1950, Simmons and Breuer 1962), with 50% of the males maturing when they reach a fork length (FL) of 529 mm and 50% of the females mature by 825 mm FL (Murphy and Taylor 1990). Smaller ripe fish are occasionally found. Mature fish have been collected in Texas as small as 425 mm TL. Males are presumed to mature at a smaller size than females and have been reported to reach maturity at 320 to 395 mm in Mississippi. Another study reported ripe males 500 mm SL and ripe females 550 mm SL from Texas samples (Gunter 1945, Miles 1950, Perret et al. 1980). In Florida, some males and females are mature by 400 and 600 mm FL, respectively (Yokel 1966, Murphy and Taylor 1990). A Louisiana study reported spawnable males ranging 779 to 1130 mm TL and spawnable females ranging 850 to 1135 mm TL (Hein and Shepard 1986a). Wilson and Nieland (1994) reported that both males and females reach maturity in the northern Gulf of Mexico at four years of age, when females are 690-700 mm fork length (FL) and 4.0-4.1 kg total weight (TW), and males are 660-670 mm FL and 3.4-3.5 kg TW.

Age and Size of Adults: Average adult size is 800 to 850 mm SL (Pearson 1928, Miles 1949). This is a long lived species with fish surviving over 37 years (Johnson 1978, Mercer 1984, Beckman et al. 1988, Murphy and Taylor 1990). A 36 year old female was 995 mm FL and weighed 11.96 kg, and a 37 year old male was 940 mm FL and weighed 10.49 kg (Beckman et al. 1988). Pearson (1928) recorded a 1520 mm TL fish. The largest red drum caught by hook and line was caught in North Carolina waters and weighed 42.69 kg (WRGF 1991). The red drum fishery is largely comprised of newly recruited fish. The mean size and age of this population depends heavily on recent recruitment (Tilmant et al. 1989). Beckman et al. (1988) have derived Von Bertalanffy growth equations for both sexes of red drum by length and by weight.

**Food and Feeding**

Trophic Mode: All free swimming life stages are carnivorous. Juveniles appear to hunt for food using a sweep style method to search for suitable prey (Fuiman and Ottey 1993).

Food Items: The red drum diet consists of food items from five major groups: copepods, mysid shrimp, amphipods, decapods, and fish (Bass and Avault 1975, Levine 1980). Utilization of these groups is determined by prey size and availability (Boothby and Avault 1971, Bass and Avault 1975, Overstreet and Heard 1978, Morales and Dardeau 1987), and so their dominance in the diet of red drum may vary among locations.

Larvae: The major prey of larval red drum are copepods, including cyclopoids, calanoids, and harpacticoids, as well as various other zooplankton (Bass and Avault 1975, Benson 1982, Peters and McMichael 1987). Larvae up to 9 mm TL subsist on copepods and their nauplii that range from 0.06 to 1.5 mm TL (Bass and Avault 1975, Comyns et al. 1989). The calanoid *Acartia* sp. is eaten most frequently, but species of cyclopoids, harpacticoids, and other calanoids are also consumed.

Juveniles: Although they appear in the diet of juveniles 10 to 39 mm TL, copepods cease to be important in volume by 10 to 19 mm TL. Mysid shrimp, particularly

*Mysidopsis almyra*, are eaten by fish 10 to 169 mm TL, but are most important in small juveniles 10 to 49 mm TL, constituting 70 to 100% of their diet (Bass and Avault 1975, Peters and McMichael 1987). Fish 30 mm TL and over eat small crustaceans like schizopods and amphipods (Darnell 1958). Gammarid amphipods are consistently found in 10-109 mm TL fish and are a dominant food item in fish 30 to 60 mm TL (Bass and Avault 1975, Peters and McMichael 1987). Generally, at least five species of amphipods, including *Ampelisca* sp. and *Carinogammarius* sp., are a minor part of the diet, but are moderately important in fish 30 to 49 mm TL. A large variety of decapods are eaten by fish 8 to 120 mm TL. The first to appear in the diet are caridean shrimp, usually grass shrimp (*Palaemonetes* sp.), as well as zostera shrimp (*Hippolyte zostericola*), bay shrimp (*Crangon* sp.), and snapping shrimp (*Alpheus* sp.). These are eaten until fish reach 150 to 159 mm TL. Penaeid shrimp, including white shrimp, pink shrimp, and brown shrimp, enter the diet of fish 70 to 79 mm, and become important for fish 90 to 99 mm TL and larger (Miles 1949, Bass and Avault 1975, Overstreet and Heard 1978, Peters and McMichael 1987). Crabs, though insignificant in the size classes from 30-69 mm SL, begin to gain importance in juveniles >70 mm long but remain secondary to shrimp (Morales and Dardeau 1987). At 100 to 175 mm TL, the chief food items are small penaeid shrimp, palaemonetid shrimp, small mullet, silversides, gobies, and small crabs (Simmons and Breuer 1962, Morales and Dardeau 1987). Blue crab and other portunid crabs are eaten by fish 40 to 49 mm TL, and are a common food item for fish 70 to 79 mm TL. Other crabs are found predominantly in larger juveniles (>105 mm TL) and include fiddler crabs (*Uca* sp.), heavy marsh crab (*Sesarma reticulatum*), mud crabs, *Eupagurus* spp., and spider crab (*Libinia dubia*), but these are generally unimportant (Miles 1949, Bass and Avault 1975, Peters and McMichael 1987, Morales and Dardeau 1987). Crabs predominate in the diet of fish 184 to 625 mm TL, particularly blue crab and Harris mud crab (*Rhithropanopeus harrisii*), and some fish as well (Darnell 1958). Fish play a substantial role in the diet of juveniles ≥15 mm TL, but were most abundant in juveniles > 90 mm TL (Bass and Avault 1975, Peters and McMichael 1987). Juveniles 20 to 29 mm TL began eating other sciaenids, usually spot, but also some Atlantic croaker. Other fish consumed include: speckled worm eel (*Myrophis punctatus*), gulf menhaden, anchovies (*Anchoa* sp.), inshore lizardfish (*Synodus foetens*), mullet, inland silverside (*Menidia beryllina*), darter goby (*Gobionellus boleosoma*), and bay whiff (*Citharichthys spilopterus*).

Food habits vary little in fish 250 to 924 mm SL (Boothby and Avault 1971). Smaller fish generally eat smaller sized items, but the three main groups, shrimp, crabs, and fish, are eaten by all size classes. No noticeable difference has been observed between the diets of males and females (Boothby and Avault 1971). Red drum 245 to 745 mm TL have been found to consume algae, grass, eggs, cysts, detritus, mud and sand, annelids, ostracods, amphipods, fish, penaeid shrimp, and squid. Specific prey items include grass shrimp, blue crab, mud crabs, bay shrimp (*Crangon* sp.), estuarine ghost shrimp (*Callianassa jamaicense*), mullet, speckled worm eel (*Myrophis punctatus*), naked goby (*Gobiosoma bosci*), sheepshead minnow, gulf pipefish (*Sygnathus scovelli*), anchovies, menhaden, hardhead catfish, rainwater killifish (*Lucania parva*), spot, and blackcheek tonguefish (*Symphurus plagiusa*) (Pearson 1928, Gunter 1945, Knapp 1949, Reid 1955, Reid et al. 1956, Simmons 1957, Breuer 1957, Bryan 1971, Diener et al. 1974). Although crustaceans as a group exceed fish in frequency of occurrence and per cent volume of stomach contents, fish are consumed more frequently, in greater numbers, and in greater volume than shrimp or crabs alone. Plant and substrate material that occurs in stomach contents are probably taken incidentally during feeding activities. Fish are generally more prevalent in the diet of red drum during winter and spring months, menhaden being a favorite. Crustaceans become increasingly more important during late spring and by summer are the main staple and continue as such until late fall. Shrimp appear more frequently in stomach contents in the spring, summer, and fall. Crabs are more frequent than shrimp only in the winter (Boothby and Avault 1971). Other organisms eaten by juveniles contributed little to stomach contents volume with the possible exception of polychaetes, especially *Glycera americana* (Bass and Avault 1975, Peters and McMichael 1987, Morales and Dardeau 1987). These were eaten by 30-139 mm TL fish, but were most important to 60-79 mm TL fish (Bass and Avault 1975, Overstreet and Heard 1978). Echinoderms are eaten regularly by large fish, but are not an important diet item (Overstreet and Heard 1978). Other species consumed in addition to the main food species are: molluscs- Atlantic mud-piddock (*Barnea truncata*), false angelwing (*Petricola pholodiformes*), white baby-ear (*Sinum perspectivum*); crustaceans- lesser blue crab (*Callinectes simulis*), calico box crab (*Hepatus epheliticus*), lady crab (*Ovalipes ocellatus*), longwrist hermit crab (*Pagurus longicarpus*), iridescent swimming crab (*Portunus gibbesi*), sea lice (*Squilla* sp.); echinoderms- *Mellita quinquiesperforata*, *Sclerodactyla briareus*; fishes- striped killifish (*Fundulus majalis*), southern kingfish (*Menticirrhus americanus*), pinfish, oyster toadfish (*Opsanus tau*), Florida pompano, and hogchoker (*Trinectes maculatus*) (Pearson 1928, Miles 1949, Boothby and Avault 1971, Overstreet and Heard 1978). Bivalve molluscs, bivalve mollusc siphons, isopod crustaceans, and a marsh rat have also been reported from stomach contents, but these items are not typical

(Pearson 1928, Peters and McMichael 1987).

**Biological Interactions**

Predation: Predation on red drum has not been well studied (Killam et al. 1992). Larvae and juveniles are potential prey items of larger piscivorous fish including larger red drum. Juvenile red drum feeding along the shorelines of mariculture ponds are subject to predation by piscivorous wading birds (Castiglione pers. comm).

Factors Influencing Populations: Red tides, caused by the blooms of certain dinoflagellates, that occur during the spawning season can affect larval survival rates and possibly impact recruitment of the affected year-class in following years (Riley et al. 1989, Killam et al. 1992). Several organisms are known to parasitize red drum possibly as a consequence of the diverse foods consumed, and these can affect health and mortality (Yokel 1966, Perret et al. 1980, Overstreet 1983, Landsberg 1993). Known parasites include: Sporozoans- *Hennequya ocellata*; *Parvicapsula renalis*, Trematodes- unidentified; Cestodes- *Poecilan cistrium robustum* (known as spaghetti worm) infecting muscles and often resulting in fish being discarded by fishermen; Copepods, which parasitize red drum the most heavily, include- *Brachiella qulosa*, *B. intermedia*, *Echetus typicus*, *Lernaennicus radiatus*, *Caliqus latifrons*, *C. repax*, *C. bonito*, *C. elongatus*, *C. haemulonis*, and *Lernanthropus paenulatus*, *Lernaennicus affixus*; Isopods- *Nerocila* sp. (Simmons 1957, Yokel 1966, Perret et al. 1980, Hein and Shepard 1986b, Landsberg et al. 1991, Landsberg 1993); Barnacles- *Balanus improvisus*, are known to attach to the flanks of red drums (Overstreet 1983). The destruction of estuarine nursery habitat utilized by late larval and juvenile stages, as well as growth overfishing and recruitment overfishing, are thought to have a serious impact on red drum (NMFS 1986).

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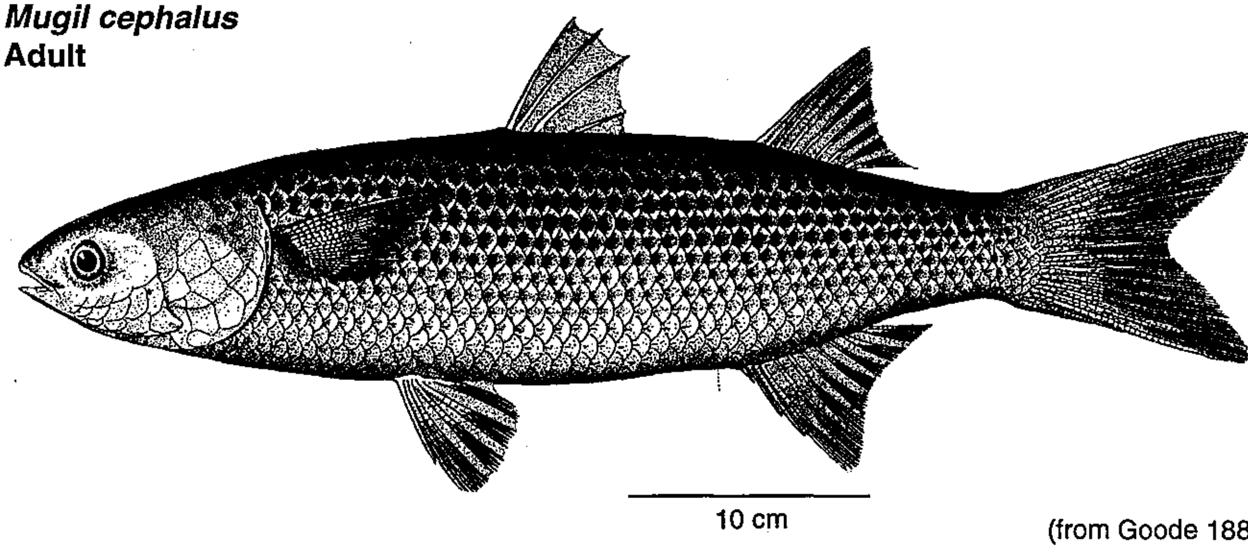
# Striped mullet

***Mugil cephalus***
**Adult**




(from Goode 1884)

**Common Name**: striped mullet
**Scientific Name**: *Mugil cephalus*
**Other Common Names**: common mullet, black mullet, Biloxi bacon, liza, gray mullet, *mulet cabot* (French), *lisa pardete* (Spanish) (Broadhead 1953, Breuer 1957, Christmas and Waller 1973, Kuo et al. 1973, Finucane et al. 1978, Fischer 1978, NOAA 1985).

**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Perciformes |
| Family: | Mugilidae |

**Value**

Commercial: Mullet comprise one of the most important fisheries of the southern United States with combined 1993 Gulf of Mexico landings for black and striped mullet totaling over 14,319 mt and selling for an average of $0.41 per pound (Anderson 1958, Lee et al. 1980, Newlin 1993, O'Bannon 1994). Commercial fishing for mullet takes place mainly from September to December (NOAA 1985), and Gulf coast landings contributed 84% of the total U.S. catch in 1992 (Newlin 1993). Florida contributes the greatest amount to Gulf of Mexico mullet production (5,104 mt), and this comes primarily from the west central coast of the state (Killam et al. 1992, Newlin 1993). This production amount is followed by Louisiana (2,733 mt), Alabama (580 mt), Mississippi (215 mt), and Texas (16 mt). Striped mullet is considered an important food fish, and is usually marketed locally. It is also taken for its roe, which is prized as a delicacy and exported to Asian markets (Render et al. 1995). Mullet are most frequently marketed as fresh or salted (Fischer 1978, Shipp 1986). This is also considered a prime species for mariculture (Broadhead 1953, Christmas and Waller 1973, Bishop and Miglarese 1978). Despite this good reputation as a food fish, striped mullet is commonly considered oily and poor tasting west of the Mississippi (although one researcher reports it as being quite palatable) and is primarily used only as bait (Kilby 1949, Reid 1955, Arnold et al. 1960). Recent efforts to enhance the image of both mullet and mullet roe as an export product have met with considerable success, thus its commercial importance may increase further in the future (Shipp 1986, Killam et al. 1992). Mullet are caught by gill nets, trammel nets, stop nets, haul seines, yard seines, hook and line, and cast nets (Broadhead 1953, Broadhead and Mefford 1956, Anderson 1958, Fischer 1978). The gill nets and trammel nets are the most effective means of capture, with haul and yard seine second in choice. Hook and line, and cast net catches are incidental. The rising popularity of mullet flesh and roe as food items, and the use of more efficient fishing gear and methods have led to increasing harvest regulation by the Gulf coast states. In order to manage the Gulf of Mexico fishery, the Gulf States Marine Fisheries Commission has developed a fishery management plan (FMP) for this species (Leard et al. 1995).

Recreational: Striped mullet is valued as a bait fish by sport fishermen, and is also indirectly important as a forage species for game fishes (Kilby 1949, Arnold et al. 1960). Fishery information for the recreational catch in the Gulf of Mexico showed a total of over 1.6 million mullet caught in 1992 (O'Bannon 1993). Sport fishermen take striped mullet with the same gear that commercial fishermen use (Manooch 1984, Collins 1985). The importance of mullet as a recreational species may be underestimated. When recently compared to a

Table 5.40. Relative abundance of striped mullet in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ◉ | | ● | ○ | |
| Ten Thousand Islands | ◉ | | ● | | |
| Caloosahatchee River | ○ | | ● | | |
| Charlotte Harbor | ◉ | | ● | √ | |
| Tampa Bay | ○ | | ● | | |
| Suwannee River | ◉ | | ◉ | ○ | |
| Apalachee Bay | ● | | ● | ◉ | |
| Apalachicola Bay | ◉ | | ◉ | ○ | |
| St. Andrew Bay | ● | | ● | ○ | |
| Choctawhatchee Bay | ◉ | | ◉ | ◉ | |
| Pensacola Bay | ◉ | | ◉ | ◉ | |
| Perdido Bay | ○ | | ◉ | ○ | |
| Mobile Bay | ◉ | | ◉ | ◉ | |
| Mississippi Sound | ● | ● | ◉ | ● | ◉ |
| Lake Borgne | ● | | ◉ | √ | |
| Lake Pontchartrain | ○ | | ◉ | | |
| Breton/Chandeleur Sounds | ◉ | | ○ | | |
| Mississippi River | ◉ | | ◉ | | |
| Barataria Bay | ○ | | ◉ | ○ | |
| Terrebonne/Timbalier Bays | ○ | | ◉ | | |
| Atchafalaya/Vermilion Bays | ◉ | | ◉ | | |
| Calcasieu Lake | | | ◉ | | |
| Sabine Lake | ○ | | ○ | | |
| Galveston Bay | ○ | | ◉ | | |
| Brazos River | ○ | | ○ | | |
| Matagorda Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| San Antonio Bay | ○ | | ◉ | | |
| Aransas Bay | ○ | | ◉ | | |
| Corpus Christi Bay | ○ | | ◉ | | |
| Laguna Madre | ○ | ○ | ◉ | ○ | ○ |
| Baffin Bay | ◉ | | ◉ | | |
| | A | S | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

group of other popular recreational species from the inshore Gulf (spotted seatrout, sand seatrout, sheepshead, red drum, and black drum), mullet ranked second in Florida, third in Mississippi, and fourth in Alabama (Leard pers. comm.).

Indicator of Environmental Stress: This species has been used by the U.S. Environmental Protection Agency (EPA) to study the toxicology of crude oil (Minchew and Yarbrough 1977). Another study indicates that the results of striped mullet responses to DDT at different temperatures have application for the development of water quality criteria in Australia (Powell and Fielder 1982).

Ecological: Striped mullet is an important forage fish and forms a major component in the flow of energy through the estuarine system by feeding at the lowest trophic levels and providing food to birds and many important commercial and game fish (Kilby 1949, Fontenot and Rogillio 1970, Moore 1974, Sogard et al. 1989).

**Range**

Overall: Striped mullet occur world-wide in warm tropical, sub-tropical, and temperate waters 42° N to 42° S (46° N in Mediterranean and Black Sea), but are less common in equatorial areas (Anderson 1958, Moore 1974, Hoese and Moore 1977, Martin and Drewry 1978, Lee et al. 1980, Ward and Armstrong 1980, NOAA 1985, Shipp 1986). Juveniles are often collected outside the above latitudes, usually in the fall. On the U.S. east coast, they are most abundant from Cape Hatteras southward, but also occur in the Chesapeake and Mid-Atlantic region, and occasionally as far north as Nova Scotia (Lee et al. 1980). They are found on the U.S. west coast from San Francisco Bay southward, and in coastal waters of the Hawaiian Islands where they are known as *'ama'ama* (Squire and Smith 1977).

Within Study Area: Striped mullet occurs throughout the Gulf of Mexico in shallow marine and estuarine habitats (Gunter 1945, Moore 1974, Ward and Armstrong 1980). This fish is very common along the west coast of Florida, and is most abundant along the south Florida coasts. It is also one of the most numerous species in the bay flats along the Texas coast (Gunter 1945, Broadhead 1953, Collins 1985, Killam et al. 1992) (Table 5.40).

**Life Mode**

All stages are pelagic, occurring primarily in the shallow part of the water column, although some deep recoveries have been reported (Arnold and Thompson 1958, Thomson 1966, Hoese and Moore 1977, Finucane et al. 1978, Martin and Drewry 1978, Ward and Armstrong 1980). Fertilized eggs are spherical, positively buoyant, and non-adhesive. Eggs and larvae are generally neustonic. Larvae are planktonic until 10 to 12 days from hatching and are then capable of sustained swimming (Kuo et al. 1973, Martin and Drewry 1978). Pre-juveniles, juveniles, and adults are nektonic and form schools ranging from a few individuals up to several hundred (Breder 1940, Kilby 1949, Arnold and Thompson 1958, Arnold et al. 1960, Thomson 1966, Hoese and Moore 1977). Activity related to feeding has been recorded during both day and night (Hiatt 1944, Darnell 1958, Tabb and Manning 1961), although light is believed necessary for schooling (Thomson 1966). A Florida study observed diurnal activity (Sogard et al. 1989).

**Habitat**

Type: Striped mullet live in a wide range of habitats and depths depending on life stage, season, and location. It is one of the most abundant fishes in shallow Gulf waters, and often has the highest biomass (Hellier 1962). It is most abundant in waters near shore, occupying virtually all shallow marine and estuarine habitats including open beaches, flats, lagoons, bays, rivers, salt marshes, and grass beds (Gunter 1945, Kilby 1949, Breuer 1957, Renfro 1960, Hellier 1962, Franks 1970, Perret et al 1971, Swingle 1971, Christmas and Waller 1973, Moore 1974, Henley and Rauschuber 1981, Cech and Wohlschlag 1982, Sogard et al. 1989). Spawning occurs near the surface of offshore waters, but larvae sink during post-hatch growth periods (Ditty and Shaw 1996). Eggs and larvae occupy offshore marine habitat where they undergo early development, then as prejuveniles enter the bays and estuaries to mature. This occurs from November to June after they have reached 15 to 32 mm in total length (TL), with the greatest occurrence from December to February (Gunter 1945, Renfro 1960, Hellier 1962, Hoese 1965, Franks 1970, Perret et al. 1971, Swingle 1971, Christmas and Waller 1973, Swingle and Bland 1974, Hildebrand and King 1975, Tarver and Savoie 1976, Ward and Armstrong 1980, Nordlie et al. 1982). This species has been reported from fresh to hypersaline waters and from waters with depths of a few centimeters to 1,385 m, but most are collected within 40 m of the surface (Gunter 1945, Breuer 1957, Simmons 1957, Arnold and Thompson 1958, Perret et al. 1971, Swingle 1971, Christmas and Waller 1973, Moore 1974, Pineda 1975, Finucane et al. 1978, Martin and Drewry 1978, Ward and Armstrong 1980, Henley and Rauschuber 1981, Cech and Wohlschlag 1982, Cornelius 1984, NOAA 1985). This species appears to prefer depths of $\leq$3 m in inshore waters.

Substrate: The striped mullet prefers softer sediments such as mud and sand which contain decaying organic detritus, but it also occurs over finely ground shell, clay, mud and sand mixtures, silt, and silt-clay mixtures (Kilby 1949, Breuer 1957, Tabb and Manning 1961, Franks 1970, Swingle 1971, Ward and Armstrong 1980, Cornelius 1984). In inshore areas, it also frequents grass beds of *Thalassia* and other macrophytes, especially at night (Thomson 1966, Zimmerman 1969, Bishop and Miglarese 1978, Henley and Rauschuber 1981), and has also been observed around patches of *Ruppia* (Franks 1970).

Physical/Chemical Characteristics:

Temperature - Eggs: Egg development has been recorded over a range of 10° to 31.9°C in both laboratory and field observations with the optimum range occurring at 21° to 24°C (Kuo et al. 1973, Nash et al. 1974, Sylvester et al. 1975, Sylvester and Nash 1975, Finucane et al. 1978, Ward and Armstrong 1980).

Temperature - Larvae: Ditty and Shaw (1996) collected 1,983 larval mullet in the northern Gulf of Mexico, at temperatures ranging from 16.7 to 27.0°C (mean 34.4°C). Larval development occurs from 15.9° to 29.1°C, with optimum growth and survival occurring at 20° to 22°C (Kuo et al 1973, Nash et al. 1974, Sylvester and Nash 1975, Ward and Armstrong 1980). The ability to survive and grow over a broad thermal range, despite the probability of temperatures at spawning sites varying very little, may be a preadaptation to accommodate temperature changes as the larvae sink vertically through the water (Sylvester and Nash 1975). Pre-juveniles occur at minimum temperatures of 5.0° to 9.0°C up to a maximum exceeding 30°C (Christmas and Waller 1973, Martin and Drewry 1978, Ward and Armstrong 1980).

Temperature - Juveniles and Adults: Juveniles and adults appear able to adjust to a wide range of temperatures (Breuer 1957, Ward and Armstrong 1980). Recorded collections are from 5.9° to 37.0°C, but the ability to withstand short periods of 40°C has been observed (Gunter 1945, Kilby 1949, Hellier 1962, Franks 1970, Perret et al. 1971, Swingle 1971, Dunham 1972, Moore 1974, Pineda 1975, Tarver and Savoie 1976, Ward and Armstrong 1980). Reported temperature preferences are 20° to 30°C for juveniles, and >16° to 30°C for adults (Ward and Armstrong 1980).

Salinity - Eggs: Striped mullet eggs are stenohaline. Spawning and development are reported to occur at 28 to 36.5‰, with optimum egg survival occurring at 30 to 33‰ (Kuo et al. 1973, Sylvester et al. 1975, Finucane et al. 1978, Ward and Armstrong 1980). Eggs have much less tolerance to salinity variation than larvae, but have a greater tolerance to sea water (Sylvester et al. 1975).

Salinity - Larvae: Larvae are stenohaline at hatching and become increasingly euryhaline with size (Nordlie et al. 1982). Early larvae are poly- to euhaline in salinities from 26 to 35‰ and are unable to tolerate fresh water. Older larvae are able to tolerate salinities from 16 to 36.5‰ with reported optimal ranges being 32 to 33‰ and 26 to 28‰ (Kuo et al. 1973, Sylvester et al. 1975, Finucane et al. 1978, Ward and Armstrong 1980, Nordlie et al. 1982). Ditty and Shaw (1996) collected 1,983 larval mullet in the northern Gulf of Mexico, at salinities ranging from 23.5 to 36.8‰, with a mean of 23.4‰. By the pre-juvenile stage, osmotic regulatory abilities and salinity tolerances reach a definitive state, and the mullet becomes euryhaline (Nordlie et al. 1982). Pre-juveniles have been recorded from a range of 0 to 54‰ with a preference for <1 to 40‰ (Gunter 1945, Swingle 1971, Christmas and Waller 1973, Ward and Armstrong 1980).

Salinity - Juveniles and Adults: Both juveniles and adults are euryhaline with similar tolerances. They have been observed in salinities ranging from 0.0 to 75‰, but adults appear to prefer median salinities of approximately 26‰, and juveniles range from 20 to 28‰ (Gunter 1945, Kilby 1949, Simmons 1957, Hoese 1960, Renfro 1960, Hellier 1962, Perret et al. 1971, Dunham 1972, Christmas and Waller 1973, Swingle and Bland 1974, Pineda 1975, Tarver and Savoie 1976, Finucane et al. 1978, Martin and Drewry 1978, Ward and Armstrong 1980, Cornelius 1984). The capability to tolerate salinities ranging from 0 to 35‰ appears when individuals have reached a standard length (SL) of 40-69 mm and are 7.5-8.5 months old (Nordlie et al. 1982).

Dissolved Oxygen (DO): Eggs and larvae prefer higher concentrations of oxygen (about 4 mg/l) and are not able to tolerate ranges as low as juveniles and adults can (Ward and Armstrong 1980, Cech and Wohlschlag 1982). Two possible mechanisms for tolerance to low oxygen levels have been examined. Enhanced hemoglobin concentrations found in striped mullet would enable it to meet seasonally heavy oxygen demands during the warmest months and the autumn spawning period (Cech and Wohlschlag 1982). Aerial respiration in the upper posterior portion of the pharynx using air obtained by jumping, rolling, or holding the head above water and moving air into the upper pharyngeal chamber may also provide supplementary oxygen for respiration (Hoese 1985).

Movements and Migrations: The striped mullet generally does not make long migrations. Movements are predominantly inshore-offshore and occur during fall and winter when large schools leave bays and estuaries in order to spawn in offshore Gulf waters. After spawning, adults return to inshore habitats. Most striped mullet move less than 33 km from their spawning site (Kilby 1949, Broadhead 1953, Broadhead and Mefford 1956, Moe 1972, Hoese and Moore 1977, Ward and Armstrong 1980). However, a tagging study conducted in Florida Bay and along the west coast of Florida showed a northwesterly coastwise movement, especially during the spawning season, with one individual recaptured 500 km from where it was released (Funicelli et al. 1989). One study found that a preference existed for bay waters and suggested an organic compound present in these waters may guide mullet back to their native area (Kristensen 1964). At lengths of 16 to 20 mm SL (40 to 45 days old), pre-juveniles migrate to inshore and estuarine waters in the spring months. Entry of juveniles into estuarine areas begins in November, and continues through February (Ditty and Shaw 1996). After entering bay systems from offshore waters, they migrate to nursery areas which are thought to be secondary and tertiary bays. Most juveniles spend the end of their first year in these coastal waters, salt marshes, and estuaries, and overwinter in deeper parts of these areas. However, some migrate offshore during the fall as sub-adults to mature and spawn when colder temperatures set in (Henley and Rauschuber 1981, Collins 1985). Movement of mullet is otherwise random and usually restricted to a broad coastal area (Broadhead 1953, Broadhead and Mefford 1956, Broadhead 1958, Moe 1972).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe into the water column. Development is oviparous. There are occasional occurrences of hermaphrodites, but they are considered atypical (Thomson 1966).

Spawning: Spawning may begin in October to mid-November and last until March. Peak spawning generally occurs from December through February in the Gulf of Mexico, but there is regional variation. Peak spawning in the northern Gulf of Mexico in November-December, over or beyond the Continental Shelf at sea surface temperatures >25°C (Ditty 1986, Ditty and Shaw 1996). In Florida, the general spawning period is from December to February, while off the Texas coast, the spawning season usually extends from October to December (Breder 1940, Gunter 1945, Broadhead 1953, Reid 1955, Anderson 1958, Arnold and Thompson 1958, Broadhead 1958, Arnold et al. 1960, Christmas and Waller 1973, Wagner 1973, Moore 1974, Sabins and Truesdale 1974, Fahay 1975, Finucane et al. 1978, Ward and Armstrong 1980). Ripe adults collect in passes in large schools and migrate offshore. The return of spent adults begins 10 days later and continues until May (Gunter 1945, Arnold and Thompson 1958, Moore 1974, Sabins and Truesdale

1974, Hoese and Moore 1977). Spawning takes place in offshore marine waters of the Gulf of Mexico over a broad area of the continental shelf (Anderson 1958, Arnold and Thompson 1958, Finucane et al. 1978, Henley and Rauschuber 1981, Nordlie et al. 1982). Adults have been observed spawning during the night 40 to 50 miles southeast of the Mississippi River delta at the surface of waters 915-1647 m deep (Arnold and Thompson 1958). Newly spawned eggs have been recovered in plankton trawls 89 to 98 km off the Texas coast in the northwest Gulf of Mexico in waters 131 to 183 m deep. These eggs were probably spawned over the edge of the continental shelf (Finucane et al. 1978). Spawners occur in small groups of 3 to 6 fish swimming close to the surface in an erratic manner (Arnold and Thompson 1958). Males stay slightly behind a single female pressing against her and from time to time visibly quiver (Breder 1940, Arnold and Thompson 1958). No direct evidence on spawning salinities and temperatures is available, but spawning is apparently unsuccessful at low salinities (Christmas and Waller 1973, Martin and Drewry 1978). Hormonal spawning in a laboratory study was best induced at 23.8° to 23.5°C, and natural spawning at 21°C (Kuo et al. 1973, Sylvester et al. 1975) in salinities ranging from 30 to 32‰ (Kuo et al. 1973, Nash et al. 1974, Sylvester et al. 1975).

Fecundity: Fecundity has been estimated in laboratory studies as being 648 ± 62 to 849 ± 62 eggs/g body weight (Shehadeh et al. 1973, Nash et al. 1974) with recorded releases ranging from 0.76 to 7.2 million eggs/female (Martin and Drewry 1978, Ward and Armstrong 1980). Field studies of Louisiana mullet report individual fecundities of 270,000 to 1,600,000 eggs, and relative fecundities of 798 to 2,616 eggs per gram body weight, for females in a size range of 290 to 445 mm FL (Render et al. 1995). Total individual fecundity correlates with female size, but relative fecundity does not. Females generally produce only one set of ova per year (i.e. isochronal) (Render et al. 1995). However, it has been suggested that Florida striped mullet may spawn more than once in a season (i.e. heterochronal or batch) (Thomson 1966). Fertilization rates in the laboratory have ranged from 53 to 95% (Kuo et al. 1973, Shehadeh et al. 1973, Nash et al. 1974).

**Growth and Development**

Egg Size and Embryonic Development: Render et al. (1995) report that oocyte diameter prior to spawning is 0.6 to 0.7 mm, swelling to 0.9 to .95 mm during hydration. Eggs are nonadhesive, spherical, and transparent to straw-colored (Martin and Drewry 1978, Ward and Armstrong 1980). Sizes average 0.93 to 0.95 mm (Kuo et al. 1973, Shehadeh et al. 1973, Nash et al. 1974, Sylvester et al. 1975, Finucane et al. 1978). They are characterized by a single large oil globule with a uniform diameter ranging 0.30 to 0.36 mm and averaging 0.33 mm (Kuo et al. 1973, Nash et al. 1974, Finucane et al. 1978). Kuo et al. (1973) and Nash et al. (1974) have made thorough descriptions of the striped mullet's embryonic development. Hatching time is temperature dependent. Incubation period is 36 to 38 hours after fertilization (AF) at 24°C and 48 to 50 hours AF at 22°C (Kuo et al. 1973, Nash et al. 1974).

Age and Size of Larvae: The TL at hatching is 2.1 mm to 2.88 mm TL with a reported average of 2.65 ± 0.23 mm TL (Kuo et al. 1973, Nash et al. 1974, Sylvester et al. 1975, Finucane et al. 1978). At hatching, the yolk sac is ovoid or oblong-ellipsoidal with the oil globule near the center or rear of the yolk sac (Martin and Drewry 1978). The mouth opens on day 2 to 3. Larvae are independently active at this point, and their eyes are sufficiently pigmented for finding food. The yolk sac is absorbed by day 5 (24°C) (Kuo et al. 1973, Nash et al. 1974, Ward and Armstrong 1980). Most growth during the yolk sac stage occurs during day 1 with larval TL's increasing from 2.65±0.23 mm to 3.36±0.03 mm. The oil globule is still present after the yolk sac is absorbed. Feeding commences at day 5 (24°C) and becomes intensive on day 9 (24°C) or day 14 (22°C) (Kuo et al. 1973). Silvering begins in the abdominal area, spreading dorsally, and is complete on day 25 (24°C) when larvae are approximately 10.9 mm TL. This marks the end of the larval stage (Kuo et al. 1973, Martin and Drewry 1978). Pre-juveniles are referred to as being in the "querimana" stage (Thomson 1966). The duration of this stage is temperature dependent, and lasts from 30 to 90 days and has a size range of about 11 to 52 mm TL (Anderson 1958, Martin and Drewry 1978). Growth rates in the wild include: 25 mm SL fish in January of class 0 year increasing to 116 mm SL in January of class 1 year; 18 mm SL fish in October increasing to 65 mm SL by mid-April; and 26 mm TL fish increasing to 88 mm TL from February to July (Gunter 1945, Kilby 1949, Hellier 1962). However, reported growth rates for this and other classes vary widely with climate and other factors (Martin and Drewry 1978). Scales begin forming when individuals are about 8 to 10 mm SL and 11 mm TL, and are complete by 12 to 14 mm SL and 18 mm TL (Anderson 1958, Kuo et al. 1973, Martin and Drewry 1978). Nostrils double and the full number of fin rays form at 11.9 mm TL (Martin and Drewry 1978). Fish 20 mm SL weigh 2.3 g (Franks 1970). The adipose eyelid is evident at 28 mm TL, and is well developed by 50 mm TL. The third anal ray changes to a hard spine at 41 to 50 mm TL and this marks the end of the prejuvenile stage (Anderson 1958, Martin and Drewry 1978).

Juvenile Size Range: Juveniles have a size range of about 44 to 200 mm SL (Gunter 1945, Anderson 1958, Martin and Drewry 1978). Fin morphology is the same as that of adults (Martin and Drewry 1978). The caudal fin achieves its final form when the fish has a fork length (FL) of 110 mm, and the scales change suddenly from that of a prejuvenile to an adult when above 30 mm TL. The circuli of the posterior (exposed) region become complete and less densely packed than those of anterior region. Lateral stripes are generally like those of adults, becoming increasingly distinct from 44 to 60 mm SL (Martin and Drewry 1978).

Age and Size of Adults: The life span for the striped mullet is up to 7 years for males, and 8 years for females (Martin and Drewry 1978, Ward and Armstrong 1980) with a probable average life span of about 5 years (Hellier 1962), although a 13 year old fish has been reported (Collins 1985). Adults grow at a rate of 38-64 mm per year (Broadhead 1953). The recorded size range for adults in the study area is 200 to 760 mm TL (Kilby 1949, Breuer 1957, Hellier 1962, Franks 1970, Perret et al. 1971, Moore 1974, Pineda 1975, Tarver and Savoie 1976, Hoese and Moore 1977, Collins 1985). Average sizes for size classes 1 through 5 have been recorded in SL as 116 mm, 181 mm, 230 mm, 277 mm, and 324 mm with mean weight increases of 31 g, 84 g, 116 g, and 167 g for the first through the fourth year (Hellier 1962). One weight recorded for a 238 mm SL fish was 345.0 g (Franks 1970). Adults become reproductively mature at 3 years of age or greater when they reach lengths of 200 to 255 mm TL for males and 250 to 350 mm TL for females, or 230 mm to 285 mm FL for males and 243 to 290 mm FL for females (Gunter 1945, Broadhead 1953, Arnold and Thompson 1958, Moore 1974). The weight of spawning females ranges from 600 to 1400 g (Sylvester et al. 1975). Thomson (1966) has developed a Von Bertalanffy equation to describe the growth of striped mullet.

**Food and Feeding**

Trophic Mode: Larvae are carnivorous, with a diet consisting of planktonic material that probably includes microcrustaceans (Harrington and Harrington 1961, Bishop and Miglarese 1978, De Silva 1980, Ward and Armstrong 1980). Pre-juveniles change from carnivores to omnivores to herbivores as size increases. The trophic transition begins at 15 mm SL and is completed before metamorphosis, usually by 35 mm SL. Feeding by juveniles and adults occurs littorally in shallows by sucking up bottom surface material, straining it through an elaborate pharyngeal sieving mechanism (Hiatt 1944, Broadhead 1958, Darnell 1958, Tabb and Manning 1961), and spitting filtered debris from the mouth (Thomson 1966). Feeding occurs day and night, and digestion is aided by a gizzard which grinds up the tough food items ingested (Hiatt 1944, Broadhead 1958, Darnell 1958, Thomson 1966). Although chiefly herbivorous, striped mullet may opportunistically feed on animal matter, especially in the fall when an above-normal protein intake may be required for gonad maturation (Bishop and Miglarese 1978).

Food Items: The prejuvenile diet consists of plant debris, algae (diatoms), copepods (eggs, nauplii, adults), mosquito larvae, and fish residue (Harrington and Harrington 1961). Juveniles and adults generally prefer organic detritus, diatoms, filamentous algae, organic matter, benthic organisms, plant tissue, foraminifera, and plankton of correct particle size, but they have also been observed with fish scales, sponge spicules, and minute gastropods in their stomach contents (Hiatt 1944, Broadhead 1958, Darnell 1958, Tabb and Manning 1961, Moore 1974). Juvenile striped mullet may feed on "marine snow", macroscopic suspended aggregates of mixed mineral, detrital, algal, and bacterial composition (Larson and Shanks 1996). Mullet that graze on submerged sediments may filter out and reject the coarser particles, and ingest the smaller ones, which contain a higher proportion of absorbed organic matter and adsorbed microorganisms (Odum 1968b). In coastal Georgia, mullet have been observed feeding on dinoflagellates during "red tide" events (Odum 1968a). Adult striped mullet have been observed actively feeding on a swarm of swimming polychaetes, *Nereis succinea* (Bishop and Miglarese 1978).

**Biological Interactions**

Predation: Piscine predators include: red drum, spotted seatrout, hardhead catfish, southern flounder, bull shark, alligator gar (*Lepisosteus spatula*), and longnose gar (*L. osseus*) (Gunter 1945, Breuer 1957, Simmons 1957, Darnell 1958). Wading birds also prey upon this species (Sogard et al. 1989).

Factors Influencing Populations: An EPA study has shown that crude oil may serve as a non-specific stress agent that lowers resistance of mullet to disease (Minchew and Yarbrough 1977). It is also considered possible that crude oil can act as a medium for pathogenic bacteria growth, and adversely affect the zooplankton serving as food for mullet. A number of parasites have been isolated from mullet including: nematodes, leeches, blood trypanosomes, ciliates, spiny-headed worms, bacteria, protozoa, copepods, and tapeworms (Reid 1955, Overstreet 1974, Paperna 1975). There is concern that the expanding roe fishery may result in overharvest of mullet populations in some areas (Clement and McDonough 1997).

**Personal communications**

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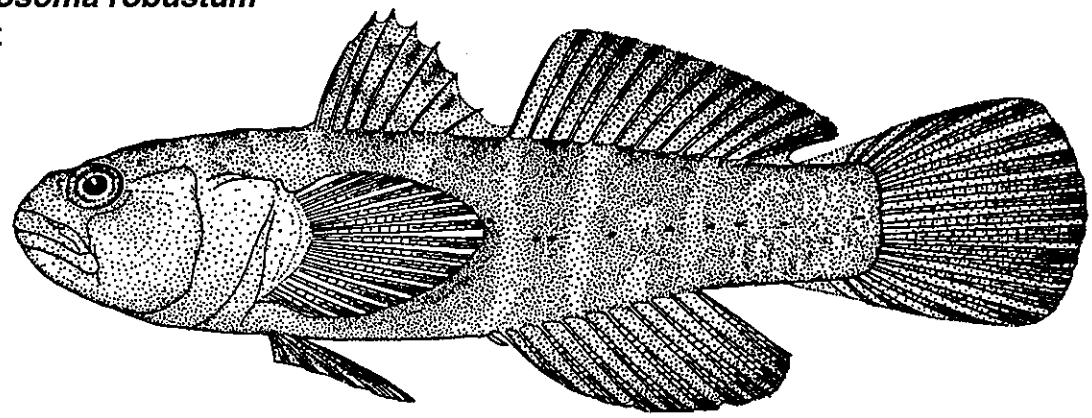
# Code goby

***Gobiosoma robustum***
**Adult**



1 cm (from Fritzsche 1978)

**Common Name**: Code goby
**Scientific Name:** *Gobiosoma robustum*
**Other Common Names**: robust goby
**Classification** (Robins et al. 1991)

| | |
|---|---|
| Phylum: | Chordata |
| Class: | Osteichthyes |
| Order: | Perciformes |
| Family: | Gobiidae |

**Value**

Commercial: The code goby has no commercial value, other than as a minor forage fish for commercially important species.

Recreational: The code goby has little recreational value, although it is somtimes kept in marine aquaria, and may be observed by recreational divers and snorkelers.

Indicator of Environmental Stress: This species is generally not used in studies of environmental stress.

Ecological: The code goby is a small predator, and is one of the dominant species of shallow grass flats (Hildebrand 1954, Springer and Woodburn 1960, Hoese and Jones 1964, Zimmerman 1969, Odum 1971). It is also considered the most abundant goby in the saline waters of northern Florida Bay (Tabb and Manning 1961).

**Range**

Overall: This species is found from the Chesapeake Bay to Florida and throughout the Gulf of Mexico to the Yucatan (Ginsburg 1933, Dawson 1969, Schwartz 1971, Hoese and Moore 1977). It is abundant in shallow sea grass meadows especially in Florida and northern Gulf of Mexico (Ginsburg 1933, Hildebrand 1954, Springer and Woodburn 1960).

Within Study Area: The code goby is common along the Gulf coast from the Laguna Madre, Texas to Florida Bay, Florida in shallow grass flats (Ginsburg 1933, Hildebrand 1954, Bohlke and Robins 1968, Zimmerman 1969). It is considered absent from many of the low-salinity estuaries of Louisiana (Czapla et al. 1991) (Table 5.41).

**Life Mode**

This is a demersal species (Zimmerman 1969, Odum 1971). Observations from different activity studies are inconclusive, possibly due to the difficulty in collecting this "secretive" resident of sea grass beds (Springer and Woodburn 1960, Hoese and Jones 1964, Zimmerman 1969, Krull 1976, Shipp 1986).

**Habitat**

Type: The habitat preferences of early life stages are well known. Eggs have been found attached to shells or sponges (Fritzsche 1978). Adults are primarily collected from oligohaline to euhaline estuaries in shallow water seagrasses, particularly *Thalassia*, but also in *Diplanthera*, *Ruppia*, *Halodule*, and *Cymodocea* grass beds. Adults are also found in bays, beach ponds, oyster reefs, river sloughs, rocky channels, and among mangrove roots (Breder 1942, Bailey et al. 1954, Hildebrand 1954, Kilby 1955, Springer and Woodburn 1960, Springer and McErlean 1961, Tabb and Manning 1961, Tabb et al. 1962, Hoese and Jones 1964, Hoese 1965, Zimmerman 1969, Bonin 1977, Hoese and Moore 1977, Huh 1984, Thayer et al. 1987). They are uncommon in deeper waters, with most collections occurring at depths of a few centimeters to

Table 5.41. Relative abundance of code goby in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | S | J | L | E |
|---|---|---|---|---|---|
| | *Life stage* | | | | |
| Florida Bay | ● | ● | ● | ● | ● |
| Ten Thousand Islands | ● | ● | ● | ● | ● |
| Caloosahatchee River | ◉ | ◉ | ◉ | ◉ | ◉ |
| Charlotte Harbor | ● | ● | ● | ● | ● |
| Tampa Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Suwannee River | ○ | ○ | ○ | ○ | ○ |
| Apalachee Bay | ○ | ○ | ○ | ○ | ○ |
| Apalachicola Bay | ○ | ○ | ○ | ○ | ○ |
| St. Andrew Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| Choctawhatchee Bay | ○ | ○ | ○ | ○ | ○ |
| Pensacola Bay | ○ | ○ | ○ | ○ | ○ |
| Perdido Bay | √ | √ | √ | √ | √ |
| Mobile Bay | | | | | |
| Mississippi Sound | ◉ | ◉ | ◉ | ◉ | ○ |
| Lake Borgne | ○ | ● | ◉ | ● | ● |
| Lake Pontchartrain | ○ | ○ | ○ | ○ | ○ |
| Breton/Chandeleur Sounds | | | | | |
| Mississippi River | | | | | |
| Barataria Bay | √ | | √ | | |
| Terrebonne/Timbalier Bays | | | | | |
| Atchafalaya/Vermilion Bays | | | | | |
| Calcasieu Lake | | | | | |
| Sabine Lake | | | | | |
| Galveston Bay | √ | √ | √ | √ | √ |
| Brazos River | na | na | na | na | na |
| Matagorda Bay | ○ | ○ | ○ | ○ | ○ |
| San Antonio Bay | √ | √ | √ | √ | √ |
| Aransas Bay | ○ | ○ | ○ | ○ | ○ |
| Corpus Christi Bay | ○ | ○ | ○ | ○ | ○ |
| Laguna Madre | ◉ | ◉ | ◉ | ◉ | ◉ |
| Baffin Bay | ◉ | ◉ | ◉ | ◉ | ◉ |
| | A | S | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present
- na No data available

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

6.1 m (Breder 1942, Springer and Woodburn 1960, Springer and McErlean 1961, Huh 1984). They are found in association with pigfish (*Orthopristis chrysopteris*), gulf pipefish (*Syngnathus scovelli*), and dusky pipefish (*Syngnathus floridae*) (Hildebrand 1954).

Substrate: Adults are primarily collected over muddy bottoms of grass beds, but they also occur over sand bottoms with covering vegetation such as mangrove roots or seagrasses (*Thalassia*). They can also occur over bottoms of sand, and mud with shell (Bailey et al. 1954, Kilby 1955, Tabb and Manning 1961, Tabb et al. 1962, Dawson 1969, Wang and Raney 1971, Zimmerman 1969, Lee et al. 1980, Huh 1984).

Physical/Chemical Characteristics:
Temperature: Egg development has been observed from 15.5° to 18.5°C (Fritzsche 1978). Temperature tolerances are unknown for both larvae and juveniles. Adults have been collected over a range of 10.0° to 34.8°C (Bailey et al. 1954, Reid 1954, Springer and Woodburn 1960, Dawson 1966, Wang and Raney 1971, Bonin 1977, Fritzsche 1978). Peak abundance has been reported to occur at an average temperature of 23°C (Krull 1976, Bonin 1977).

Salinity: Salinity tolerances of eggs, larvae, and juveniles are not well known. Adults have been found over a wide salinity range, occurring from 2.1 to 37.6‰. They are reported to prefer intermediate to moderately high salinities ranging from 22 to 32‰ (Bailey et al. 1954, Reid 1954, Kilby 1955, Gunter 1956, Springer and Woodburn 1960, Tabb et al. 1962, Dawson 1966, Wang and Raney 1971, Bonin 1977, Lee et al. 1980, Loftus and Kushlan 1987).

Movements and Migrations: The code goby is thought to reside throughout the year in seagrass beds (Zimmerman 1969), with no reported migratory behavior. Some movements associated with temperature fluctuations have been observed (Huh 1984, Krull 1976). Studies in Florida bays report movement of this fish to shore during the coldest months, and then back out into bays as temperatures increase (Kilby 1955, Reid 1954).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, and development is oviparous.

Spawning: Spawning has been observed throughout the year in the Gulf of Mexico particularly during late spring and early summer with a peak reported in May (Dawson 1966, Dokken et al. 1984, Huh 1984). This extended spawning season may be due to the short mild winters found in the study area coupled with frequent warming periods. Variations in spawning behavior are possibly due to the different temperature patterns found throughout the range of this species (Dawson 1966, Dokken et al. 1984). Temperatures greater than 19°C may be necessary for spawning to occur, but repression has been noted at temperatures greater than 30°C in Florida populations (Springer and McErlean 1961, Dokken et al. 1984). Spawning occurs during falling salinities (<45‰) in Texas (Dokken et al. 1984) and from 19.2 to 23.0‰ in Florida populations (Springer and McErlean 1961). Eggs are usually attached to the underside of shells or sponges and are guarded by males (Breder 1942).

Fecundity: Both left and right ovaries ripen equally with approximately equal numbers of eggs. In Tampa Bay, a 27 mm standard length (SL) female was reported with 349 eggs in the right ovary, and 346 eggs in its left. The number of eggs produced appears to be related to the size of the female with 56 per ovary observed in a 15 mm SL fish and 397 per ovary observed in a 28 mm SL fish. Eggs are apparently spawned *in toto*, but two spawnings per season are considered possible (Springer and McErlean 1961).

**Growth and Development**

Egg Size and Embryonic Development: Ovarian eggs are transparent until a diameter of 0.102-0.136 mm is attained, and then they become more opaque. Eggs are ripe at 0.476-0.782 mm (Springer and McErlean 1961). Fertilized eggs are elliptical, opaque, slightly yellowish with a clear envelope. Their length varies from 1.30-1.40 mm in June to 1.55-1.70 mm in March, while width varies from 0.50 mm in June to 0.60-0.70 mm in March (Breder 1942, Fritzsche 1978). Eggs are fastened by filaments attached to the chorion at the germinal end, and have an opaque, slightly yellowish yolk with a widely variable number of oil droplets scattered over its surface (Springer and McErlean 1961, Fritzsche 1978). In fertilized eggs of unknown age collected on March 14, near Charlotte Harbor, Florida, the head was large and prominent 22.25 hours after collection. After another 26.25 hours, the embryo formed, somites were visible after another 41.25 hours, and the heart was visible and beating after another 27.5 hours. Total observation period covered 117.25 hours with the embryos dying before hatching (Breder 1942, Fritzsche 1978).

Age and Size of Larvae: Little information is available on the larval stage of this species.

Juvenile Size Range: Described specimens of juvenile code goby are 5.6 to 8.78 mm SL (Shropshire 1932, Springer and McErlean 1961). All fin elements are present by 5.6-8.5 mm SL (Springer and McErlean). Increase in pigmentation, appearance of tubular nostrils and a series of rows of papillae on lower jaw, forehead, and cheeks occur by 8.78 mm SL (Shropshire 1932). Growth rate is moderate with 0-class fish reaching 26.9 to 28.4 mm total length (TL) by the end of their first year (Springer and Woodburn 1960, Dawson 1966).

Age and Size of Adults: Young of the year can achieve sexual maturity when only a few months old. Minimum sizes noted for sexually mature adults are 13.1 mm TL and 14.6 mm SL for females (Springer and McErlean 1961, Dawson 1966), and 16.5 mm TL for males (Fritzsche 1978). Maximum reported sizes are 31.5 mm TL for females (Dawson 1966), and 44 mm SL for males with males being larger on the average than females (Springer and McErlean 1961). Maximum reported size for this species is 55.5 mm TL or 45.0 mm SL for an unsexed fish (Ginsburg 1933). The code goby is considered an annual fish with very few individuals living over one year, although some males are reported to live up to 2 years (Springer and McErlean 1961).

**Food and Feeding**

Trophic mode: The code goby is a small benthic predator.

Food Items: Code gobies feed principally on amphipods, mysids, chironomid larvae, decapod shrimp, copepods, isopods, gamarids, cladocerans, ostracods, small molluscs, and some algal filaments and detritus when 15 to 35 mm SL (Reid 1954, Springer and Woodburn 1960, Odum 1971). Smaller individuals, 7-15 mm SL, have been found to eat harpacticoid copepods, juvenile mysids, cumaceans, and many penate diatoms (Odum 1971).

**Biological Interactions**

Predation: Reported predators include inshore lizardfish (*Synodus foetens*), spotted seatrout, and gray snapper (Springer and Woodburn 1960, Tabb and Manning 1961, Thayer et al. 1987).

Factors Influencing Populations: The size and abundance of seagrass beds and drift algae biomass may affect the abundance of the code goby by providing both habitat and refuge for this species (Kulczycki et al. 1981).

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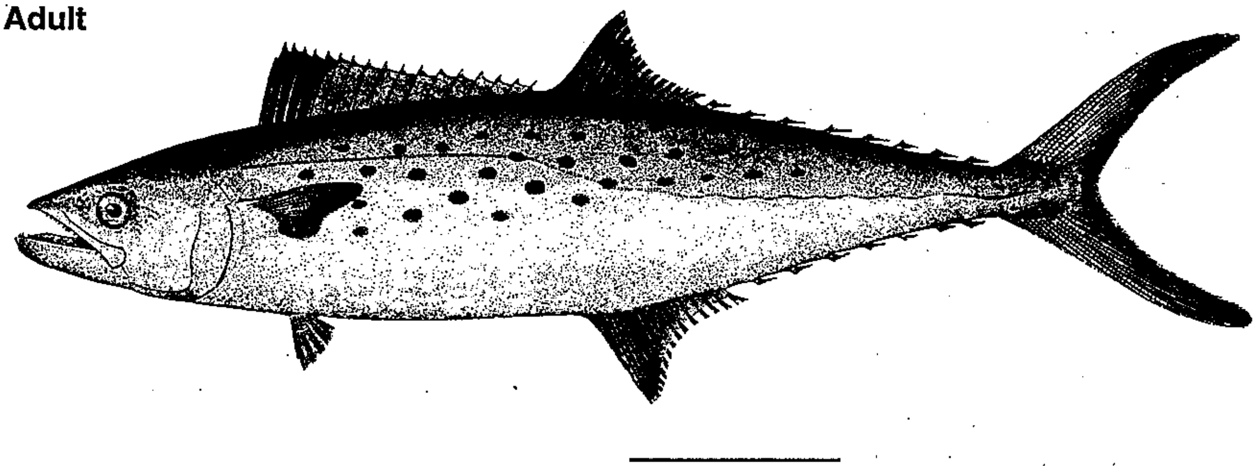
# Spanish mackerel

*Scomberomorus maculatus*
**Adult**




(from Goode 1884)

**Common Name:** Spanish mackerel
**Scientific Name:** *Scomberomorus maculatus*
**Other Common Names:** mackerel, horse mackerel, bay mackerel, spotted mackerel, Spaniard, spotted cybium (Earll 1883, Pew 1966); *thazard tachete* (French); *carite pintado, sierra* (Spanish) (Fischer 1978, NOAA 1985).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Perciformes
Family: Scombridae

**Value**
Commercial: This is a prized commercial species. Most fishing occurs along the south Atlantic coast from Cape Hatteras, North Carolina to the Florida Keys, and in the eastern Gulf of Mexico from the Florida Keys to the Mississippi River delta (Moe 1972, Dwinell and Futch 1973, Powell 1975, Trent and Anthony 1978, Sutherland and Fable 1980, Johnson 1981, Fable et al. 1987, Palko et al. 1987). The fishery is seasonal, and peak harvest periods vary in different areas of the Gulf (Collette and Nauen 1983, Klima pers. comm.). Commercial landings for the Gulf of Mexico in 1992 were 804.2 mt with 152.4 mt landed 0 to 4.8 km offshore and 651.8 mt landed 4.8 to 322 km offshore (Newlin 1993). Florida produced nearly 90% of the commercial catch with landings totaling about 709 mt in 1992. The peak harvest in Florida has historically been from December through February (Klima pers. comm.). However, the commercial fishery in Florida has been practically eliminated by a recent net ban (DeVries pers. comm.). Landings in Alabama, Mississippi, and Louisiana for 1992 were 66.7, 2.3, and 26.3 mt respectively (Newlin 1993), while annual landings in Texas have been less than 907 kg (Dwinell and Futch 1973, Hoese and Moore 1977, Trent and Anthony 1978). The principal commercial gear used has been run-around gill nets with some hook and line catches, but in Mississippi most of the commercial harvest comes as bycatch from shrimping trawls in offshore waters (Klima 1959, Trent and Anthony 1978, Sutherland and Fable 1980, Benson 1982). In U.S. federal waters of the Gulf of Mexico, regulations have been enacted pertaining to minimum size, gear type, harvest quotas, and closed season (GMFMC 1996a). Most of the catch is marketed fresh, frozen, or smoked (Collette and Nauen 1983, Shipp 1986). The flesh becomes rancid very quickly, and is often treated with antioxidants and EDTA to prolong shelf life.

Recreational: Spanish mackerel is an important game fish along the U.S. Atlantic and Gulf of Mexico coasts. It is prized for both its fighting ability and high food quality (Klima 1959, Moe 1972, Dwinell and Futch 1973, Powell 1975, Hoese and Moore 1977, Trent and Anthony 1978, Sutherland and Fable 1980, Johnson 1981, Benson 1982, Fable et al. 1987). The most productive recreational fishing area is along the Atlantic coast from Cape Hatteras, North Carolina to the Florida Keys, followed by the eastern Gulf of Mexico from the Florida Keys to the Mississippi River, and then from the Mississippi River to the Mexican border in waters $\leq$4.8 km from shore. The principal fishing method is hook and line while trolling or drifting, with some catches in Florida made from boats, piers, jetties, and beaches by casting, live bait fishing, jigging, and drift fishing (Trent and Anthony 1978, Palko et al. 1987). Regulations for recreational fishing of this species vary among the Gulf states (GSMFC 1993). Minimum length and bag limits have also been enacted

Table 5.42. Relative abundance of Spanish mackerel in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ○ | | ○ | | |
| Ten Thousand Islands | ○ | | ○ | | |
| Caloosahatchee River | √ | | √ | | |
| Charlotte Harbor | ○ | | ○ | | |
| Tampa Bay | ○ | | √ | | |
| Suwannee River | √ | | ○ | | |
| Apalachee Bay | √ | | √ | | |
| Apalachicola Bay | √ | | √ | | |
| St. Andrew Bay | ◉ | | ◉ | | |
| Choctawhatchee Bay | ○ | | ○ | | |
| Pensacola Bay | ○ | | ○ | | |
| Perdido Bay | ◉ | | ○ | | |
| Mobile Bay | ○ | | ○ | | |
| Mississippi Sound | ◉ | √ | ○ | √ | √ |
| Lake Borgne | | | √ | | |
| Lake Pontchartrain | | | √ | | |
| Breton/Chandeleur Sounds | ○ | | ○ | | |
| Mississippi River | | | √ | | |
| Barataria Bay | ○ | | ○ | | |
| Terrebonne/Timbalier Bays | √ | | ○ | | |
| Atchafalaya/Vermilion Bays | | | ○ | | |
| Calcasieu Lake | | | ○ | | |
| Sabine Lake | ○ | | √ | | |
| Galveston Bay | | | ○ | | |
| Brazos River | | | √ | | |
| Matagorda Bay | | | √ | | |
| San Antonio Bay | √ | | √ | | |
| Aransas Bay | √ | | √ | | |
| Corpus Christi Bay | √ | | √ | | |
| Laguna Madre | | | √ | | |
| Baffin Bay | | | | | |
| | A | S | J | L | E |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

in U.S. federal waters of the Gulf of Mexico (GMFMC 1996b).

Indicator of Environmental Stress: This species, along with others, has been used to study heavy metal contamination in marine fish. No levels of contamination were found that might constitute a threat to public health (Meaburn 1978).

Ecological: This is a high trophic level, pelagic carnivore that feeds predominantly on fish in the marine environment and in higher salinity, seaward portions of estuaries (Benson 1982, Shipp 1986, NOAA 1993).

**Range**

Overall: This species is distributed along the western Atlantic coast from Nova Scotia to Florida, along the north coast of Cuba, and in the Gulf of Mexico from the Florida Keys to the Yucatan Peninsula, Mexico (Erdman 1949, Powell 1975, Collette and Russo 1978, Collette et al. 1978, Sutherland and Fable 1980, Collette and Nauen 1983, Shipp 1986, Fable et al. 1987, Gilhen and McAllister 1989). This is a summer visitor all along the U.S. Atlantic coast as far north as New York, and occurs less regularly along the southern coasts of New England. It occasionally strays into colder waters northward with captures of single fish reported from Maine (Bigelow and Schroeder 1953) and Nova Scotia (Gilhen and McAllister 1989), but is most common in subtropical and tropical coastal waters (Shipp 1986). The center of abundance appears to be the Atlantic coast of Florida (Dwinell and Futch 1973, Trent and Anthony 1978, Fable et al. 1987). Populations of the Gulf of Mexico and Atlantic may comprise two distinct stocks (Johnson 1981, Skow and Chittenden 1981).

Within Study Area: The Spanish mackerel occurs from the Florida Keys to the Rio Grande River (Table 5.42), but is generally less common west of the Mississippi River delta (Dwinell and Futch 1973, Collette and Russo 1978, Fable et al. 1987).

**Life Mode**

The Spanish mackerel is an epipelagic and neritic species and is often found in large schools (Higgins and Lord 1926, Franks et al. 1972, Moe 1972, Christmas and Waller 1973, Powell 1975, Rice 1979, Benson 1982, Collette and Nauen 1983). Schools occur near the water surface and, in the past, have covered several square kilometers of area (Berrien and Finan 1977). Activity and feeding appear to be evenly distributed between day and night (Tabb and Manning 1961, Zimmerman 1969, Moe 1972).

## Habitat

Type:

Larvae occur most frequently offshore over the inner continental shelf (12 to 34 m) in polyhaline to euhaline waters (Wollam 1970, McEachran and Finucane 1978). Abundance appears to be greatest in the northeastern Gulf of Mexico (Lukens 1989). The most frequent collections of larvae are made in water depths ranging 5.0 to 12.8 m, but larvae have been found in waters as deep as 91.5 m (Dwinell and Futch 1973, Lyczkowski-Shultz 1987).

Juveniles are found offshore and in beach surf. They are sometimes reported from lower river outflows, estuaries, sounds, bays, lagoons, and marshes, but are generally not considered estuarine dependent (Gunter 1945, Baughman 1947, Reid 1956a, Reid 1956b, Zimmerman 1969, Swingle 1971, Franks et al. 1972, Christmas and Waller 1973, Dwinell and Futch 1973, McEachran and Finucane 1978, Benson 1982, Lukens 1989). They occur in oligohaline to euhaline salinities, but appear to prefer euhaline water (Gunter 1945, Reid 1956, Franks et al. 1972, Christmas and Waller 1973, Dwinell and Futch 1973, McEachran and Finucane 1978). Most juveniles are collected from waters 9.1 to 18.3 m deep, but collection depths can range from the surface down to 91.5 m (Franks et al. 1972, Dwinell and Futch 1973).

Adults are typically found offshore in neritic waters and along coastal areas, usually very near barrier islands and particularly their passes. They frequent shallower depths and are seldom found deeper than 73.2 m (Earll 1883, Higgins and Lord 1926, Gunter 1945, Klima 1959, Springer and Woodburn 1960, Pew 1966, Franks et al. 1972, Christmas and Waller 1973, Rice 1979). In Florida, most inhabit coral reefs, off-shore currents, and tide rips of clear tropical waters (Klima 1959, Moe 1972). Adults are seldom taken near river mouths or in low salinity waters (Earll 1883), but one study from Florida reports that they enter tidal rivers on flood tides to feed on shrimp migrating seaward (Tabb and Manning 1961). One fish has also been captured in the tidal portion of a south Texas river (Bryan 1971). They will enter estuaries and bays, especially high salinity areas, during seasonal migrations, but are considered rare and infrequent in many Gulf estuaries (Reid 1956a, Simmons 1957, Klima 1959, Parker 1965, Pew 1966, Zimmerman 1969, Powell 1975, Benson 1982). They are collected from salinities ranging from oligohaline to euhaline with an apparent preference for euhaline waters (Gunter 1945, Reid 1956a, Franks et al. 1972, Christmas and Waller 1973, Dwinell and Futch 1973, McEachran and Finucane 1978).

Substrate: Juvenile mackerel seem to prefer clean sand (Benson 1982), but substrate preferences for other life stages of this pelagic fish have not been reported.

Physical/Chemical Characteristics:

Temperature: This species prefers warmer waters, and generally favors water temperatures 20° C or greater (Shipp 1986). Larvae are found in the northwestern Gulf of Mexico from 19.6° to 29.8°C, and are reported to prefer ranges of 21° to 27°C and 20.2° to 29.8°C (McEachran and Finucane 1978, Benson 1982). They have been found in Florida from 28.4° to 30.5°C (Dwinell and Futch 1973). Juveniles occur over a range from 10° to 34.9°C (Gunter 1945, Perret et al. 1971, Wang and Raney 1971, Franks et al. 1972, Christmas and Waller 1973, Dwinell and Futch 1973, Perret and Caillouet 1974). The occasional appearances of juveniles in Texas bays seem to be limited to waters above 24°C (Zimmerman 1969), and they are most abundant in samples at 25°C or higher (Perret et al. 1971). Adults have been reported occurring over a range of 21° to 32°C and to seldom enter waters below 18°C (Earll 1883, Gunter 1945, Springer and Woodburn 1960, Fritzsche 1978).

Salinity: Salinities at larvae collection sites range from 28.3 to 37.4‰ (Dwinell and Futch 1973, McEachran and Finucane 1978, Benson 1982), and larvae are most abundant at 28.3 to 34.4‰ (McEachran and Finucane 1978). Juveniles can be found over a salinity range of 0.21 to 37.4‰ (Kelley 1965, Dugas 1970, Bryan 1971, Perret et al. 1971, Swingle 1971, Wang and Raney 1971, Franks et al. 1972, Christmas and Waller 1973, Dwinell and Futch 1973, Perret and Caillouet 1974), but occur most often in salinities exceeding 10‰ (Perret et al. 1971, Swingle 1971, Benson 1982). Adults are generally associated with marine salinities (Fritzsche 1978), and reported salinities range from 31.1 to 36.7‰ in Texas and Florida (Gunter 1945, Springer and Woodburn 1960).

Movements and Migrations: This species migrates seasonally. Its movements are along coastlines and can be extensive, depending on water temperature (Powell 1975, Moe 1972, Benson 1982, Collette and Nauen 1983). Three major migration routes are hypothesized: along the Mexican-Texan coast; along the northern Gulf of Mexico coast and west coast of Florida; and along the Atlantic (Johnson 1981). In the eastern Gulf, these fish move northward in the Gulf during late winter and spring appearing off the central west coast of Florida about the first of April (Moe 1972, Sutherland and Fable 1980). Movements continue westward and terminate along the northern Gulf coast. During fall, migration is back southward to the wintering grounds in south Florida waters (Moe 1972, Sutherland and Fable

1980). In the western Gulf, spring migration apparently occurs as schools move to the north and east along the coast (Wollam 1970, Benson 1982). This movement also terminates in the northern Gulf of Mexico, with abundant numbers off Alabama and Mississippi from April through late fall, and in Texas from March to October with an August peak (Gunter 1945, Springer and Pirson 1958, Pew 1966, Franks et al. 1972, Helser and Malvestuto 1987). Movement in the fall is back southward beginning about September (Gunter 1945, Wollam 1970, Benson 1982). The wintering ground for both eastern and western fish is believed to be in the Campeche-Yucatan area (Sutherland and Fable 1980, Johnson 1981). Fish are caught throughout the year, indicating that some fish move offshore during cold weather and do not migrate (Perret et al. 1971, Moe 1972, Christmas and Waller 1973).

**Reproduction**

Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe into the water column (Berrien and Finan 1977). Development is oviparous.

Spawning: The onset of spawning probably varies with latitude, with fish in the northern part of the range ripening later than those in the southern part (Berrien and Finan 1977). Active and ripening oocytes are present throughout the spring and summer (April through mid-September) in Florida, with spawning probably occurring May through September (Klima 1959, Moe 1972, Powell 1975, Berrien and Finan 1977, Schmidt et al. 1993). In the western Gulf of Mexico, developing gonads are seen May through September when water temperatures reach 22°C, and spent individuals become increasingly abundant from July to September (Earll 1883, Hoese 1965, Wollam 1970, Rice 1979, Finucane and Collins 1986, Lyczkowski-Shultz 1987). Some spawning may occur in April or October and spawning throughout the year is considered possible in Florida (Finucane and Collins 1986). Based on the presence of larval Spanish mackerel in the northern Gulf of Mexico, it can be inferred that spawning occurs April through October, with a peak from August to September (Ditty 1986, Ditty et al. 1988). Spawning can occur day or night with multiple spawnings possible over a prolonged season (Ryder 1882, Klima 1959, Powell 1975, Benson 1982, Collette and Nauen 1983, Lyczkowski-Shultz 1987). Spawning takes place in inner shelf waters probably in the vicinity of barrier islands and passes at depths of 12 to 18 m. Spawning also occurs occasionally over the middle and outer shelf, possibly as deep as 200 m (McEachran and Finucane 1978, Benson 1982). Spawning temperatures range from 21 to 31°C, but are usually in excess of 22°C and seldom below 18°C (Hoese 1965, Benson 1982). Salinities for spawning range from 30 to 36.5‰ (Hoese 1965, Benson 1982). Peak spawning seems to be during June through August with the eastern and northeastern Gulf of Mexico probably being the most important spawning area (Klima 1959, Moe 1972, McEachran and Finucane 1978). There is some evidence of spawning near Mississippi Sound (Lukens 1989).

Fecundity: This species is a fractional spawner (Berrien and Finan 1977). Fish in south Florida are sexually mature in their second or third year of life according to otolith annulations counted in one study (Klima 1959). Another investigator considers these observations to have been overestimated by one year; therefore, fish less than 1 year old may have been mature (Powell 1975). Many class I fish observed had ripe oocytes, but examinations made of these fish during the spawning season suggested eggs were not advanced enough to be spawned that season. Spanish mackerel are probably not fully mature until age class II with the bulk of the spawning population composed of class III and older fish (Powell 1975, Lukens 1989). Fecundity increases with length and weight (Earll 1883, Godcharles and Murphy 1986). Estimates of fecundity are 1.5 million for a 2.7 kg female while a 0.45 kg fish had an estimated 300,000 eggs (Earll 1883). Fecundity ranges from 100,000 to 2,000,000 eggs for fish ranging 295 to >2,415 g and with fork lengths (FL) of 312 mm to 626 mm (Berrien and Finan 1977, Finucane and Collins 1986).

**Growth and Development**

Egg Size and Embryonic Development: Development is oviparous. Eggs are buoyant, transparent and smooth with a single oil droplet 0.25 mm in diameter. They are round in shape and 0.91-1.15 mm in diameter (Earll 1883, Ryder 1882, Benson 1982). The perivitelline space is approximately 0.1 mm across. Hatching is primarily during summer months and occurs about 25 hours after fertilization at 26°C (McEachran and Finucane 1978, Fritzsche 1978, Godcharles and Murphy 1986).

Age and Size of Larvae: The larval stage lasts from 2.56 to 13 mm TL. Larvae are 2.56 mm TL or 2.0 mm standard length (SL) at hatching and attain 2.8 SL within 3 days (Fritzsche 1978, McEachran and Finucane 1978). Other investigators have reported preserved specimens ranging in size from 1.6 to 11.8 mm SL (Richardson and McEachran 1981, Lyczkowski-Shultz 1987). The yolk sac is absorbed by 3.18 mm TL on the fourth day (Wollam 1970, Fritzsche 1978). Larval growth rate has been estimated as 1.15 mm/day (DeVries et al. 1990).

Juvenile Size Range: Juveniles range from 13.5 to 225 mm TL in size. Eight preopercular spines are present at 14 mm TL, and two at 22-25 mm TL (Fritzsche 1978, Lukens 1989). Females mature at lengths ranging from 250 mm to 450 mm FL, while males can reach maturity anywhere from 209 mm to 336 mm FL. The longest immature fish were a 320 mm FL female and a 340 mm FL male. Some age class 0 fish reach sexual maturity, but 100% maturity of a cohort is not reached until at least age class II for males and age class III for females. The majority of spawning fish is probably made up of age class III fish >350 mm FL (Powell 1975, Helser and Malvestuto 1987, Lukens 1989, Schmidt et al. 1993).

Age and Size of Adults: The average weight range of fish taken by recreational and commercial anglers is 0.7-1.8 kg, with most larger fish averaging about 4-5 kg. The maximum reported weight is 11 kg (Pew 1966, Meaburn 1978, Benson 1982). Growth rates among adults are rapid until year 5 in females and year 6 in males, and then slow appreciably (Fable et al. 1987). Females reach up to 802 mm FL and grow faster than males which have been recorded up to 723 mm FL (Collette and Russo 1978, Fable et al. 1987). Maximum life spans reported for Spanish mackerel have been 11 years for females and 7 years for males (Collette and Russo 1978, Fable et al. 1987, Schmidt et al. 1993). However, males have been reported up to 10 years in Florida (DeVries pers. comm.). It is believed that females generally live longer than males (Fable et al. 1987). Von Bertalanffy growth equations have been developed from otolith samples for male and female Spanish mackerel (Helser and Malvestuto 1987, Schmidt et al. 1993).

**Food and Feeding**

Trophic mode: The Spanish mackerel is a fast moving surface feeder in pelagic waters, and is primarily piscivorous (Finucane et al. 1990).

Food Items: The Spanish mackerel is a fast moving voracious predator. They usually feed in loose schools, and feed on schooling prey that occupy the same pelagic habitat, including herrings and sardines (Clupeidae), jacks (Carangidae), anchovies (Engraulidae), and squids (Saloman and Naughton 1983, Shipp 1986 Lukens 1989, Finucane et al. 1990). Shallow continental shelf waters are the favored feeding areas, but the mackerel will occasionally forage in the lower, saltier portions of estuaries. Larvae and post larvae are principally piscivorous (Finucane et al. 1990). Larval jacks, herrings, and anchovies occur frequently in larval mackerel stomach contents. Other fish species consumed by mackerel larvae include: lanternfishes, flatfishes, and puffers. Fish eggs were also found to be a food item as well as invertebrates such as nudibranch larvae, amphipods, penaeid shrimp, and euphausiids. Older juveniles and adults prefer various small fish which can form up to 100% of their diet. Juveniles and small adults (70-420 mm FL) prey chiefly on various anchovies, and also herrings and wrasses. Larger adults (525-675 mm FL) consume other fishes mainly herrings and jacks (Saloman and Naughton 1983, Lukens 1989, Finucane et al. 1990). Spanish mackerel probably become more opportunistic as they increase in size with food items varying according to availability. Other animals such as squid, crabs, and shrimp can become important diet components at this point (Saloman and Naughton 1983, Pew 1966, Rice 1979, Benson 1982). Fish that are preyed on include: sciaenids, alewife, flatfish, menhaden, cutlassfish (*Trichiurus lepturus*), scaled sardine (*Harengula jaguna*), Atlantic thread herring (*Opisthonema oglinum*), Spanish sardine (*Sardinela aurita*), striped mullet and other mullet, needlefish (*Strongylura* spp.), jacks (*Caranx* spp.), lookdown (*Selene vomer*), inland silverside (*Menidia beryllina*) and other silversides, striped anchovy (*Anchoa hepsetus*) and other anchovies, butterfish (*Peprilus triacanthus*), northern harvestfish (*Peprilus paru*), spadefish (*Chaetodipterus faber*), silver perch, and round scad (*Decapturas punctatus*) (Earll 1883, Kemp 1949, Breuer 1949, Knapp 1949, Miles 1949, Simmons and Breuer 1964, Pew 1966, Rice 1979, Naughton and Saloman 1981, Lukens 1989, Finucane et al. 1990). Anchovies may be more important in juvenile diets because of their smaller size being more easily swallowed by the smaller juvenile mackerel mouth parts (Naughton and Saloman 1981). Important invertebrate components include various penaeid shrimp (white, pink, and brown shrimp), sealice (*Squilla* sp.), grass shrimp (*Palaemonetes* sp.), sand shrimp (*Crangon* sp.), squid (*Loligo* sp.), swimming crabs (Portunidae), and mud crabs (Xanthidae) (Kemp 1949, Miles 1949, Naughton and Saloman 1981, Saloman and Naughton 1983).

**Biological Interactions**

Predation: This species is a major prey item of sharks, including bull shark, dusky shark (*C. obscurus*), smooth hammerhead (*Sphyrna zygaem*), porbeagle (*Lamna nasas*), tiger shark (*Galeocerdo cuvieri*); and also of dolphins (*Tursiops truncatus*) (Kemp 1949, Lukens 1989).

Factors Influencing Populations: A potential exists for damage of eggs and larvae present near the water surface by oil pollution (Lukens 1989). The popularity of this species as a food and game fish may have contributed to a decline in its abundance.

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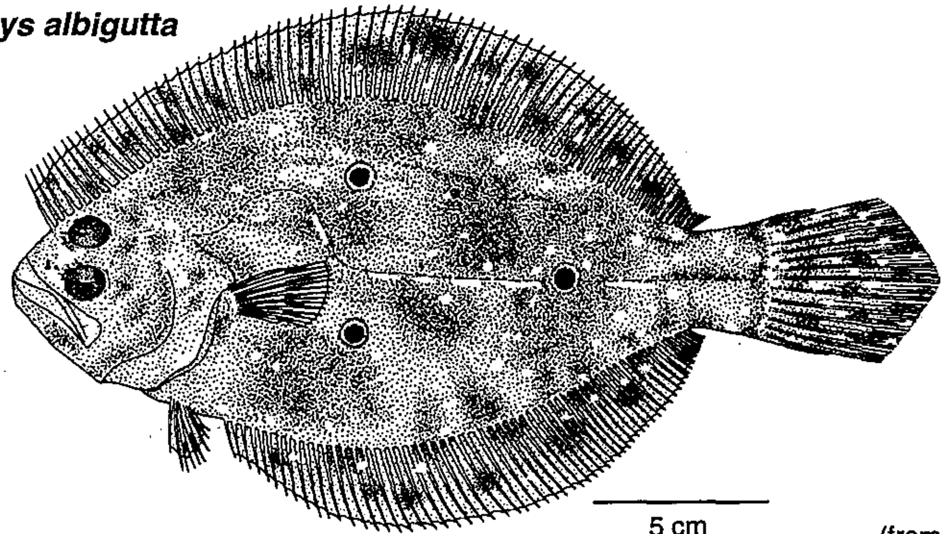
# Gulf flounder




(from Fischer 1978)

**Common Name**: gulf flounder
**Scientific Name**: *Paralichthys albigutta*
**Other Common Names**: sand flounder, flounder, fluke, *cardeau trois yeux* (French), and *lenguado tresojos* (Spanish) (Ginsburg 1952, Fischer 1978, NOAA 1985, Gilbert 1986).
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Pleuronectiformes
Family: Bothidae

**Value**
Commercial: In 1992, U.S. commercial fishery landings for flounders were fifth in quantity and eighth in value (O'Bannon 1994). Flounder landings in the Atlantic and Gulf for the group that includes this species totaled 7,098 mt and was valued at nearly 23 million dollars. The Gulf flounder contributes a varying amount to this commercial catch recorded as "fluke", depending on location. This is an important commercial species in Florida, but much less so in the other Gulf coastal states (Swingle 1971, Fischer 1978, Benson 1982, NOAA 1985, Van Voorhees et al. 1992). In 1992, approximately 77.6 mt of flounders were landed in Florida with a value of over $175,000 (Newlin 1993). Most fish are taken by otter trawls, fyke nets, weirs, fish traps, pound nets, gill nets, trammel nets, beach seines, and gigging (Ginsburg 1952, Fischer 1978, Manooch 1984). Gill and trammel nets were outlawed in Texas waters in 1988. Many are taken incidentally by commercial shrimpers (Fischer 1978, Benson 1982). Catches are marketed as either fresh or frozen product (Fischer 1978, NOAA 1985).

Recreational: Gulf flounder are more important as a game fish than as a commercial species, although most anglers do not preferentially seek them. Fish are taken by bottom fishing with hook and line, and by gigging in shallow waters at night (Warlen 1975, Manooch 1984). In 1991, reported recreational landings of gulf flounder for the Gulf coast states (except Texas) totaled 284,000 fish, most of which were landed in Florida (241,000 fish) (Van Voorhees et al. 1992). Actual sport catches were probably greater as a large number of unidentified "flounders" were also reported during the same period. Minimum size and daily bag limits may vary among the Gulf states (GSMFC 1993).

Indicator of Environmental Stress: Gulf flounder are not typically used in studies of environmental stress.

Ecological: Although this species is not especially abundant in most areas, it is important as a demersal carnivore.

**Range**
Overall: The gulf flounder is found from Oregon Inlet, North Carolina (Powell pers. comm.), to the waters off Padre Island, Texas, including the upper Laguna Madre. It is also reported from the western Bahamas (Hoese and Moore 1977, Shipp 1986). It is not known to occur in the coastal waters of Mexico (NOAA 1985).

Within Study Area: In U.S. Gulf of Mexico estuaries, gulf flounder occur from Florida Bay to Mississippi Sound, but not in the low salinity estuaries of Louisiana (Table 5.43). They occur in small numbers in Texas westward to the Rio Grande (Topp and Hoff 1972, Shipp 1986).

Table 5.43. Relative abundance of gulf flounder in 31 Gulf of Mexico estuaries (from *Volume I*).

| Estuary | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | ○ | | ○ | ○ | |
| Ten Thousand Islands | ○ | | ○ | | |
| Caloosahatchee River | √ | | √ | | |
| Charlotte Harbor | ○ | | ○ | ○ | |
| Tampa Bay | ○ | | ○ | | |
| Suwannee River | ○ | | ○ | ○ | |
| Apalachee Bay | ○ | | ○ | ○ | |
| Apalachicola Bay | ○ | | ○ | ○ | |
| St. Andrew Bay | ◉ | | ◉ | ○ | |
| Choctawhatchee Bay | ○ | | ○ | ○ | |
| Pensacola Bay | ○ | | ○ | ○ | |
| Perdido Bay | ○ | | ○ | ○ | |
| Mobile Bay | √ | | ○ | ○ | |
| Mississippi Sound | ○ | ○ | ○ | ○ | ○ |
| Lake Borgne | | | | | |
| Lake Pontchartrain | | | | | |
| Breton/Chandeleur Sounds | | | | | |
| Mississippi River | | | | | |
| Barataria Bay | | | | | |
| Terrebonne/Timbalier Bays | | | | | |
| Atchafalaya/Vermilion Bays | | | | | |
| Calcasieu Lake | | | | | |
| Sabine Lake | | | | | |
| Galveston Bay | √ | | √ | | |
| Brazos River | | | | | |
| Matagorda Bay | √ | | √ | | |
| San Antonio Bay | √ | | √ | | |
| Aransas Bay | √ | | √ | | |
| Corpus Christi Bay | √ | | √ | | |
| Laguna Madre | √ | | √ | | |
| Baffin Bay | | | √ | | |

Relative abundance:
- ● Highly abundant
- ◉ Abundant
- ○ Common
- √ Rare
- blank Not present

Life stage:
- A - Adults
- S - Spawning
- J - Juveniles
- L - Larvae
- E - Eggs

**Life Mode**
Eggs and larvae are planktonic. Postlarvae become demersal after metamorphosis. Juveniles and adults are demersal (Bond 1979).

**Habitat**
Type: Eggs are marine and neritic. Larvae are marine and neritic, becoming estuarine. Juveniles and adults are estuarine and marine. Adults are neritic, and are found offshore as far as the mid-continental shelf in depths up to 50 m. They prefer shallow waters (<30 m) of bays and the nearshore Gulf of Mexico (Ginsburg 1952, Miller 1964, Powell 1974, Stokes 1977, Benson 1982). It rarely enters areas with reduced salinities, and never enters freshwater (Gilbert 1986). It is considered probable that gulf flounder in excess of 2 or 3 years of age reside exclusively in the Gulf (Stokes 1977).

Substrate: Gulf flounder typically occur over hard sand bottoms. Juveniles have been reported in association with seagrass beds (Ginsburg 1952, Reid 1954, Springer and Woodburn 1960, Stokes 1977, Fischer 1978, Hoese and Moore 1977).

Physical/Chemical Characteristics:
Temperature: The reported range of temperatures where the Gulf flounder occurs is 8.3° to 32.5° C (Reid 1954, Springer and Woodburn 1960, Wang and Raney 1971, Stokes 1977).

Salinity: This fish ranges from the seawater zone to the seaward end of the mixing zone of estuaries. It reportedly prefers higher salinities (>20‰) (Gunter 1945, Powell and Schwartz 1977). Collections have been reported from salinities ranging from 6 to 60‰ (Reid 1954, Simmons 1957, Springer and Woodburn 1960, Williams and Deubler 1968, Wang and Raney 1971, Topp and Hoff 1972, Powell 1974, Stokes 1977, Powell and Schwartz 1977). Williams and Deubler (1968) reported that postlarvae are found in estuarine habitats at salinities ≥22‰. In North Carolina, juveniles were collected in salinities ranging from 6 to 35‰, but the majority occurred above 20‰ (Powell and Schwartz 1977).

Turbidity: Stokes (1977) stated that Gulf flounder were not present in waters with turbidity greater than 65 Jackson Turbidity Units (JTU).

Migrations and Movements: Adults migrate out of the estuaries to neritic offshore waters during fall and winter to spawn. Timing of the movement is associated with the advent of falling water temperatures. Stokes (1977) reported that the Gulf flounder begins to move offshore when water temperatures fall from 23° to 14.1°C, and that peak immigration of juveniles coincided with temperatures around 16°C. Beginning in late spring to early summer, the adults and juveniles return to the estuarine habitats (Reid 1954, Springer and Woodburn 1960, Stokes 1977).

**Reproduction**
Mode: This species has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe into the water column. The eggs float at or near the surface of the water, and development is oviparous (Gilbert 1986).

Spawning: Spawning occurs during late fall and early winter (November to February) in marine neritic waters (Ginsburg 1952, Reid 1954, Springer and Woodburn 1960, Topp and Hoff 1972, Stokes 1977). Larvae of *Paralichthys* species are known to occur in the northern Gulf of Mexico from September through April, with a peak from December to February (Ditty et al. 1988).

Fecundity: Little information on gulf flounder fecundity is available (Gilbert 1986).

**Growth and Development**
Egg Size and Embryonic Development: Eggs are spawned oviparously. Eggs are spherical, with an approximate mean diameter of 0.87 mm, and one oil globule with an approximate diameter of 0.18 mm (Powell and Henley 1995).

Age and Size of Larvae: Recently-hatched larvae are approximately 2.0 mm notochord length (NL) (Powell and Henley 1995). Larvae appear in the eastern Gulf of Mexico from December through early March (Reid 1954, Topp and Hoff 1972). The standard length (SL) of postlarvae ranges 7-10 mm SL, and averages 8.4 mm (Deubler 1958). A full complement of fin rays is present by approximately 8.5 mm SL (Powell and Henley 1995). In general, at any given size, larval gulf flounder (*P. albigutta*) are further developed than southern flounder (*P. lethostigma*) (Powell and Henley 1995). There are differences in pigmentation patterns between the two species, but these may be difficult to discern with field-collected specimens.

Juvenile Size Range: The growth rate of juveniles up to a size of 50 mm appears to be rapid (Reid 1954), and size-at-age is highly variable for this species (Fitzhugh pers. comm.). Stokes (1977) calculated total length (TL) growth rates of males and females. Males during their first year (age 0) ranged in size from 10 to >300 mm TL, and had an upper weight of 150 g, while those in their second year (age I) ranged 221-350 mm in size with an upper weight of 270 g. In first year females sizes ranged from 10 to 400 mm TL, with an upper weight of 270 g. Maturation occurs around 145 mm SL for females (Topp and Hoff 1972), and 50% of females are mature by age I (Fitzhugh pers. comm.).

Age and Size of Adults: Stokes (1977) noted ripe females were two years old and stated that females grow more rapidly and attain greater sizes than males. Females during their second year range in size from 291 to >400 mm, and have an upper weight of 0.57 kg. Third year females have a size range of 361-420 mm TL and an upper weight of 1.01 kg. The maximum reported size is 710 mm TL with a weight of 5 kg (Topp and Hoff 1972). Actual life spans probably exceed three years (Manooch 1984). Females may live up to seven years, and males up to four years (Fitzhugh pers. comm.). Length-weight relationships for North Carolina gulf flounder have been determined by Safrit and Schwartz (1988).

**Food and Feeding**
Trophic mode: The gulf flounder is a benthic carnivore.

Food Items: Small juveniles, 10-50 mm TL, feed predominantly on invertebrates; mostly crustaceans, especially mysids and amphipods. Juveniles above 45 mm consume both small fish and crustaceans, including penaeid shrimp and portunid crabs. At 100-150 mm TL they are primarily piscivorous. Noted prey include menhaden, bay anchovy and other anchovy species, inshore lizardfish (*Synodus foetens*), longnose killifish (*Fundulus similis*), pipefishes, grunts, pigfish (*Orthopristis chrysoptera*), pinfish, Atlantic croaker, mullets, and code goby (*Gobiosoma robustum*) as well as a number of unidentified forms (Reid 1954, Springer and Woodburn 1960, Topp and Hoff 1972, Stokes 1977, Benson 1982).

**Biological Interactions**
Predation: Information on predation of flounder is scarce. Juveniles are probably the most susceptible to predation due to their smaller size. Known and suspected species that prey on flounder species in the Gulf of Mexico are: tiger shark (*Galeocerdo cuvier*), gafftopsail catfish (*Bagre marinus*), inshore lizard fish (*Synodus foetens*), various searobins (family Triglidae), various sculpins (family Cottidae), jewfish (*Epinephelus itaiara*), and larger-sized southern flounder (Kemp 1949, Miles 1949, Diener et al. 1974, Tanaka et al. 1989).

Factors Influencing Populations: *Paralichthys lethostigma* and *P. albigutta* are very difficult to distinguish from each other during the larval stage (Woolcott et al. 1968). Early stages are often summarized as "*Paralichthys* species" (King 1971, Ditty et al. 1988) or just "southern flounder" (Stokes 1977). Adult southern flounder generally outnumber gulf flounder in the northern Gulf of Mexico, and catches containing the two species are not usually separated. This makes catch data for the two species difficult to analyze. The shrimp fishery unintentionally catches large numbers of juvenile flounder, almost all of which are discarded (Gunter 1945, Matlock 1991). This reduces the number of sexually immature fish available for recruitment into the population and fishery. The gulf flounder appear to be restricted to the higher salinity portions of estuaries (>20‰), unlike the southern flounder (Gilbert 1986, Nelson et al. 1992).

**Personal communications**

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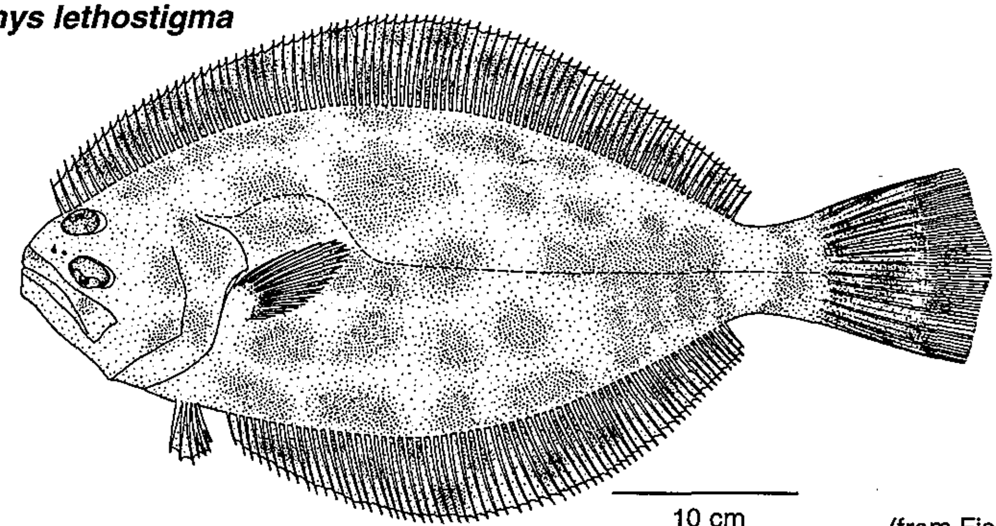
## Southern flounder



(from Fischer 1978)

**Common Name:** southern flounder
**Scientific Name:** *Paralichthys lethostigma*
**Other Common Names:** mud flounder, doormat, halibut (Reagan and Wingo 1985); southern large flounder, fluke (Gilbert 1986), *cardeau de Floride* (French), *lenguado de Florida* (Spanish) (Fischer 1978, NOAA 1985), saddleblanket.
**Classification** (Robins et al. 1991)
Phylum: Chordata
Class: Osteichthyes
Order: Pleuronectiformes
Family: Bothidae

### Value

Commercial: In 1992, U.S. commercial fishery landings for flounders were fifth in quantity and eighth in value (O'Bannon 1994). Flounder landings in the Atlantic and Gulf for the group that includes this species totaled 7,098 mt and were valued at nearly 23 million dollars. The southern flounder is fished commercially throughout its range. Landing data are often grouped with two other species (*Paralichthys albigutta* and *P. dentatus*), making the relative importance of each species difficult to ascertain. In Texas, southern flounder account for most of the flounder caught. In the northwestern Gulf of Mexico, most of the southern flounder catch is landed incidentally in commercial shrimp trawls. In 1992, approximately 451.8 mt of flounders were landed in Texas and Louisiana with a value of over $1.2 million. Most fish are taken by otter trawls, fyke nets, weirs, fish traps, pound nets, gill nets, trammel nets, beach seines, trotlines, and gigging (Ginsburg 1952, Fischer 1978, Manooch 1984, Gilbert 1986, Matlock 1991, Newlin 1993, Hightower pers. comm.). Gill and trammel nets were outlawed in Texas waters in 1988. This fish is marketed mostly as fresh product and is used primarily as table fare (Fischer 1978, Matlock 1991).

Recreational: The southern flounder is a popular recreational species throughout its range (Shipp 1978). Fish are taken by hook and line and by gigging in shallow waters at night (Warlen 1975, Manooch 1984). In 1991, recreational landings of southern flounder along the Gulf coast states (except Texas) was 102,000 fish in Florida, 126,00 fish in Mississippi, and 471,000 fish in Louisiana (Van Voorhees et al. 1992). Estimated recreational landings along the Texas coast, calculated from data provided by Osborn and Fergusson (1987), averaged 94,258 kg from 1983 to 1986. Actual sport catches were probably greater as a large number of unidentified "flounders" were also reported during the same period. Minimum size limits and daily bag limits vary among the Gulf states (GSMFC 1993).

Indicator of Environmental Stress: This species is not typically used in studies of environmental stress.

Ecological: Southern flounder are important predators in estuarine ecosystems, feeding on small crustaceans as juveniles, and becoming piscivorous as they grow (Diener et al. 1974, Fitzhugh et al. 1996). Southern flounder have been introduced into freshwater reservoirs of Texas in an experimental effort to control problem fish populations and improve recreational fishing (Lasswell et al. 1981).

### Range

Overall: On the U.S. east coast, this species ranges from Albermarle Sound, North Carolina, southward to the Loxahatchee River, Florida. In the Gulf of Mexico, it is present from Florida to Texas and northern Mexico

Table 5.44. Relative abundance of southern flounder in 31 Gulf of Mexico estuaries (from *Volume I*).

| *Estuary* | A | S | J | L | E |
|---|---|---|---|---|---|
| Florida Bay | √ | | √ | | |
| Ten Thousand Islands | √ | | √ | | |
| Caloosahatchee River | | | | | |
| Charlotte Harbor | √ | | √ | √ | |
| Tampa Bay | √ | | √ | √ | |
| Suwannee River | ○ | | ○ | ○ | |
| Apalachee Bay | ○ | | ○ | ○ | |
| Apalachicola Bay | ○ | | ○ | ○ | |
| St. Andrew Bay | ○ | | ○ | ○ | |
| Choctawhatchee Bay | ○ | | ○ | ○ | |
| Pensacola Bay | ○ | | ○ | ○ | |
| Perdido Bay | ○ | | ○ | ○ | |
| Mobile Bay | ○ | | ○ | ○ | |
| Mississippi Sound | ◉ | ◉ | ◉ | ◉ | ○ |
| Lake Borgne | ○ | | ○ | | |
| Lake Pontchartrain | ○ | | ○ | | |
| Breton/Chandeleur Sounds | ◉ | | ○ | | |
| Mississippi River | ◉ | | ◉ | | |
| Barataria Bay | ◉ | | ◉ | ○ | |
| Terrebonne/Timbalier Bays | ◉ | | ○ | | |
| Atchafalaya/Vermilion Bays | ○ | | ○ | | |
| Calcasieu Lake | ○ | | ◉ | | |
| Sabine Lake | ● | | ○ | | |
| Galveston Bay | ● | | ○ | | |
| Brazos River | ○ | | ○ | | |
| Matagorda Bay | ◉ | | ○ | | |
| San Antonio Bay | ◉ | | ○ | | |
| Aransas Bay | ○ | | ○ | | |
| Corpus Christi Bay | ○ | | ○ | | |
| Laguna Madre | ○ | | ◉ | | |
| Baffin Bay | ○ | | ○ | | |
| | A | S | J | L | E |

| Relative abundance: | | Life stage: |
|---|---|---|
| ● | Highly abundant | A - Adults |
| ◉ | Abundant | S - Spawning |
| ○ | Common | J - Juveniles |
| √ | Rare | L - Larvae |
| blank | Not present | E - Eggs |

(Hoese and Moore 1977, Lee et al. 1980, Manooch 1984). It is not common in the southwest Florida estuaries, and its range is apparently not continuous around the southern tip of Florida.

Within Study Area: The southern flounder is distributed throughout the coastal and estuarine habitats of the U.S. Gulf of Mexico from Florida to Texas, and is particularly abundant along the Texas coast (Ginsburg 1952, Hoese and Moore 1977, Manooch 1984, Reagan and Wingo 1985, Gilbert 1986) (Table 5.44).

**Life Mode**

Eggs are planktonic, buoyant, and float at or near the surface (Arnold et al. 1977). Larvae are planktonic and can be found throughout the water column (King 1971). King (1971) has shown no difference between night and day larval distributions. Juveniles and adults are demersal, and they are more active at night (Powell and Schwartz 1977).

**Habitat**

Type: Eggs are marine, occurring in neritic waters. Early larval stages are marine, while postlarvae become estuarine. Juveniles and adults are estuarine, riverine and marine in coastal areas usually depending on size of the flounder and hydrography (Fischer 1978, Lee et al. 1980, Shipp 1986). Southern flounder can be found at depths up to about 40 m (Fischer 1978).

Substrate: Southern flounder frequent fine unconsolidated substrates of clayey silts and organic-rich muddy sands (Fischer 1978, Lee et al. 1980, Gilbert 1986, Powell and Schwartz 1977). Juvenile fish have been reported in association with seagrass beds (Stokes 1977). In marshes they appear to be equally abundant in vegetated and non-vegetated habitats (Minello et al. 1989). Juveniles and adults are associated with fine sediments in flooded *Spartina* marshes, seagrasses and muddy substrates while in estuaries (Stokes 1977, Ward et al. 1980).

Physical/Chemical Characteristics:

Temperature: This is a eurythermal species. The reported temperature range for eggs is 9.1 to 22.9°C with 14°C preferred; and for larvae 2 to 30°C with a preferred range of 20 to 25°C (Ward et al. 1980). Juveniles are apparently widespread over water temperatures ranging from 2 to 31.2° C. Adults are found in temperatures ranging from 7 to 32°C and show a preference for temperature between 14 and 22° C (Pineda 1975, Ward et al. 1980, Prentice 1989). Young southern flounder appear to be more tolerant of cold than adults, and both groups show increasing tolerance to cold as salinity is increased (Prentice 1989). Temperature appears to have a greater effect on growth than salinity (Peters 1971). Adults in salt water will cease feeding below 7.3°C (Prentice 1989).

Salinity: The southern flounder is euryhaline. Larvae have been found in salinities of 10 to 30‰ (Ward et al. 1980). Salinities in which juveniles have been collected range from 2 to 60‰, but they apparently prefer waters that are 2 to 37‰ (Ward et al. 1980). Adult southern flounder have been collected in waters with salinities that range from 0 to 60‰, with a preference for 20 to 30‰ (Ward et al. 1980). Adults, while in estuaries, prefer the mixing and tidal fresh zones (Gunter 1945).

Dissolved Oxygen (DO): Deubler and Posner (1963) demonstrated avoidance behavior in juvenile southern flounder when dissolved oxygen levels fell below 3.7 mg/l, for temperatures 6.1°, 14.4°, and 25.3° C.

Migrations and Movements: Adults emigrate from the estuaries to spawn in deeper offshore waters during fall and winter. The migrations coincide with falling water temperatures (Gunter 1945, Kelley 1965, Shepard 1986). Males usually leave estuaries for the Gulf earlier than females (Stokes 1977). Hoese and Moore (1977) report severe "northers" will result in mass emigrations, while moderate to warm winters cause flounders to leave dispersed over longer periods of time. Stokes (1977) indicates that only those emigrating are gravid. Some juveniles and adults overwinter in the deeper holes and channels of bays and estuaries (Ogren and Brusher 1977, Stokes 1977, Ward et al. 1980). Postlarvae and juveniles immigrate into the bays and estuaries from late winter to spring. Williams and Deubler (1968) indicated postlarval immigration correlates with lunar phase. In addition, adults migrate back into estuarine habitats throughout spring and into summer. Juveniles tend to migrate to low salinity water, often going up into river channels (Williams and Deubler 1968, Pineda 1975). Stokes (1977) reported that local movements within and between estuaries rarely exceeded 18 km.

**Reproduction**

Mode: The southern flounder has separate male and female sexes (gonochoristic). Fertilization is external, by broadcast of milt and roe into the water column. The eggs are buoyant, and float at or near the water surface (Arnold et al. 1977, Gilbert 1986). Development is oviparous.

Spawning: Spawning occurs during late fall and early winter in marine neritic waters (Sabins and Truesdale 1974, Reagan and Wingo 1985, Gilbert 1986) with a December peak reported in Louisiana (Shepard 1986). In laboratory studies, Arnold et al. (1977) reported that males attended females for a period of 3 weeks prior to spawning. At spawning, the females would swim to the surface and release eggs which were immediately fertilized by the attending male. Larvae of *Paralichthys* species are known to occur in the northern Gulf of Mexico from September through April, with a peak from December to February (Ditty et al. 1988).

Fecundity: Arnold et al. (1977) reported that 13 spawns from 3 pairs of southern flounder produced a total of 120,000 eggs.

**Growth and Development**

Egg Size and Embryonic Development: Eggs are spawned oviparously. Eggs are spherical, with an approximate mean diameter of 0.91 to 0.92 mm, and one oil globule with an approximate diameter of 0.18 mm (Henderson-Arzapalo et al. 1988, Powell and Henley 1995). In a laboratory study, spawned eggs hatched in 61-76 hours at 17°C and 28‰ (Arnold et al. 1977).

Age and Size of Larvae: Recently-hatched larvae are approximately 2.1 mm notochord length (NL) (Powell and Henley 1995). Larvae, 40 to 46 days old and 8 to 11 mm long, begin metamorphosis into the postlarval stage. Transformation is complete by about 50 days (Arnold et al. 1977). Optimal growth in early postlarvae occurs at high salinities (Deubler 1960); while advanced postlarvae grow better at salinities of 5 to 15‰ (Stickney and White 1973). In general, at any given size, larval gulf flounder (*P. albigutta*) are further developed than southern flounder (*P. lethostigma*) (Powell and Henley 1995). There are differences in pigmentation patterns between the two species, but these may be difficult to discern with field-collected specimens.

Juvenile Size Range: The minimum size of settled juveniles overlaps that of the postlarvae in some cases (10-15 mm TL). Peters (1971) concluded *P. lethostigma* grows faster at warm temperatures and low salinities. Size-at-age is highly variable for this species, and age 0 year classes are known to develop bimodal length-frequency distributions (Fitzhugh et al. 1996). This may be the result of faster growth after an ontogenetic shift to piscivory at a size of 70 to 180 mm TL. Size estimated after the first and second year of growth is 201 and 250 mm TL for male, 225 and 364 mm TL for female southern flounder (Stokes 1977). Immature fish >170 mm TL have distinctive gonads and maturation occurs by the second year in fish ranging from 341 to 560 mm TL. Maturity occurred in one study at 243 mm TL for females and 170 mm TL for males (Shepard 1985).

Age and Size of Adults: Stokes (1977) reported a 3 to 5 year life span for this species. Females appear to grow faster, live longer, and attain greater size than males (Stokes 1977). The largest individuals reported range from 595 to 910 mm TL (Ginsburg 1952, Hoese and Moore 1977, Stokes 1977).

### Food and Feeding

Trophic Mode: The southern flounder is carnivorous during all life stages. Larvae feed on pelagic zooplankton, while juveniles and adults feed on crustaceans, and benthic and pelagic fishes (Gilbert 1986). Young southern flounder are dominant predators in Texas estuaries on small brown shrimp during the spring (Minello et al. 1989).

Food Items: Larvae feed on zooplankton (Peters 1971). Small crustaceans, particularly mysids, but also grass shrimp, penaeid shrimp, amphipods, and crabs make up the diet of small juveniles (10-160 mm TL) (Diener et al. 1974, Stokes 1977, Minello et al. 1989). Larger juveniles and adults are basically piscivorous, feeding on small benthic and pelagic fishes; but, shrimp, crabs and polychaetes are also utilized to a lesser extent (Darnell 1958, Fox and White 1969, Powell 1974, Stokes 1977, Powell and Schwartz 1979, Overstreet and Heard 1982). In a North Carolina study, invertebrate prey included the mysids *Mysidopsis bigelowi* and *Neomysis americana*, and fish prey included bay anchovy, spot, and croaker (Fitzhugh et al. 1996). The ontogenetic shift to piscivory occurred as fish grew from 70 to 180 mm TL.

### Biological Interactions

Predation: Information on predation of flounder is scarce. Larvae and juveniles are probably the most susceptible to predation due to their smaller size. Known and suspected species that prey on flounder species in the Gulf of Mexico are: tiger shark (*Galeocerdo cuvier*), gafttopsail catfish (*Bagre marinus*), inshore lizard fish (*Synodus foetens*), various searobins (family Triglidae), various sculpins (family Cottidae), jewfish (*Epinephelus itaiara*), and larger-sized southern flounder (Kemp 1949, Miles 1949, Diener et al. 1974, Tanaka et al. 1989).

Factors Influencing Populations: Southern flounder and gulf flounder are very difficult to distinguish from each other during early life stages (Woolcott et al. 1968). Early stages are often summarized as "*Paralichthys* species" (King 1971) or just "southern flounder" (Stokes 1977). Adult southern flounder generally outnumber gulf flounder in the northern Gulf of Mexico, and catches containing the two species are not usually separated. This makes catch data for the two species very hard to analyze. The shrimp fishery unintentionally catches large numbers of juvenile flounder, almost all of which are discarded (Gunter 1945, Matlock 1991). This reduces the number of sexually immature fish available for recruitment into the fishery.

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## Glossary

ABYSSAL ZONE—Ocean bottom at depths between 4,000 and 6,000 m.

ABYSSOPELAGIC—Living in the water column at depths between 4,000 and 6,000 m; the abyssopelagic zone.

ADDUCTOR MUSCLE—A muscle that pulls a part of the body toward the median axis of the body. In bivalve molluscs, this muscle is used to close the shell halves and hold them together.

ADHESIVE—Sticky and tending to adhere; e.g., adhesive eggs.

AGE-GROUP—A term used to designate year-classes in fishes; a division date of January 1 is used in the northern hemisphere. See YOUNG-OF-YEAR, YEARLING, and TWO-YEAR-OLD.

AGGREGATION—A group of individuals of the same species gathered in the same place but not socially organized or engaged in cooperative behavior. Compare to SCHOOL.

ALGAE—A collective, or general name, applied to a number of primarily aquatic, photosynthetic groups (taxa) of plants and plant-like protists. They range in size from single cells to large, multicellular forms like the giant kelps. They are the food base for almost all marine animals. Important taxa are the dinoflagellates (division Pyrrophyta), diatoms (div. Chrysophyta), green algae (div. Chlorophyta), brown algae (div. Phaeophyta), and red algae (div. Rhodophyta). Cyanobacteria are often called blue-green algae, although blue-green bacteria is a preferable term.

AMBICOASTAL—Used in reference to enclosed bay systems to denote both estuarine and marine coasts.

AMPHIPODA—An order of laterally compressed crustaceans with thoracic gills, no carapace, and similar body segments. Although most are <1 cm long, they are an important component of zooplankton and benthic invertebrate communities. A few species are parasitic.

ANADROMOUS—Life cycle where an organism spends most of its life in the sea, and migrates to fresh water to spawn. Compare to CATADROMOUS.

ANNULUS—Annual growth mark on a scale, bone (e.g., otolith), or other hard structure.

ANTHROPOGENIC—Refers to the effects of human activities.

AQUACULTURE—The rearing of aquatic (marine or freshwater) vertebrates, invertebrates, or algae, to be harvested for commercial or subsistence purposes. See MARICULTURE.

AREAL—Refers to a measure of area.

ASCIDIAN—A tunicate (class Ascidiacea) that has a generalized sac-like, cellulose body and is usually attached to the substratum.

AUTOTROPH—An organism using sunlight or inorganic chemical reactions as a source of energy to synthesize organic matter. Compare with PHOTOTROPH and HETEROTROPH.

BATCH SPAWN—Discontinuous episodes of spawning, either of gametes or offspring. Individuals or populations that release gametes or offspring with greater continuity are serial or sequential spawners.

BATHYAL—The zone of ocean bottom at depths of 200 to 4,000 m, primarily on the continental slope and rise.

BATHYMETRIC—Pertaining to depth measurement. Also refers to a migration from waters of one depth to another.

BATHYPELAGIC—Ocean depths from 1,000 to 4,000 m.

BENTHIC—Pertaining to the bottom of an ocean, lake, or river. Also refers to sessile and crawling animals which reside in or on the bottom.

BIGHT—An inward bend or bow in the coastline.

BIOMASS—The total mass of living tissues (wet or dried) of an organism or collection of organisms of a species or trophic level, from a defined area or volume.

BIVALVIA—Bilaterally symmetrical molluscs (also referred to as Pelecypoda) that have two lateral calcareous shells (valves) connected by a hinge ligament. They are mostly sedentary filter feeders. This class includes clams, oysters, scallops, and mussels.

BRANCHIAL—A structure or location on an organism associated with the gills.

BROADCAST SPAWNER—Planktonic release of floating or sinking (demersal) gametes (eggs, sperm) or of offspring. May be continuous or periodic in duration. See BATCH SPAWN.

BRYOZOA—Small moss-like colonial animals of the phylum Bryozoa.

BUOYANT—Able to remain afloat in a liquid, or rise in air or gas.

BYCATCH—See INCIDENTAL CATCH.

BYSSAL THREAD—A tuft of filament, chemically similar to silk, that attaches certain molluscs to substrates.

CALANOIDA—An order of free-living, largely planktonic copepods with very long first antennae.

CALCAREOUS—Composed of calcium or calcium carbonate.

CARAPACE—The hard exoskeletal covering of the dorsal part of a crustacean.

CARAPACE WIDTH—The total width of a crustacean's carapace, often used as a standardized measurement for crabs.

CARIBBEAN PROVINCE—A tropical marine zoogeographic province of the Atlantic continental shelf that includes southern Florida from Cape Canaveral around to the Tampa Bay region, and the Central and South American coast from near Tampico, Mexico to Venezuela.

CARNIVORE—An animal that feeds on the flesh of other animals. See PARASITISM and PREDATION.

CAROLINIAN PROVINCE—A warm-temperate marine zoogeographic province of the Atlantic continental shelf extending approximately from Cape Hatteras, North Carolina southward to Cape Canaveral, Florida on the U.S. east coast, and from Florida's Tampa Bay region westward to Cape Rojo near Tampico, Mexico on the Gulf coast.

CATADROMOUS—A life cycle in which an organism lives most of its life in fresh water, but migrates to saltwater to spawn. Compare to ANADROMOUS.

CERCARIA—A heart-shaped, tailed, larval stage of a trematode (fluke) produced in a mollusc host, which is released from the mollusc, sometimes then encysting, and subsequently infecting a vertebrate host.

CESTODE—A parasitic, ribbon-like worm having no intestinal canal; class Cestoda (e.g., tapeworms).

CHELAE—The forceps-like pincers in crustaceans.

CHELIPED—The large grasping claw of many crustaceans.

CHEMOTAXIS—A response movement by an animal either toward or away from a specific chemical stimulus.

CHORDATA—A phylum of animals which includes the subphyla Vertebrata, Cephalochordata, and Urochordata. At some stage of their life cycles, these organisms have pharyngeal gill slits, a notochord, and a dorsal hollow nerve cord.

CHROMATOPHORE—A pigment cell or group of cells which under the control of the nervous system can be altered in shape or color.

CILIA—Hair-like processes of certain cells, often capable of rhythmic beating that can produce locomotion or facilitate the movement of fluids.

CIRCULUS—A ringlike arrangement.

CIRRI—Flexible, thread-like tentacles or appendages of certain organisms.

CLEITHRUM—clavicular elements of some fishes.

CLINE—A series of differing physical characteristics within a species or population, reflecting gradients or changes in the environment (e.g., body size or color).

COLONY—A group of organisms living in close proximity. An invertebrate colony is a close association of individuals of a species which are often mutually dependent and in physical contact with each other. A vertebrate colony is usually a group of individuals brought together for breeding and rearing young.

COMMENSALISM—A relationship between two species, where one species benefits without adversely affecting the other.

COMMERCIAL VALUE—Economic attribute of marketable fishes, invertebrates, or other marine resources, the harvest, culture, processing, or distribution of which occur with sufficient financial return to support a specialized, expert and usually regulated trade.

COMMUNITY—A group of plants and animals living in a specific region under relatively similar conditions. Further definitions are often applied, such as the algal community, the invertebrate community, the benthic gastropod community, etc.

COMPETITION—Two types exist - interspecific and intraspecific. Interspecific competition exists when two or more species use one or more limited resources such as food, attachment sites, protective cover, or dissolved ions. Intraspecific competition exists when individuals of a single species compete for limited resources needed for survival and reproduction. This form of competition includes the same resources involved in interspecific competition as well as mates and territories. It is generally more intense than interspecific competition because resource needs are essentially identical among conspecifics. See NICHE.

CONGENER—Referring to other members of the same genus.

CONSPECIFIC—Referring to other members of the same species.

CONTINENTAL SHELF—The submerged continental land mass, not usually deeper than 200 m. The shelf may extend from a few miles off the coastline to several hundred miles.

CONTINENTAL SLOPE—The steeply sloping seabed that connects the continental shelf and continental rise.

COPEPODA—A subclass of crustaceans with about 4,500 species, including several specialized parasitic orders. The free-living species are small (one to several mm) and have cylindrical bodies, one median eye, and two long antennae. One order is planktonic (Calanoida), one is benthic (Harpacticoida), and one has both planktonic and benthic species (Cyclopoida). In most species, the head appendages form a complex apparatus used to sweep in and possibly filter prey (especially algae). Thoracic appendages are used for swimming or crawling on the bottom. One of the most abundant groups of animals on earth, they are a major component of aquatic food webs.

CREPUSCULAR—Relates to animals whose peak activity is during the twilight hours of dawn and dusk.

CRUSTACEA—A large class of over 26,000 species of mostly aquatic arthropods having five pairs of head appendages, including laterally opposed jaw-like mandibles and two pairs of antennae. Most have well-developed compound eyes and variously modified two-branched body appendages. The body segments are often differentiated into a thorax and an abdomen. Some common members are crabs, shrimp, lobsters, copepods, amphipods, isopods, and barnacles.

CTENIDIA—The comblike respiratory apparatus of molluscs.

CTENOPHORA—A phylum of mostly marine animals that have oval, jellylike bodies bearing eight rows of comb-like plates that aid swimming (e.g., ctenophores and comb jellies).

CYCLOPOIDA—An order of marine and freshwater, planktonic and benthic copepods.

DECOMPOSERS—Bacteria and fungi that break down dead organisms of all types to simple molecules and ions.

DEMERSAL—Refers to swimming animals that live near the bottom of an ocean, river, or lake. Often refers to eggs that are denser than water and sink to the bottom after being laid.

DEPOSIT FEEDER—An animal that ingests small organisms, organic particles, and detritus from soft sediments, or filters organisms and detritus from such substrates.

DESICCATE—To dry completely.

DETRITIVORE—An organism that eats small fragments of partially decomposed organic material (detritus) and its associated microflora. See DECOMPOSER.

DETRITUS—Small pieces of dead and decomposing plants and animals; detached and broken-down fragments of an organic structure.

DIATOMS—Single-celled protistan algae of the class Bacillariophyceae that have intricate siliceous shells composed of two halves. They range in size from about 10 to 200 microns. Diatoms sometimes remain attached after cellular divisions, forming chains or colonies. These are the most numerous and important groups of phytoplankters in the oceans, and form the primary food base for marine ecosystems.

DIEL—Refers to a 24-hour activity cycle based on daily periods of light and dark.

DIMORPHISM—A condition where a population has two distinct physical forms (morphs). In sexual dimorphism, secondary sexual characteristics are markedly different (e.g., size, color, and behavior).

DINOFLAGELLATE—A planktonic, photosynthetic, unicellular algae that typically has two flagella, one being in a groove around the cell and the other extending from the center of the cell.

DIRECT DEVELOPMENT—See EMBRYONIC DEVELOPMENT.

DISPERSAL—The spreading of individuals throughout suitable habitat within or outside the population range. In a more restricted sense, the movement of young animals away from their point of origin to locations where they will live at maturity.

DISSOCHONCH—The adult shell secreted by newly-settled clam larvae or plantigrades.

DISTRIBUTION—(1) A species distribution is the spatial pattern of its population or populations over its geographic range. See RANGE. (2) A population depth distribution is the proportion or number of all individuals, or those of various sizes or ages, at different depth strata. (3) A population age distribution is the proportions of individuals in various age classes. (4) Within a population, individuals may be distributed evenly, randomly, or in groups throughout suitable habitat.

DIURNAL—Refers to daylight activities, or organisms most active during daylight. See DIEL.

ECHINODERMATA—A phylum of radially-symmetrical marine animals, possessing a water vascular system, and a hard, spiny skeleton (e.g., sea stars, sea urchins, and sand dollars).

ECTOPARASITE—A parasite that attacks (and usually attaches to) a host animal or plant on the outside. Feeding periods and/or attachment time may be brief compared to internal (endo-) parasites.

EELGRASS—Vascular flowering plants of the genus *Zostera* that are adapted to living under water while rooted in shallow sediments of bays and estuaries.

EMBRYONIC DEVELOPMENT—The increase in cell number, body size, and complexity of organ systems as an individual develops from a fertilized egg until hatching or birth. In direct development, individuals at birth or hatching are essentially miniatures of the adults. In indirect development, newly hatched individuals differ greatly from the adult, and go through periodic, major morphological changes (larval stages and metamorphosis) before becoming a juvenile.

EMIGRATION—A movement out of an area by members of a population. See IMMIGRATION.

ENDEMIC—Refers to a species or taxonomic group that is native to a particular geographical region.

EPIBENTHIC—Located on the bottom, as opposed to in the bottom.

EPIDERMAL—Refers to an animal's surface or outer layer of skin.

EPIFAUNA—Animals living on the surface of a substrate.

EPIPELAGIC—The upper sunlit zone of oceanic water where phytoplankton live and organic production takes place (approximately the top 200 m). See EUPHOTIC.

EPIPHYTIC—Refers to organisms which live on the surface of a plant (e.g., mosses growing on trees).

EPIPODAL—A structure or location associated with the leg or foot; typically refers to arthropod anatomy.

ESCARPMENT—A steep slope in topography, as in a cliff or along the continental slope.

ESTUARY—A semi-enclosed body of water with an open connection to the sea. Typically there is a mixing of sea and fresh water, and the influx of nutrients from both sources results in high productivity.

EUHALINE—A category in the Venice system of estuarine salinity classification; water with salinity of 30 to 40 parts per thousand (‰).

EUPHOTIC—Refers to the upper surface zone of a water body where light penetrates and phytoplankton (algae) carry out photosynthesis. See EPIPELAGIC.

EURYHALINE—Refers to an organism that is tolerant of a wide range of salinities.

EURYTHERMAL—Refers to an organism that is tolerant of a wide range of temperatures.

EXTANT—Existing or living at the present time; not extinct.

FAUNA—All of the animal species in a specified region.

FECUNDITY—The potential of an organism to produce offspring (measured as the number of gametes). See REPRODUCTIVE POTENTIAL.

FILTER FEEDER—Any organism that filters small animals, plants, and detritus from water or fine sediments for food. Organs used for filtering include gills in clams and oysters, baleen in whales, and specialized appendages in crustaceans and marine worms.

FINGERLING—Refers to a small juvenile fish that is about 100 mm long.

FLAGELLATE—Refers to cells that have motility organelles or microorganisms that possess one or more flagella used for locomotion.

FLORA—All of the plant species in a specified region, including algae.

FOOD WEB (CHAIN)—The feeding relationships of several to many species within a community in a given area during a particular time period. Two broad types are recognized: 1) grazing webs involving producers (e.g., algae), herbivores (e.g., copepods), and various combinations of carnivores and omnivores, and 2) detritus webs involving scavengers, detritivores, and decomposers that feed on the dead remains or organisms from the grazing webs, as well as on their own dead. A food chain refers to organisms on different trophic levels, while a food web refers to a network of interconnected food chains. See TROPHIC LEVEL.

FORAGE SPECIES—An organism that occurs in large numbers and comprises a significant prey base for predatory animals.

FORAMINIFERIDA—A chiefly marine order of protozoans with mosty multichambered shells.

FORK LENGTH—distance from the tip of the snout to the notch in the caudal fin.

FOULING—Occurs when large numbers of marine plants and animals attach and grow on various submerged structures (floats, pipes, and pilings), often interfering with their use. Fouling organisms include algae, barnacles, mussels, bryozoans, and sponges.

FRESH WATER—Water that has a salt concentration of 0.0-0.5 parts per thousand (‰).

FRY—Very young fish; may include both larvae and young juveniles.

GAMETE—A reproductive cell. When two gametes unite they form an embryonic cell (zygote).

GAMETOGENESIS—The formation of gametes.

GASTROPODA—The largest class of the Phylum Mollusca. This group includes terrestrial snails and slugs as well as aquatic species such as whelks, turbans, limpets, conchs, abalones, and nudibranchs. Most have external shells that are often spiraled (but this has been lost or is reduced in some), and move on a flat, undulating foot. They are mostly herbivorous and scrape food with a radula, an organ analogous to a tongue.

GASTRULATION—A stage in early embryogenesis involving extensive cell movements, and in which the gut cavity is formed and the three primary layers of the animal body (ectoderm, mesoderm, and ectoderm) are placed in position for further development.

GONOCHORISTIC—Refers to a species that has separate sexes (i.e., male and female individuals).

GREGARIOUS—Living together in groups, as in schools, flocks, or herds.

GROUNDFISH—Fish species that live on or near the bottom, often called bottomfish.

GYNOGENESIS—Embryonic development of an egg without genetic contribution by a sperm, although activation by sperm during spawning is required for development to proceed. Gynogenetic development is known to occur within the unisexual *Menidia clarkhubbsi*, an all-female clonal complex which produces diploid eggs without genetic recombination.

GYRE—An ocean current that follows a circular or spiral path around an ocean basin, clockwise in the northern hemisphere and counterclockwise in the southern hemisphere.

HABITAT—The particular type of place where an organism lives within a more extensive area or range. The habitat is characterized by its biological components and/or physical features (e.g., sandy bottom of the littoral zone, or in seagrass beds within 3 m of the water surface).

HAPLOSPORIDIAN—A unicellular protozoan occurring in vertebrate and invertebrate hosts, often causing disease.

HARPACTICOIDA—An order of mostly free-living, marine and freshwater, bottom-dwelling copepods. Some are planktonic, and many are interstitial.

HATCHERY-REARED—Distinguished from naturally-occurring recruits in population, these animals are raised in captivity for the purposes of release or harvest.

HERBIVORE—An animal that feeds on plants (phytoplankton, large algae, or higher plants).

HERMAPHRODITIC—Refers to an organism having both male and female sex organs on the same individual.

HETEROTROPH-An organism (e.g. animals and fungi) which obtains nourishment by consuming exogenous organic matter. Compare to AUTOTROPH and PHOTOTROPH.

HYDROZOA—A class of the phylum Cnidaria. The primary life stage is nonmotile and has a sac-like body composed of two layers of cells and a mouth that opens directly into the body cavity. A second life stage, the free-living medusa, often resembles the common jellyfish.

HYPERSALINE—Water with a salt concentration over 40 parts per thousand (‰).

IMMIGRATION—A movement of individuals into a new population or region. See EMIGRATION, MIGRATION, and RECRUITMENT.

INCIDENTAL CATCH—Catch of a species that is not intended to be caught by a fishery, but is taken along with the species being sought; also known as BYCATCH.

INDICATOR OF STRESS—Species whose presence or absence in an environment has been documented as correlated with polluted or unpolluted conditions, or ecological stress of other forms.

INDIRECT DEVELOPMENT—See EMBRYONIC DEVELOPMENT.

INFAUNA—Animals living within a substrate.

INNER SHELF—The continental shelf extending from the mean low tide line to a depth of 20 m.

INSTAR— The intermolt stage of a young arthropod.

INSULAR—Of or pertaining to an island or its characteristics (i.e., isolated).

INTERTIDAL—The ocean or estuarine shore zone exposed between high and low tides.

ISOBATH—A contour mapping line that indicates a specified constant depth.

ISOPODA—An order of about 4,000 species of dorsoventrally compressed crustaceans that have abdominal gills and similar abdominal and thoracic segments. Terrestrial pillbugs and thousands of benthic marine species are included. Most species are scavengers and/or omnivores; a few are parasitic.

ISOTHERM—A contour line connecting points of equal mean temperature for a given sampling period.

ITEROPAROUS—Refers to an organism that reproduces several times during its lifespan (i.e., does not die after spawning); compare with SEMELPAROUS.

JACKSON TURBIDITY UNITS—Measurement of turbidity that relates levels of sample liquid in a graduated cylinder to visible loss or merging of the image of a standardized candle, viewed from the top of the column of water, with the lighted candle at a defined distance from the bottom of the graduated column.

JUVENILE—A young organism essentially similar to an adult, but not sexually mature.

KINESIS—A randomly directed movement by an animal in response to a sensory stimulus such as light, heat, or touch. When the response is directed, it is called a taxis. See CHEMOTAXIS.

LACUSTRINE—Pertaining to, or living in, lakes or ponds.

LAGOON—A shallow pond or channel linked to the ocean, but often separated by a reef or sandbar.

LARVA—An early developmental stage of an organism that is morphologically different from the juvenile or adult form, intervening between the times of hatching and of juvenile transformation. See EMBRYONIC DEVELOPMENT.

LATERAL LINE—A pressure sensory system located in a line of pores under the skin on both sides of most fishes. The system is connected indirectly with the inner ear and senses water pressure changes due to water movement (including sound waves).

LC50—The measured concentration of a toxic substance that kills 50% of a group of test organisms within a specified time period.

LITTORAL—The shore area between the mean low and high tide levels. Water zones in this area include the littoral pelagic zone and the littoral benthic zone.

MACROALGAE—Relatively large, multicellular, non-vascular marine or estuarine plants that float, drift along the bottom, or have hold-fasts that anchor them to sand, rock, or shell. Larger than and different from planktonic or benthic unicellular (micro-) algae.

MANTLE—The upper fold of skin in molluscs that encloses the gills and most of the body in a cavity above the muscular foot. In squids and allies, the mantle is below the body and behind the tentacles (derived from the foot) due to the shift in the dorsal-ventral axis. The mantle produces the shell in species having them.

MANTLE LENGTH—The total length of the mantle of squids and allies.

MARICULTURE—The rearing of marine vertebrates, invertebrates, or algae, to be harvested for commercial or subsistence purposes. See AQUACULTURE.

MARINE—Of, pertaining to, living in, or related to the seas or oceans.

MARSH—Plant community developing on wet, but not peaty, soil in either tidal or non-tidal areas.

MEAN LOWER LOW WATER (MLLW)—The arithmetic mean of the lower low water heights of a mixed tide over a specific 19-year Metonic cycle (the National Tidal Datum Epoch). Only the lower low water of each tidal day is included in the mean.

MEDUSA—A free-swimming sexual form in coelenterates.

MEGALOPA—The larval stage of a crab characterized by an adult-like abdomen, thoracic appendages, and a developed carapace; occurs after the zoeal stage. See ZOEA.

MEIOFAUNA—Very small animals, usually < 0.5 mm in diameter, and often planktonic.

MELANOPHORE—A pigment cell containing melanin that is present in many animals and is responsible for pigmentation and color changes.

MERISTIC—Refers to countable measurements of segments or features such as vertebrae, fin rays, and scale rows. Counts of these are used in population comparisons and classifications.

MEROPLANKTON—Temporary plankton, consisting of eggs and larvae; seasonal plankton.

MESOHALINE—A category in the Venice system of estuarine salinity classification; water with salinity of 5 to 18 parts per thousand (‰).

MESOPELAGIC—Ocean zone of intermediate depths from about 200-1,000 m below the surface, where light penetration drops rapidly and ceases.

METAMORPHOSIS—Process of transforming from one body form to another form during development (e.g., tadpole changing to a frog). See EMBRYONIC DEVELOPMENT.

METRIC TON (t)—A unit of mass or weight equal to 2,204.6 lb.

MIGRATION—Movement by a population or subpopulation from one location to another (often periodic or seasonal, and over long distances). Vertical migrations in the water column may be daily or seasonal within the same area. Migrations between deep and shallow areas are usually seasonal and related to breeding. Many marine birds and mammals have seasonal latitudinal migrations associated with breeding. See EMIGRATION, IMMIGRATION, RANGE, and RECRUITMENT.

MILT—The seminal fluid and sperm of male fish.

MIXING ZONE—The portion of an estuary with annual depth-averaged salinities of 0.5 to 25 parts per thousand (‰).

MOLLUSC—Any invertebrate of the phylum Mollusca, unsegmented animals with a body consisting of a ventral foot and a dorsal visceral mass. Most possess a mantle which secretes a calcareous shell. Common representatives are snails, mussels, clams, oysters, and squid.

MOLT—The process of shedding and regrowing an outer skeleton or covering at periodic intervals. Crustaceans and other arthropods molt their exoskeletons, grow rapidly, and produce larger exoskeletons. Most reptiles, birds, and mammals molt skin, feathers, and fur, respectively.

MORPHOLOGY—The appearance, form, and structure of an organism.

MORPHOMETRICS—The study of comparative morphological measurements.

MORTALITY—Death rate expressed as a proportion of a population or community of organisms. Mortality is caused by a variety of sources, including predation, disease, environmental conditions, etc.

MOTILE—Capable of or exhibiting movement or locomotion.

MUTUALISM—An interaction between two species where both benefit. Some authorities consider true mutualism to be obligatory for both species, while mutually beneficial relationships that are not essential for either species are classified as protocooperative.

NACREOUS MATERIAL—A calcareous, lustrous secretion in the inner surface of the shell of many molluscs. Foreign particles lodging between the inner shell surface and mantle are covered by nacre, often forming pearls.

NANOPLANKTON—Microscopic, planktonic organisms smaller than 20 microns in diameter.

NATAL—Pertaining to birth or hatching.

NAUPLIUS—A free-swimming larva, the first stage in the development of certain crustaceans such as shrimps.

NEARSHORE—Consists of those waters extending from the beach out to 6 fathoms of depth.

NEKTONIC—Refers to pelagic animals that are strong swimmers, live above the substrate in the water column, and can move independently of currents.

NEMERTEA—A phylum of unsegmented, elongate marine worms having a protrusible proboscis and no body cavity, and live mostly in coastal mud or sand; nemerteans.

NERITIC—An oceanic zone extending from the mean low tide level to the edge of the continental shelf. See INNER SHELF, LITTORAL, and OCEANIC ZONES.

NEUSTON—Organisms that live on or just under the water surface, often dependent on surface tension for support.

NICHE—The fundamental niche is the full range of abiotic and biotic factors under which a species can live and reproduce. The realized niche is the set of actual conditions under which a species or a population of a species exists, and is largely determined by interactions with other species.

NIDAMENTAL APPARATUS—A pair of glands that in squids and their allies lies in the mantle cavity, with their openings situated close to the oviductal outlet(s). This structure secretes a mucinous material that aids in the encapsulation of eggs as they leave the oviduct.

NOCTURNAL—Refers to night, or animals that are active during the night.

NUDIBRANCH—A group of shell-less marine molluscs commonly known as sea slugs.

OCEANIC—Living in or produced by the ocean.

OCEANIC ZONE—Pelagic waters of the open ocean beyond the continental shelf. See BATHYPELAGIC, EPIPELAGIC, ABYSSOPELAGIC, MESOPELAGIC, and NERITIC.

OLIGOHALINE—A category in the Venice system of estuarine salinity classification; water with salinity of 0.5 to 5.0 parts per thousand (‰).

OMNIVORE—An animal that eats both plant and animal matter.

OOCYTES—The cells in ovaries that will mature into eggs.

OSMOREGULATION—The maintenance of proper water and electrolyte balance in an organism's body.

OSTRACODS—A class of widely distributed marine and freshwater crustaceans whose bodies are completely enclosed in a bivalve carapace.

OTOLITHS—Small calcareous nodules located in the inner ear of fishes used for sound reception and equilibration. They are often used by biologists to assess daily or seasonal growth increments.

OUT-MIGRATION—Movement of animals out of or away from an area (e.g., juvenile sciaenids moving from estuaries to the ocean).

OVIGEROUS—The condition of being ready to release mature eggs; egg-bearing.

OVIPAROUS—Refers to animals that produce eggs that are laid and hatch externally. See OVOVIVIPAROUS and VIVIPAROUS.

OVIPOSITION—The process of placing eggs on or in specific places, as opposed to randomly dropping or broadcasting them.

OVOVIVIPAROUS—Refers to animals whose eggs are fertilized, developed, and hatched inside the female, but receive no nourishment from her. See OVIPAROUS and VIVIPAROUS.

PALP—An organ attached to the head appendages of various invertebrates; usually associated with feeding functions.

PARALARVA—A cephalopod mollusc in its first post-hatching growth stage that is pelagic in near-surface waters during the day, and that has a different life mode than older conspecifics.

PARASITISM—An obligatory association where one species (parasite) feeds on, or uses the metabolic mechanisms of the second (host). Unlike predators, parasites usually do not kill their hosts, although hosts may later die from secondary causes that are related to a weakened condition produced by the parasite. Parasitism may also be fatal when high parasite densities develop on or in the host.

PARTS PER THOUSAND—A standard unit for measuring salinity, abbreviated as ‰ or ppt.

PARTURITION—The act of giving birth, e.g., the live birth of bull shark pups. Compare to SPAWN.

PATHOGEN—A microorganism or virus that produces disease and can cause death.

PEDIVELIGER—The larval stage of bivalves during which a functional pedal (footlike) organ develops.

PELAGIC—Pertaining to the water column, or to organisms that live in the water column and not near the bottom.

PELAGIVORE—A carnivore that feeds in the water column.

PELECYPODA—A synonym for the mollusc class BIVALVIA.

PHOTOPERIODISM—The responses of an organism to changes in light intensity or in length of days; e.g., seasonal and cyclic events such as migrations or reproductive cycles of animals.

PHOTOTROPH—An organism (e.g. phytoplankton and other plants) using sunlight as a source of energy to synthesize organic matter. Compare with AUTOTROPH and HETEROTROPH.

PHYLLOSOMA—The larval stage of lobsters, being a broad, thin, schizopod larva.

PHYLOGENY—Refers to evolutionary relationships and lines of descent.

PHYTOPLANKTON—Microscopic plants and plant-like protists (algae) of the epipelagic and neritic zones that are the base of marine food webs. They drift with currents, but may have some ability to control their level in the water column. See ALGAE and DIATOMS.

PISCIVOROUS—Refers to a carnivorous animal that eats fish.

PLANKTIVOROUS—Refers to an animal that eats phytoplankton and/or zooplankton.

PLANKTON—Microscopic aquatic plants, animals, and protists have limited means of locomotion and drift with currents. See PHYTOPLANKTON and ZOOPLANKTON.

PLANTIGRADE—A young, newly settled post-larval clam.

PLEOPODS—Paired swimming appendages on the abdomen of crustaceans.

PNEUMATOPHORE—A root rising above the level of water or soil and acting as a respiratory organ in some trees (e.g., mangroves).

POLYCHAETA—A class of segmented, mostly marine, annelid worms that bear bristles and fleshy appendages on most segments.

POLYHALINE—A category in the Venice system of estuarine salinity classification; water with salinity of 18 to 30 parts per thousand (‰).

POPULATION—All individuals of the same species occupying a defined area during a given time. Environmental barriers may divide the population into local breeding units (demes) with restricted immigration and interbreeding between the localized units. See SPECIES, SUBSPECIES, and SUBPOPULATION.

POSTLARVA—larva following the time of absorption of yolk; applied only when the structure and form continue to be strikingly unlike that of the juvenile.

PREDATION—An interspecific interaction where one animal species (predator) feeds on another animal or plant species (prey) while the prey is alive or after killing it. The relationship tends to be positive (increasing) for the predator population and negative (decreasing) for the prey population. See PARASITISM, SYMBIOTIC, CARNIVORE, and TROPHIC LEVEL.

PRODUCTION—Gross primary production is the amount of light energy converted to chemical energy in the form of organic compounds by autotrophs such as algae. The amount left after respiration is net primary production and is usually expressed as biomass or calories/unit area/unit time. Net production for herbivores and carnivores is based on the same concept, except that chemical energy from food, not light, is used and partially stored for life processes. Efficiency of energy transfers between trophic levels may range from 10 to 65%, depending on the organisms and trophic levels. Organisms at high trophic levels have only a fraction of the energy available to them that was stored in plant biomass. After respiration loss, net production goes into growth and reproduction, and some is passed to the next trophic level. See FOOD WEB and TROPHIC LEVEL.

PROTANDRY-A type of hermaphroditism in which and individual initially develops as a male, then reverses to function as a female. Common among some species of shrimps.

PROTISTAN-Pertaining to the eukaryotic unicellular organisms of the kingdom Protista, including such groups as algae, fungi, and protozoans.

PROTOGYNY—The condition of hermaphrodite plants and animals in which female gametes mature and are shed before maturation of male gametes.

PROTOZOA—A varied group of either free-living or parasitic unicellular flagellate and amoeboid organisms.

PROTOZOEA—A post-naupliar, pre-zoeal larval stage in penaeid shrimp. See NAUPLIUS and ZOEA.

PTEROPODS—Group of marine gastropod molluscs with wing-like extensions to the foot, commonly called sea butterflies.

PUERULUS—A brief (several weeks), nonfeeding, oceanic postlarval phase in the development of spiny lobster.

PYCNOCLINE—A zone of marked water density gradient that is usually associated with depth; the density gradient may be due to salinity and/or temperature.

QUERIMANA—Prejuvenile stage in striped mullet that is identical to the adult form except that it has two anal spines instead of three, that the adipose eyelid is not yet apparent, and that the axillary scales are quite short.

RACE—An intraspecific group or subpopulation characterized by a distinctive combination of physiological, biological, geographical, or ecological traits.

RADULA—A toothed belt or tongue in the buccal cavity of most molluscs that is used to scrape food particles from a surface, or modified otherwise to serve a variety of feeding habits.

RANGE—(1) The geographic range is the entire area where a species is known to occur or to have occurred (historical range). The range of a species may be continuous, or it may have unoccupied gaps between populations (discontinuous distribution). (2) Some populations, or the entire species, may have different seasonal ranges. These may be overlapping, or they may be widely separated with intervening areas that are at most briefly occupied during passage on relatively narrow migration routes. (3) Home range refers to the local area that an individual or group uses for a long period or life. See DISTRIBUTION and TERRITORY.

RECREATIONAL VALUE—Economic and social attributes of fishes and invertebrates sought by individual persons as leisure activity.

RECRUITMENT—The addition of new members to a population or stock through successful reproduction and immigration.

RED TIDE—A reddish coloration of sea waters caused by a large bloom of red flagellates. The accumulation of metabolic by-products from these organisms is toxic to fish and many other marine species. The accumulation of these metabolites in shellfish makes shellfish toxic to humans.

REPRODUCTIVE POTENTIAL—The total number of offspring possible for a female of a given species to produce if she lives to the maximum reproductive age. This is found by multiplying the number of possible reproductive periods by the average number of eggs or offspring produced by females of each age class. This potential is seldom realized, but this and the age of first reproduction, or generation time, determine the maximum rate of population increase under ideal conditions.

RHEOTAXIS—A response movement by an animal toward or away from stimulation by a water current.

RIVERINE—Pertaining to a river or formed by a river or stream.

ROE—The egg-laden ovary of a fish, or the egg mass of certain crustaceans.

RUN—A group of migrating fish (e.g., a shad run).

SALT WEDGE—A wedge-shaped layer of salt water that intrudes upstream beneath a low-density freshwater lens that has "thinned" while flowing seaward.

SCAVENGER—Any animal that feeds on dead animals and remains of animals killed by predators. See DECOMPOSER and DETRITIVORE.

SCHOOL—A group of aquatic organisms, usually of the same size, mutually attracted to each other, that swim together in an organized fashion.

SEAWATER ZONE—The portion of an estuary with annual depth-averaged salinities of greater than 25 parts per thousand.

SEDENTARY—Refers to animals that are attached to a substrate or confined to a very restricted area (or those that do not move or move very little). See SESSILE.

SEMELPAROUS—Animals that have a single reproductive period during their lifespan; compare with ITEROPAROUS.

SESSILE—Refers to an organism that is permanently attached to the substrate. See SEDENTARY.

SESTON—Microplankton; all bodies, living and non-living, floating or swimming in water.

SETTLEMENT—The act of or state of making a permanent residency. Often refers to the period when fish and invertebrate larvae change from a planktonic to a benthic existence.

SHOAL—(1) A sand bar in a body of water that is exposed at low tide. (2) An area of shallow water. (3) A group of fish (school). (4) As a verb, to collect in a crowd or school.

SILT—Soil with particles intermediate in size between sand and clay.

SIPHONS—The "necks" or tubes of clams and other bivalves that carry water containing food and oxygen into the gills (inhalant siphon), and then expel water containing waste products (exhalent siphon).

SLOUGH-A shallow inlet or backwater area whose bottom may be exposed at low tide. Sloughs are often adjacent to open estuarine waters, and may have a channel passing through them.

SPAT—Juvenile bivalve molluscs which have settled from the water column to the substrate to begin a benthic existence.

SPAWN—The release of eggs and sperm during mating. Also, the bearing of offspring by species with internal fertilization. See PARTURITION.

SPECIES—(1) A fundamental taxonomic group ranking after a genus. (2) A group of organisms recognized as distinct from other groups, whose members can interbreed and produce fertile offspring. See POPULATION, SUBPOPULATION, and SUBSPECIES.

SPERMATOPHORE—A capsule or gelatinous packet (extruded by a male) containing sperm and used to transfer sperm to females. Spermatophores are produced by certain invertebrates and some primitive vertebrates.

SPICULE—A sharp, pointed, siliceous or calcareous body, as in those forming the endoskeleton of sponges, corals, and certain protozoans.

SPIT—A long, narrow sand bar or peninsula extending into a body of water which is at least partly connected to the shore. See SHOAL.

SPOROCYST—A simple larval stage of parasitic trematode worms. Contact with the host causes a metamorphosis from an earlier stage to this stage.

STANDARD LENGTH—Distance from the tip of a fishes snout or lips to the end of the last vertebrae at the base of the caudal fin.

STENOHALINE—Pertaining to organisms that are restricted to a narrow range of salinities, in contrast to EURYHALINE.

STENOPHAGOUS—Subsisting on a limited variety of food items.

STENOTHERMAL—Pertaining to organisms that are restricted to a narrow range of temperatures, in contrast to EURYTHERMAL.

STOCK—A related group or subpopulation. See POPULATION and SUBPOPULATION.

STOMATOPODA—An order of highly specialized carnivorous crustaceans commonly referred to as mantis shrimp.

SUBADULTS—Maturing individuals that are not yet sexually mature.

SUBLITTORAL—The benthic zone along a coast or lake that extends from mean low tide to depths of about 200 m.

SUBPOPULATION—A breeding unit (deme) of a larger population. These units may differ little genetically and taxonomically. See SUBSPECIES. Subpopulations may intergrade with some interbreeding, or they may occupy a common seasonal range prior to the mating season. The units may have different reproduction times and be separated spatially or temporally. See RACE, STOCK, and POPULATION.

SUBSPECIES—A taxonomic class assigned to populations and/or subpopulations when interbreeding (gene flow) between populations is limited, and there are significant differences in some combination of characteristics between subspecies (e.g., appearance, anatomy, ecology, physiology, and behavior). While successful interbreeding can occur when the groups are in contact, under natural conditions reproductive isolation is complete and the groups are considered distinct. Classification of such groups is based on the comparative study and judgement of phylogenists. A second epithet for each subspecies is added to the binomial for the species (e.g., Oncorhynchus clarki clarki). See SPECIES, POPULATION, and SUBPOPULATION.

SUBTIDAL—See SUBLITTORAL.

SUPRALITTORAL—The splash zone of land (adjacent to the sea) that is above the mean high tide level.

SUSPENSION FEEDER—An animal that feeds directly or by filtration on minute organisms and organic debris that is suspended in the water column.

SYMBIOSIS—The relationship between two interacting organisms that is positive, negative, or neutral in its effects on each species. See COMPETITION, MUTUALISM, PARASITISM, and PREDATION.

SYMPATRIC—Species inhabiting the same or overlapping geographic areas.

TAXONOMY—A system of describing, naming, and classifying animals and plants into related groups based on common features (e.g., structure, embryology, and biochemistry).

TEMPORAL—Pertaining to time. Used to describe organism activities, developmental stages, and distributions as they relate to daily, seasonal, or geologic time periods.

TERRITORY—An area occupied and used by an individual, pair, or larger social group, and from which other individuals or groups of the species are excluded, often with the aid of auditory, olfactory, and visual signals, threat displays, and outright combat.

TEST—A rigid calcareous exoskeleton produced by some echinoderms in the class Echinoidea (e.g., sea urchins and sand dollars).

THERMOCLINE—A relatively narrow boundary layer of water where temperature decreases rapidly with depth. Little water or solute exchange occurs across the thermocline, which is maintained by solar heating of the upper water layers.

TIDAL FRESH ZONE—The portion of an estuary with annual depth-averaged salinities of less than 0.5 parts per thousand (‰).

TINTINNIDAE—A family of ciliated protozoans.

TOTAL LENGTH—Length of a fish measured as a straight line from the anterior end of the snout to the distal end of the caudal fin.

TREMATODA—A class of parasitic flatworms of the phylum Platyhelminthes. Trematodes have one or more muscular, external suckers and are also known as flukes.

TROCHOPHORE—A molluscan larval stage (except in Cephalopoda) following gastrulation (embryonic stage characterized by the development of a simple gut). It is commonly ciliated, biconically shaped, and free-swimming; it establishes an evolutionary link between annelids and molluscs, since both groups display a similar life stage.

TROPHIC LEVEL—The feeding level in an ecosystem food chain characterized by organisms that occupy a similar functional position. At the first level are autotrophs or producers (e.g., algae and seagrass); at the second level are herbivores (e.g., copepods and molluscs); at the third level and above are carnivores (e.g., fishes). Omnivores feed at the second and third levels. Decomposers and detritivores may feed at all trophic levels. See FOOD WEB and PRODUCTION.

TURBELLARIA—A class of mostly aquatic, non-parasitic flatworms that are leaf-shaped and covered with cilia.

TWO-YEAR-OLD—A fish that is a member of age-group II, in its third calendar year.

UMBO—A dorsal protuberance on each shell (valve) of a bivalve mollusc, which rises above the line of articulation and is the oldest part of the shell.

UPWELLING—The process whereby prevailing seasonal winds create surface currents that allow nutrient-rich cold water from the ocean depths to move into the euphotic or epipelagic zone. This process breaks down the thermocline and increases primary productivity, and ultimately fish abundance.

VELICONCHA—A bivalve larval stage. A veliconcha has two larval shells and moves by using its velum.

VELIGER—A ciliated larval stage common in molluscs. This stage forms after the trochophore larva and has some adult features, such as a shell and foot.

VELUM—The ciliated swimming organ of a larval mollusc.

VIVIPAROUS—Refers to animals that produce live offspring; eggs are retained and fertilized in the female (as compared to OVIPAROUS).

WATER COLUMN—The water mass between the surface and the bottom.

YEAR-CLASS—Refers to animals of a species population hatched or born in the same year at about the same time; also known as a cohort. Strong year-classes result when there is high larval and juvenile survival; the reverse is true for weak year-classes. The effects of strong and weak year-classes on population size and structure may persist for years in long-lived species. Variation in year-class strength often affects fisheries. See DISTRIBUTION and STOCK.

YEARLING—A fish that is a member of age-group I, in its second calendar year.

YOLK SAC LARVA—A larval fish still bearing yolk, also called a prolarva.

YOUNG-OF-YEAR—Young fish of age-group 0, from transformation into juvenile until January 1.

ZOEA—An early larval stage of various marine crabs and shrimp; zoea have many appendages and long dorsal and anterior spines.

ZOOPLANKTON—Animal members of the plankton. Most range in size from microscopic to about 2.54 cm (1 inch) in length. They reside primarily in the epipelagic zone and feed on phytoplankton and each other. Although they have only a limited ability to swim against currents, many undertake diel migrations. Taxa include protozoa, jellyfish, comb jellies, arrowworms, lower chordates, copepods, water fleas, krill, and the larvae of many fish and invertebrates that are not planktonic as adults.

## Table 6. Habitat Associations

**Terms used in Table 6, Habitat Associations:**

**Domain** - General habitat of life stages.

- *Freshwater*- Rivers and lakes above head-of-tide; freshwater lentic and lotic habitats.
  - *Lacustrine* - Freshwater lentic areas (lakes) with riverine connections to the sea..
  - *Riverine - coastal plain* - River portions in the relatively flat land along a coast.
  - *Riverine - inland* - River portions away from the coast.
- *Estuarine* - Embayment with tidal fresh, mixing, and seawater zones.
  - *Inlet mouth* - The seaward end of an estuary.
  - *Channel* - The drowned river channel or tributary channels of an estuary.
  - *Inter- and subtidal flats* - Broad, shallow estuarine areas.
  - *Salinity range, NEI* - Three salinity zones used by the ELMR program for compilation of distribution and abundance data.
    - *Tidal fresh zone* - Salinities of 0.0-0.5‰.
    - *Mixing zone* - Salinities of 0.5-25.0‰.
    - *Seawater zone* - Salinities >25‰.
  - *Salinity range, Venice system* - Five salinity zones according to the Venice system of estuarine classification.
    - *Limnetic* - Salinities of 0.0-0.5‰.
    - *Oligohaline* - Salinities of 0.5-5.0‰.
    - *Mesohaline* - Salinities of 5-18‰.
    - *Polyhaline* - Salinities of 18-30‰.
    - *Euhaline* - Salinities >30‰.
  - *Temperature range* - The temperatures at which a life stage is typically found, from 0°C to >30°C
- *Marine* - Coastal and offshore
  - *Beach/surf* - Shore areas receiving ocean waves and wash.
  - *Neritic* - Residing from the shore to the edge of the continental shelf.
  - *Oceanic* - Residing beyond the edge of the continental shelf.

**Substrate preference** - Size of substrate that life stages reside on or in.

- *Mud/clay/silt* - Fine substrates <0.0625 mm in diameter.
- *Sand* - Substrates 0.0625-4.0 mm in diameter.
- *Pebble/cobble/gravel* - Substrates 4-256 mm in diameter.
- *Boulder/rocky outcrop/reef*- Large substrate >256 mm in diameter, exposed solid bedrock, or coral reef.
- *Shell* - Mollusc shell substrate, such as oyster.
- *Submergent vegetation* - Rooted aquatic vegetation that does not grow above the water's surface, e.g., turtle grass (*Thalassia testudinum*), shoal grass (*Halodule wrightii*), and widgeon grass (*Ruppia maritima*).
- *Emergent vegetation* - Rooted aquatic vegetation that grows above the water's surface, e.g., cordgrass (*Spartina*) and mangrove.
- *Floating vegetation* - Non-rooted aquatic vegetation, e.g., *Sargassum*, and other vegetation that can form floating mats.
- *None* - No known substrate preferences.

**Depth preference** -

- *Littoral* -
  - *Intertidal* - From the high tide mark to depths of 1 m.
  - *Subtidal* - At depths of 1-10 m.
- Sublittoral -
  - *Inner shelf* (10-50 m) - On or over the continental shelf at depths of 10-50 m.
  - *Middle shelf* (50-100) - On or over the continental shelf at depths of 50-100 m.
  - *Outer shelf* (100-200 m) - On or over the continental shelf at depths of 100-200 m.

**Table 6. Habitat Associations**

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs

| | | Habitat Associations | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Domain | | | | | | | | | | | | | | | | | | | | | | | | Substrate preference | | | | | | | | | Depth preference | | | | |
| | | Freshwatr. | | | Estuarine | | | | | | | | | | | | | | | | | | Marine | | | | | | | | | | | | Littoral | Sublittoral | | | |
| | | | | | | | | Salinity range | | | | | | | | Temperature range | | | | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | NEI | | | Venice system | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Species / life stage | | Lacustrine | Riverine - coastal plain | Riverine - inland | Inlet mouth | Channel | Inter- and subtidal flats | Tidal fresh (0-0.5‰) | Mixing (0.5-25‰) | Seawater (>25‰) | Limnetic (0-0.5‰) | Oligohaline (0.5-5‰) | Mesohaline (5-18‰) | Polyhaline (18-30‰) | Euhaline (>30‰) | 0-5°C | 5-10°C | 11-15°C | 16-20°C | 21-25°C | 26-30°C | >30°C | Beach/surf | Neritic | Oceanic | Mud/silt/clay | Sand | Pebble/cobble/gravel | Boulder/rocky outcrop | Shell | Submergent vegetation | Emergent vegetation | Floating vegetation | None | Intertidal | Subtidal | Inner shelf (10-50 m) | Middle shelf (50-100 m) | Outer shelf (100-200 m) |
| Bay scallop | A | | | | | | ● | | ● | ● | | | | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | | ● | | | | ● | ● | ● | | |
| *Argopecten* | S | | | | | | ● | | ● | ● | | | | ● | ● | | | | | | ● | | | ● | | ● | ● | | | | ● | | | | ● | ● | ● | | |
| *irradians* | J | | | | | | ● | | ● | ● | | | | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | ● | ● | | ● | | ● | ● | ● | | |
| | L | | | | | | ● | | ● | ● | | | | ● | ● | | | | ● | ● | ● | | | ● | | | | | | ● | ● | ● | ● | | ● | ● | ● | | |
| | E | | | | | | ● | | ● | ● | | | | ● | ● | | | | ● | ● | | | | ● | | | | | | | | | | ● | ● | ● | ● | | |
| American oyster | A | | | | | | ● | | ● | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | | | | | ● | ● | | | |
| *Crassostrea* | S | | | | | | ● | | ● | ● | | | ● | ● | ● | | | | | ● | ● | | ● | | | ● | ● | ● | ● | ● | | | | | ● | ● | | | |
| *virginica* | J | | | | | | ● | | ● | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | | | | | ● | ● | | | |
| | L | | | | | | ● | | ● | ● | | | ● | ● | ● | | | | | ● | ● | ● | ● | | | | | | | ● | | | | | ● | ● | | | |
| | E | | | | | | ● | | ● | ● | | | ● | ● | ● | | | | ● | ● | ● | | ● | | | | | | | | | | | ● | ● | ● | | | |
| Atlantic rangia | A | | ● | | | | ● | ● | ● | | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | | | ● | ● | | | ● | | | |
| *Rangia* | S | | ● | | | | ● | ● | ● | | ● | ● | ● | ● | | | | | ● | ● | | | | | | ● | ● | | | | | ● | ● | | | ● | | | |
| *cuneata* | J | | ● | | | | ● | ● | ● | | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | | | ● | ● | | | ● | | | |
| | L | | ● | | | | ● | ● | ● | | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | | | ● | ● | | | ● | | | |
| | E | | ● | | | | ● | ● | ● | | ● | ● | ● | ● | | | | | ● | ● | ● | ● | | | | | | | | | | | | ● | | ● | | | |
| Hard clam | A | | | | | | ● | | ● | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | ● | ● | | ● | | ● | ● | ● | | |
| *Mercenaria* | S | | | | | | ● | | ● | ● | | | | ● | ● | | | | | ● | ● | | | ● | | ● | ● | | | ● | ● | | ● | | ● | ● | ● | | |
| species | J | | | | | | ● | | ● | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | ● | ● | | ● | | ● | ● | ● | | |
| | L | | | | | | ● | | ● | ● | | | | ● | ● | | | ● | ● | ● | ● | ● | | ● | | | | ● | ● | ● | ● | | | | ● | ● | ● | | |
| | E | | | | | | ● | | ● | ● | | | | ● | ● | | | ● | ● | ● | ● | ● | | ● | | | | | | | | | | ● | ● | ● | ● | | |
| Bay squid | A | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | ● | | |
| *Lolliguncula* | S | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | | | ● | ● | ● | | | | ● | | | | | | | | | | ● | | ● | ● | | |
| *brevis* | J | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | ● | | |
| | L | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | | | ● | ● | ● | | | | ● | | | | | | | | | | ● | | ● | ● | | |
| | E | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | | | ● | ● | ● | | | | ● | | | ● | ● | ● | | | | | | | ● | ● | | |
| Brown shrimp | A | | | | ● | | | | ● | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | | | | | | | | ● | ● | |
| *Penaeus* | S | | | | | | | | | ● | | | | | ● | | | | ● | ● | ● | | | ● | | ● | ● | | | | | | | | | | | ● | |
| *aztecus* | J | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | | | | | ● | ● | | | ● | ● | | | |
| | L | | | | | ● | | | ● | ● | | | | ● | ● | | | ● | ● | ● | ● | ● | | ● | | ● | | | | | ● | | | ● | | | ● | ● | |
| | E | | | | | | | | | ● | | | | | ● | | | | | | ● | ● | | ● | | | | | | | | | | ● | | | | ● | |

Table 6, continued. Habitat Associations

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs
M - Mating

| | | Habitat Associations | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Domain | | | | | | | | | | | | | | | | | | | | | | | | Substrate preference | | | | | | | | | Depth preference | | | | |
| | | Freshwatr. | | | Estuarine | | | | | | | | | | | | | | | | | | Marine | | | | | | | | | | | | Littoral | | Sublittoral | | |
| | | | | | | | | Salinity range | | | | | | | | Temperature range | | | | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | NEI | | | Venice system | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Species / life stage | | Lacustrine | Riverine - coastal plain | Riverine - inland | Inlet mouth | Channel | Inter- and subtidal flats | Tidal fresh (0-0.5‰) | Mixing (0.5-25‰) | Seawater (>25‰) | Limnetic (0-0.5‰) | Oligohaline (0.5-5‰) | Mesohaline (5-18‰) | Polyhaline (18-30‰) | Euhaline (>30‰) | 0-5°C | 5-10°C | 11-15°C | 16-20°C | 21-25°C | 26-30°C | >30°C | Beach/surf | Neritic | Oceanic | Mud/silt/clay | Sand | Pebble/cobble/gravel | Boulder/rocky outcrop | Shell | Submergent vegetation | Emergent vegetation | Floating vegetation | None | Intertidal | Subtidal | Inner shelf (10-50 m) | Middle shelf (50-100 m) | Outer shelf (100-200 m) |
| Pink shrimp | A | | | | ● | ● | ● | | | ● | | | | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | ● | | | | | | ● | ● | ● | |
| *Penaeus* | S | | | | | | | | | ● | | | | | ● | | | | ● | ● | ● | ● | | ● | | ● | ● | | | ● | | | | | | ● | ● | | |
| *duorarum* | J | | | | | | ● | | ● | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | ● | ● | ● | | ● | ● | ● | | |
| | L | | | | | | | | | ● | | | | | ● | | | | | ● | ● | | | ● | ● | | | | | | | | | ● | | ● | ● | | |
| | E | | | | | | | | | ● | | | | | ● | | | | | ● | ● | ● | | ● | ● | | | | | | | | | ● | | ● | ● | | |
| White shrimp | A | | | | | ● | | | ● | ● | | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | | | | ● | | | | ● | | |
| *Penaeus* | S | | | | | | | | | ● | | | | | ● | | | | ● | ● | ● | | | ● | | ● | ● | | | | | | | | | | ● | | |
| *setiferus* | J | | | | | ● | ● | | ● | ● | | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | | ● | ● | ● | | ● | ● | | | |
| | L | | | | | | | | | ● | | | | | ● | | | ● | ● | ● | ● | | | ● | | | | | | | ● | | | ● | | | ● | | |
| | E | | | | | | | | | ● | | | | | ● | | | | ● | ● | ● | | | ● | | | | | | | | | | ● | | | ● | | |
| Grass shrimp | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | | | | | ● | ● | ● | ● | | ● | ● | | | |
| *Palaemonetes* | S | | | | | | ● | | ● | ● | | | ● | ● | ● | | | | ● | ● | ● | ● | | | | | | | | | | | ● | | ● | ● | | | |
| *pugio* | J | | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | | | | | ● | ● | ● | | | ● | ● | | | |
| | L | | | | | | ● | | ● | ● | | | ● | ● | ● | | | | | ● | ● | | | | | | | | | | | | ● | ● | ● | ● | | | |
| | E | | | | | | ● | | ● | ● | | | ● | ● | ● | | | | ● | ● | ● | | | | | | | | | | | | | ● | ● | ● | | | |
| Spiny lobster | A | | | | ● | ● | | | ● | ● | | | ● | ● | ● | | | ● | ● | ● | ● | ● | | ● | | | | ● | ● | ● | ● | | | | | ● | ● | ● | |
| *Panulirus* | M | | | | | | | | | ● | | | | | ● | | | | | ● | ● | | | ● | | | | ● | ● | | | | | | | ● | ● | | |
| *argus* | J | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | | | ● | ● | ● | ● | ● | | ● | | | | ● | ● | ● | ● | ● | | | | ● | | | |
| | L | | | | | | | | | ● | | | | | ● | | | | | ● | ● | | | ● | ● | | | | | | | | | ● | | | ● | ● | |
| | E | | | | | | | | | ● | | | | | ● | | | | | ● | ● | | | ● | ● | | | | | | | | | ● | | | ● | ● | |
| Blue crab | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | ● | ● | ● | | | | ● | ● | ● | | |
| *Callinectes* | M | | ● | | | ● | ● | | ● | ● | | ● | ● | ● | | | | | ● | ● | ● | | | | | ● | ● | | | | | | | | ● | ● | | | |
| *sapidus* | J | | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | | ● | ● | ● | | | | ● | ● | ● | | |
| | L | | | | ● | ● | ● | | ● | ● | | | | ● | ● | | | | ● | ● | ● | | | ● | | | | | | | | | | ● | ● | ● | ● | | |
| | E | | | | | | ● | | ● | ● | | | | ● | ● | | | | ● | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| Gulf stone crab | A | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | | | ● | ● | ● | ● | ● | | ● | ● | ● | | |
| *Menippe* | M | | | | | | ● | | ● | ● | | | | | | | | | | ● | ● | | | ● | | | | | ● | ● | ● | ● | ● | | ● | ● | | | |
| *adina* | J | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | | | | ● | ● | ● | ● | ● | | ● | ● | ● | | |
| | L | | | | | | ● | | ● | ● | | | | ● | ● | | | | | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| | E | | | | | | ● | | ● | ● | | | | ● | ● | | | | | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |

Table 6, continued. Habitat Associations

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs
M - Mating
P - Parturition

| Species / life stage | | Lacustrine | Riverine - coastal plain | Riverine - inland | Inlet mouth | Channel | Inter- and subtidal flats | Tidal fresh (0-0.5‰) | Mixing (0.5-25‰) | Seawater (>25‰) | Limnetic (0-0.5‰) | Oligohaline (0.5-5‰) | Mesohaline (5-18‰) | Polyhaline (18-30‰) | Euhaline (>30‰) | 0-5°C | 5-10°C | 11-15°C | 16-20°C | 21-25°C | 26-30°C | >30°C | Beach/surf | Neritic | Oceanic | Mud/silt/clay | Sand | Pebble/cobble/gravel | Boulder/rocky outcrop | Shell | Submergent vegetation | Emergent vegetation | Floating vegetation | None | Intertidal | Subtidal | Inner shelf (10-50 m) | Middle shelf (50-100 m) | Outer shelf (100-200 m) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Habitat Associations** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | Domain | | | | | | | | | | | | | | | | | | | | | | | | Substrate preference | | | | | | | | | Depth preference | | | | |
| | | Freshwatr. | | | Estuarine | | | | | | | | | | | | | | | | | | Marine | | | | | | | | | | | | Littoral | Sublittoral | | | |
| | | | | | | | | Salinity range | | | | | | | | Temperature range | | | | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | NEI | | | Venice system | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Florida stone crab | A | | | | ● | ● | ● | | ● | ● | | | | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | | | | ● | ● | ● | ● | ● | | | ● | ● | | |
| *Menippe* | M | | | | | | ● | | ● | ● | | | | ● | ● | | | | | ● | ● | | | ● | | | | | ● | ● | | ● | | | | ● | ● | | |
| *mercenaria* | J | | | | ● | ● | ● | | ● | ● | | | | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | | | | ● | ● | ● | ● | ● | | | ● | ● | | |
| | L | | | | | | ● | | | ● | | | | ● | ● | | | | | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| | E | | | | | | ● | | | ● | | | | ● | ● | | | | | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| Bull shark | A | | ● | | ● | ● | | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | ● | | |
| *Carcharhinus* | M | | | | | ● | | | | | | | | | | | | | | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| *leucas* | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | ● | | |
| | P | | | | | | ● | | ● | | | ● | ● | ● | | | | | | ● | ● | | | ● | | | | | | | | | | ● | | ● | | | |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Tarpon | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | ● | ● | ● | ● | | ● | ● | | | | | | | | | ● | ● | | |
| *Megalops* | S | | | | | | | | | | | | | | | | | | | | | | | ● | | | | | | | | | | ● | | | ● | ● | |
| *atlanticus* | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | ● | ● | | | | ● | ● | | | | | | | | ● | ● | | | |
| | L | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | ● | ● | ● | ● | | | | | | | | | | ● | | ● | ● | ● | |
| | E | | | | | | | | | | | | | | | | | | | | | | | ● | | | | | | | | | | ● | | | | ● | |
| Alabama shad | A | | ● | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | | | | ● | | | | | | | | | | ● | ● | ● | | | |
| *Alosa* | S | | ● | ● | | | | | | | | | | | | | | | ● | | | | | | | | ● | ● | | | | | | | | | | | |
| *alabamae* | J | | ● | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | | | ● | | | | | | | | | | ● | ● | ● | | | |
| | L | | ● | ● | | | | | | | | | | | | | | | ● | ● | | | | | | | | | | | | | | ● | | | | | |
| | E | | ● | ● | | | | | | | | | | | | | | | ● | ● | | | | | | | | | | | | | | ● | | | | | |
| Gulf menhaden | A | | | | ● | ● | ● | | ● | ● | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | | | | | | | | | ● | ● | ● | ● | ● | |
| *Brevoortia* | S | | | | | | | | | | | | | | | | | | ● | ● | | | | ● | | | | | | | | | | ● | | ● | ● | ● | |
| *patronus* | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | | | | | | | | | ● | ● | ● | ● | | |
| | L | | | | | | | | | | | | | | | | | | ● | ● | | | | ● | | | | | | | | | | ● | | ● | ● | ● | |
| | E | | | | | | | | | | | | | | | | | | ● | ● | | | | ● | | | | | | | | | | ● | | ● | ● | ● | |
| Yellowfin menhaden | A | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | ● | | |
| *Brevoortia* | S | | | | | | | | ● | ● | | | | ● | ● | | | | ● | ● | | | | ● | | | | | | | | | | ● | | ● | ● | | |
| *smithi* | J | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | ● | | |
| | L | | | | | | | | ● | ● | | | | ● | ● | | | | ● | ● | | | | ● | | | | | | | | | | ● | | ● | ● | | |
| | E | | | | | | | | ● | ● | | | | ● | ● | | | | ● | ● | | | | ● | | | | | | | | | | ● | | ● | ● | | |

Table 6, continued. Habitat Associations

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs

| Species / life stage | | Lacustrine | Riverine - coastal plain | Riverine - inland | Inlet mouth | Channel | Inter- and subtidal flats | Tidal fresh (0-0.5‰) | Mixing (0.5-25‰) | Seawater (>25‰) | Limnetic (0-0.5‰) | Oligohaline (0.5-5‰) | Mesohaline (5-18‰) | Polyhaline (18-30‰) | Euhaline (>30‰) | 0-5°C | 5-10°C | 11-15°C | 16-20°C | 21-25°C | 26-30°C | >30°C | Beach/surf | Neritic | Oceanic | Mud/silt/clay | Sand | Pebble/cobble/gravel | Boulder/rocky outcrop | Shell | Submergent vegetation | Emergent vegetation | Floating vegetation | None | Intertidal | Subtidal | Inner shelf (10-50 m) | Middle shelf (50-100 m) | Outer shelf (100-200 m) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Habitat Associations | | Domain: Freshwatr | | | Estuarine | | | Salinity range: NEI | | | Venice system | | | | | Temperature range | | | | | | | Marine | | | Substrate preference | | | | | | | | | Depth preference: Littoral | | Sublittoral | | |
| Gizzard shad | A | ● | ● | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | ● | ● | ● | | ● | | ● | ● | | | |
| *Dorosoma* | S | ● | ● | ● | | | | ● | | | ● | | | | | | | ● | ● | ● | ● | | | | | | | | | | | | | | ● | ● | | | |
| *cepedianum* | J | ● | ● | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | ● | ● | ● | | ● | | ● | ● | | | |
| | L | ● | ● | ● | | | | ● | | | ● | | | | | | | ● | ● | ● | ● | | | | | | | | | | | | | ● | ● | ● | | | |
| | E | ● | ● | ● | | | | ● | | | ● | | | | | | | ● | ● | ● | ● | | | | | | | | | | | | | ● | ● | ● | | | |
| Bay anchovy | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | | | | | | ● | ● | ● | | |
| *Anchoa* | S | | | | | ● | ● | | | ● | | | | | ● | | | | | ● | ● | | | ● | | | | | | | | | | ● | ● | ● | ● | | |
| *mitchilli* | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | | | | | | ● | ● | ● | | |
| | L | | | | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | | | | | | | | | ● | ● | ● | ● | | |
| | E | | | | | ● | | | ● | ● | | | ● | ● | ● | | | | | ● | ● | ● | | ● | | | | | | | | | | ● | ● | ● | ● | ● | ● |
| Hardhead catfish | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | ● | ● | | | | ● | ● | ● | | |
| *Arius* | S | | | | | | | | ● | ● | | ● | ● | ● | ● | | | | | | ● | ● | | ● | | | | | | | | | | | ● | ● | ● | | |
| *felis* | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | ● | | | | ● | ● | ● | | |
| | L | | | | | | | | ● | ● | | ● | ● | ● | ● | | | | ● | ● | ● | ● | | | | | | | | | | | | ● | ● | ● | ● | | |
| | E | | | | | | | | ● | ● | | ● | ● | ● | ● | | | | | | ● | ● | | | | | | | | | | | | ● | ● | ● | ● | | |
| Sheepshead minnow | A | | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | | | | | ● | ● | | | |
| *Cyprinodon* | S | | | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | ● | | | | | ● | ● | | | ● | | | | | ● | ● | | | |
| *variegatus* | J | | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | | | | | ● | ● | | | |
| | L | | | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | | | | | ● | ● | | | |
| | E | | | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | ● | | | | | ● | ● | | | ● | | | | | ● | ● | | | |
| Gulf killifish | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | | ● | | | ● | ● | | | |
| *Fundulus* | S | | ● | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | ● | ● | | | ● | ● | | | |
| *grandis* | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | | ● | | | ● | ● | | | |
| | L | | | | | | ● | | ● | ● | | | ● | ● | ● | | | | | ● | ● | ● | | | | ● | ● | | | ● | ● | ● | | | ● | ● | | | |
| | E | | | | | | ● | | ● | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | ● | ● | | | ● | ● | | | |
| Silversides | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | ● | ● | | | ● | ● | | | |
| *Menidia* | S | | ● | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | ● | ● | | | | | | | | | ● | ● | | | ● | ● | | | |
| species | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | ● | ● | | | ● | ● | | | |
| | L | | ● | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | | ● | ● | | | | | ● | ● | | | ● | ● | ● | | | ● | ● | | | |
| | E | | ● | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | ● | ● | | | ● | ● | | | |

Table 6, continued. Habitat Associations

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs

| Species / life stage | | Habitat Associations | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Domain | | | | | | | | | | | | | | | | | | | | | | | | Substrate preference | | | | | | | | | Depth preference | | | | |
| | | Freshwatr. | | | Estuarine | | | | | | | | | | | | | | | | | | | Marine | | | | | | | | | | | Littoral | Sublittoral | | | |
| | | | | | | | | Salinity range | | | | | | | | Temperature range | | | | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | NEI | | | Venice system | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | Lacustrine | Riverine - coastal plain | Riverine - inland | Inlet mouth | Channel | Inter- and subtidal flats | Tidal fresh (0-0.5‰) | Mixing (0.5-25‰) | Seawater (>25‰) | Limnetic (0-0.5‰) | Oligohaline (0.5-5‰) | Mesohaline (5-18‰) | Polyhaline (18-30‰) | Euhaline (>30‰) | 0-5°C | 5-10°C | 11-15°C | 16-20°C | 21-25°C | 26-30°C | >30°C | Beach/surf | Neritic | Oceanic | Mud/silt/clay | Sand | Pebble/cobble/gravel | Boulder/rocky outcrop | Shell | Submergent vegetation | Emergent vegetation | Floating vegetation | None | Intertidal | Subtidal | Inner shelf (10-50 m) | Middle shelf (50-100 m) | Outer shelf (100-200 m) |
| Snook | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | | ● | | ● | ● | ● | | ● | ● | ● | | | ● | ● | | | |
| *Centropomus* | S | | | | | | | | ● | ● | | | | ● | ● | | | | | | ● | | ● | | | | | | | | | | | ● | ● | ● | | | |
| *undecimalis* | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | | | | ● | ● | ● | | ● | ● | ● | | | ● | ● | | | |
| | L | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | | ● | ● | | | | | | | | | | | | | ● | ● | ● | | | |
| | E | | | | ● | ● | ● | | ● | ● | | | | ● | ● | | | | | | ● | | | | | | | | | | | | | ● | ● | ● | | | |
| Bluefish | A | | | | ● | ● | | | ● | ● | | | | ● | ● | | | | ● | ● | | | ● | ● | | | | | | | | | | ● | | ● | ● | ● | ● |
| *Pomatomus* | S | | | | | | | | | | | | | | | | | ● | ● | ● | ● | | | ● | | | | | | | | | | ● | | | | | |
| *saltatrix* | J | | | | ● | ● | ● | | ● | ● | | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | ● | ● | | | ● | | | ● | | | | | ● | ● | ● | | |
| | L | | | | | | | | | | | | | | | | | | | ● | ● | | | ● | | | | | | | | | | ● | | | ● | ● | ● |
| | E | | | | | | | | | | | | | | | | | | ● | ● | ● | | | ● | | | | | | | | | | ● | | | | ● | ● |
| Blue runner | A | | | | ● | ● | | | ● | ● | | | | ● | ● | | | | | ● | ● | | | ● | ● | ● | | | | ● | | | | | | | ● | ● | ● |
| *Caranx* | S | | | | | | | | | | | | | | | | | | | | | | | ● | | | | | | | | | | ● | | | ● | ● | ● |
| *crysos* | J | | | | ● | ● | | | ● | ● | | | | ● | ● | | | | | ● | ● | | | ● | | ● | | | | ● | | | ● | | | | ● | ● | ● |
| | L | | | | | | | | | | | | | | | | | | | ● | ● | | | ● | | | | | | | | | | ● | | | | ● | ● |
| | E | | | | | | | | | | | | | | | | | | | | | | | ● | | | | | | | | | | ● | | | | ● | ● |
| Crevalle jack | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | | ● | | ● | ● | | | ● | | | | | | ● | ● | ● | |
| *Caranx* | S | | | | | | | | | | | | | | | | | | | | | | | ● | | | | | | | | | | ● | | | ● | ● | |
| *hippos* | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | | ● | | ● | ● | | | ● | | | | | ● | ● | ● | | |
| | L | | | | | | | | | | | | | | ● | | | | | ● | ● | | | ● | | | | | | | | | | ● | | | ● | ● | |
| | E | | | | | | | | | | | | | | ● | | | | | | | | | ● | | | | | | | | | | ● | | | ● | ● | |
| Florida pompano | A | | | | ● | ● | | | ● | ● | | | ● | ● | ● | | | | ● | ● | ● | ● | ● | ● | | ● | ● | | ● | ● | | | | | | ● | ● | | |
| *Trachinotus* | S | | | | | | | | | | | | | | | | | | | | | | | ● | | | | | | | | | | ● | | | ● | | |
| *carolinus* | J | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | | | ● | ● | ● | ● | ● | ● | ● | | | ● | | | ● | | | ● | | ● | ● | | | |
| | L | | | | | | | | | | | | | | | | | | | | | | | ● | | | | | | | | | | ● | ● | ● | | | |
| | E | | | | | | | | | | | | | | | | | | | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | ● | | |
| Gray snapper | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | | ● | | ● | ● | ● | ● | ● | ● | | ● | | | ● | ● | | |
| *Lutjanus* | S | | | | | | | | | ● | | | | | ● | | | | | ● | ● | | | ● | | | | | ● | ● | | | | | | ● | ● | | |
| *griseus* | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | ● | ● | | ● | | ● | ● | | ● | ● | ● | | ● | | | ● | ● | | |
| | L | | | | | | | | ● | ● | | ● | ● | ● | | | | | ● | ● | ● | | | ● | | ● | | | | | ● | | ● | | | ● | ● | | |
| | E | | | | | | | | | ● | | | | ● | ● | | | | | ● | ● | | | ● | | | | | ● | ● | | | | | | ● | ● | | |

Table 6, continued. Habitat Associations

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs

| Species / life stage | | Habitat Associations: Domain | | | | | | | | | | | | | | | | | | | | | | | | Substrate preference | | | | | | | | | Depth preference | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Freshwatr | | | Estuarine | | | | | | | | | | | | | | | | | | | Marine | | | | | | | | | | | | Littoral | | Sublittoral | | |
| | | | | | | | | Salinity range | | | | | | | | Temperature range | | | | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | NEI | | | Venice system | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | Lacustrine | Riverine - coastal plain | Riverine - inland | Inlet mouth | Channel | Inter- and subtidal flats | Tidal fresh (0-0.5‰) | Mixing (0.5-25‰) | Seawater (>25‰) | Limnetic (0-0.5‰) | Oligohaline (0.5-5‰) | Mesohaline (5-18‰) | Polyhaline (18-30‰) | Euhaline (>30‰) | 0-5°C | 5-10°C | 11-15°C | 16-20°C | 21-25°C | 26-30°C | >30°C | Beach/surf | Neritic | Oceanic | Mud/silt/clay | Sand | Pebble/cobble/gravel | Boulder/rocky outcrop | Shell | Submergent vegetation | Emergent vegetation | Floating vegetation | None | Intertidal | Subtidal | Inner shelf (10-50 m) | Middle shelf (50-100 m) | Outer shelf (100-200 m) |
| Sheepshead | A | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | | | ● | ● | | ● | ● | | | ● | ● | | |
| *Archosargus probatocephalus* | S | | | | | | | | | ● | | | | | ● | | | | | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| | J | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | | | | | ● | | | ● | ● | ● | | ● | | ● | | | | |
| | L | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | | | | | ● | ● | | | ● | | | | | | | ● | | ● | | ● | ● | ● | | |
| | E | | | | | | | | | ● | | | | | ● | | | | | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| Pinfish | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | | | | | | ● | | ● | | | | ● | | |
| *Lagodon rhomboides* | S | | | | | | | | | ● | | | | | ● | | | | ● | ● | ● | | | | | | | | | | | | | ● | | | ● | | |
| | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | | | | | | ● | | ● | | ● | ● | | | |
| | L | | | | | ● | ● | | | | | | | ● | ● | | | | ● | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| | E | | | | | | | | | | | | | | ● | | | | ● | ● | ● | | | ● | | | | | | | | | | ● | | | ● | | |
| Silver perch | A | | | | ● | ● | | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | | ● | | ● | | | ● | ● | | |
| *Bairdiella chrysoura* | S | | | | ● | ● | | | ● | ● | | | ● | ● | ● | | | | ● | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | | ● | | ● | | | ● | | | |
| | L | | | | | ● | ● | | ● | ● | | ● | ● | ● | ● | | | | ● | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | ● | | |
| | E | | | | | ● | | | ● | ● | | | ● | ● | ● | | | | ● | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| Sand seatrout | A | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | | | ● | ● | ● | ● | ● | | ● | | ● | ● | | | ● | | | | | | ● | ● | ● | |
| *Cynoscion arenarius* | S | | | | | | | | ● | ● | | | ● | ● | | | | | ● | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | ● | ● | |
| | J | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | | | | | ● | | ● | | | ● | ● | | |
| | L | | | | | ● | ● | | ● | ● | | | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | | | | | ● | | ● | | | ● | ● | | |
| | E | | | | | ● | | | ● | ● | | | | ● | ● | | | | ● | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | ● | ● | |
| Spotted seatrout | A | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | | | | ● | | | ● | | | ● | | | |
| *Cynoscion nebulosus* | S | | | | | ● | ● | | ● | ● | | | ● | ● | ● | | | | ● | ● | ● | | ● | | | | ● | | | | | | ● | | | ● | | | |
| | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | | | ● | | | | ● | ● | ● | ● | | | ● | | | |
| | L | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | | | ● | | | | | ● | | ● | | | ● | | | |
| | E | | | | | | ● | | ● | ● | | | ● | ● | ● | | | | ● | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | | | |
| Spot | A | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | ● | | | | | | ● | ● | ● | |
| *Leiostomus xanthurus* | S | | | | | | | | | ● | | | | | | | | | ● | ● | | | | ● | | | | | | | | | | ● | | | ● | ● | |
| | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | | | | | ● | | ● | | | | ● | ● | |
| | L | | | | | | | | | ● | | | | ● | ● | | | | ● | ● | | | | ● | | | | | | | | | | ● | | ● | ● | ● | |
| | E | | | | | | | | | ● | | | | | | | | | ● | ● | | | | ● | | | | | | | | | | ● | | | ● | ● | |

Table 6, continued. Habitat Associations

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs

| Species / life stage | | Habitat Associations | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Domain | | | | | | | | | | | | | | | | | | | | | | | | Substrate preference | | | | | | | | | Depth preference | | | | |
| | | Freshwatr. | | | Estuarine | | | | | | | | | | | | | | | | | | | Marine | | | | | | | | | | | Littoral | | Sublittoral | | |
| | | | | | | | | Salinity range | | | | | | | | Temperature range | | | | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | NE! | | | Venice system | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | Lacustrine | Riverine - coastal plain | Riverine - inland | Inlet mouth | Channel | Inter- and subtidal flats | Tidal fresh (0-0.5‰) | Mixing (0.5-25‰) | Seawater (>25‰) | Limnetic (0-0.5‰) | Oligohaline (0.5-5‰) | Mesohaline (5-18‰) | Polyhaline (18-30‰) | Euhaline (>30‰) | 0-5°C | 5-10°C | 11-15°C | 16-20°C | 21-25°C | 26-30°C | >30°C | Beach/surf | Neritic | Oceanic | Mud/silt/clay | Sand | Pebble/cobble/gravel | Boulder/rocky outcrop | Shell | Submergent vegetation | Emergent vegetation | Floating vegetation | None | Intertidal | Subtidal | Inner shelf (10-50 m) | Middle shelf (50-100 m) | Outer shelf (100-200 m) |
| Atlantic croaker | A | | ● | | ● | ● | | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | ● | | | | | | ● | ● | ● | |
| *Micropogonias undulatus* | S | | | | | | | | | | | | | | | | | | ● | ● | | | | ● | | | | | | | | | | ● | | | ● | ● | |
| | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | | | | | | ● | ● | ● | | |
| | L | | | | ● | ● | ● | | ● | ● | | | | ● | ● | | | ● | ● | ● | | | | ● | | | | | | | | | | ● | | | | ● | ● |
| | E | | | | | | | | | ● | | | | | ● | | | | ● | ● | | | | ● | | | | | | | | | | ● | | | | ● | ● |
| Black drum | A | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | ● | | | | | | | ● | | |
| *Pogonias cromis* | S | | | | ● | ● | | | ● | ● | | | ● | ● | ● | | | | ● | ● | | | | ● | | | | | | | | | | ● | | | ● | | |
| | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | ● | | | | | ● | ● | ● | | |
| | L | | | | | ● | ● | | ● | ● | | | ● | ● | ● | | | ● | ● | | | | | ● | | | | | | | | | | ● | ● | ● | ● | | |
| | E | | | | | ● | | | ● | ● | | | ● | ● | ● | | | | ● | | | | | ● | | | | | | | | | | ● | | ● | ● | | |
| Red drum | A | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | | | ● | | | | | | ● | ● | ● | |
| *Sciaenops ocellatus* | S | | | | | | | | | | | | | | | | | | | ● | | | | ● | | | | | | | | | | ● | | ● | ● | | |
| | J | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | | | ● | ● | | ● | | ● | ● | | | |
| | L | | | | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | ● | ● | ● | | ● | | ● | ● | | | | ● | | ● | ● | ● | ● | | | |
| | E | | | | | | ● | | ● | ● | | | | ● | ● | | | | | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| Striped mullet | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | | ● | | | | ● | ● | ● | | |
| *Mugil cephalus* | S | | | | | | | | | | | | | | | | | | | ● | | | | ● | | | | | | | | | | | | ● | ● | | |
| | J | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | | | ● | ● | | | | ● | | | | ● | ● | | | |
| | L | | | | | | | | | | | | | | | | | | ● | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| | E | | | | | | | | | | | | | | | | | ● | ● | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | ● | | |
| Code goby | A | | | | | ● | ● | | ● | ● | | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | | | | ● | ● | | | ● | ● | | | | ● | ● | | | |
| *Gobiosoma robustum* | S | | | | | | | | | | | | | | | | | | ● | ● | ● | | | | | ● | | | | | ● | | | | ● | ● | | | |
| | J | | | | | ● | ● | | ● | ● | | ● | ● | ● | ● | | | | | | | | | | | ● | | | | | ● | | | | ● | ● | | | |
| | L | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | ● | ● | ● | | | |
| | E | | | | | | | | | | | | | | | | | | ● | | | | | | | | | | | | | | | ● | ● | ● | | | |
| Spanish mackerel | A | | | | ● | | | | | ● | | | | ● | ● | | | | | ● | ● | ● | | ● | | | | | | | | | | ● | | ● | ● | | |
| *Scomberomorus maculatus* | S | | | | | | | | | | | | | | | | | | | ● | ● | ● | | ● | | | ● | | | | | | | | | | ● | | |
| | J | | | | ● | ● | ● | | ● | ● | | ● | ● | ● | ● | | | ● | ● | ● | ● | ● | ● | ● | | | | | | | | | | ● | | ● | ● | | |
| | L | | | | | | | | | | | | | | | | | | ● | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| | E | | | | | | | | | | | | | | | | | | | ● | ● | ● | | ● | | | | | | | | | | ● | | | ● | | |

Table 6, continued. Habitat Associations

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs

| Species / life stage | | Lacustrine | Riverine - coastal plain | Riverine - inland | Inlet mouth | Channel | Inter- and subtidal flats | Tidal fresh (0-0.5‰) | Mixing (0.5-25‰) | Seawater (>25‰) | Limnetic (0-0.5‰) | Oligohaline (0.5-5‰) | Mesohaline (5-18‰) | Polyhaline (18-30‰) | Euhaline (>30‰) | 0-5°C | 5-10°C | 11-15°C | 16-20°C | 21-25°C | 26-30°C | >30°C | Beach/surf | Neritic | Oceanic | Mud/silt/clay | Sand | Pebble/cobble/gravel | Boulder/rocky outcrop | Shell | Submergent vegetation | Emergent vegetation | Floating vegetation | None | Intertidal | Subtidal | Inner shelf (10-50 m) | Middle shelf (50-100 m) | Outer shelf (100-200 m) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Habitat Associations** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | Domain | | | | | | | | | | | | | | | | | | | | | | | | Substrate preference | | | | | | | | | Depth preference | | | | |
| | | Freshwatr. | | | Estuarine | | | | | | | | | | | | | | | | | | Marine | | | | | | | | | | | | Littoral | Sublittoral | | | |
| | | | | | | | | Salinity range | | | | | | | | Temperature range | | | | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | NEI | | | Venice system | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Gulf flounder *Paralichthys albigutta* | A | | | | | | ● | | ● | ● | | | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | | ● | | | | | | | | ● | ● | ● | | |
| | S | | | | | | | | | | | | | | | | | | ● | ● | | | | ● | | | ● | | | | | | | | | ● | ● | | |
| | J | | | | | | ● | | ● | ● | | | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | | ● | | | | ● | | ● | | ● | ● | ● | | |
| | L | | | | | ● | ● | | | ● | | | | | ● | | | | ● | ● | | | | ● | | | | | | | | | | ● | ● | ● | ● | | |
| | E | | | | | | | | | ● | | | | | ● | | | | ● | ● | | | | ● | | | | | | | | | | ● | | ● | ● | | |
| Southern flounder *Paralichthys lethostigma* | A | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | | | | | | | ● | ● | | |
| | S | | | | | | | | ● | ● | | | ● | ● | ● | | | ● | ● | ● | | | | ● | | | | | | | | | | ● | | ● | ● | | |
| | J | | ● | | ● | ● | ● | | ● | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | ● | ● | | | | ● | | ● | | | ● | ● | | |
| | L | | | | ● | ● | ● | | ● | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |
| | E | | | | | | | | ● | ● | | | ● | ● | ● | | ● | ● | ● | ● | ● | | | ● | | | | | | | | | | ● | | ● | ● | | |

## Table 7. Biological Attributes

**Terms used in Table 7. Biological Attributes:**

**Life Mode** - The usual location within the water column.
- *Benthic* - In the bottom sediments.
- *Epibenthic* - On, but not in, the bottom.
- *Demersal* - In the water column, but near the bottom.
- *Nektonic* - In the water column away from the bottom, and capable of locomotion.
- *Planktonic* - In the water column, but not capable of extensive movements.

**Spatial strategy** - Use of habitats by life stages.
- *Freshwater resident* - Resides primarily in freshwater habitats.
- *Estuarine resident* - Resides primarily in estuarine habitats (salinities ≥0.5 and ≤25‰).
- *Marine resident* - Resides primarily in seawater habitats (salinities >25‰).
- *Coastal migrant* - Migrates within nearshore waters of the continental shelf.
- *Ocean migrant* - Migrates in ocean waters beyond the continental shelf.

**Mobility** -
- *Non-mobile* - Sessile or sedentary.
- *Low mobility* - Capable of limited directed movements.
- *High mobility* - Capable of extensive directed movements.

**Feeding Type** -
- *Filter feeder* - Obtains food items by filtering water or fine sediments.
- *Non-filter feeder* - Obtains food items by other means, such as selective predation.

**Prey Items** - Food items typically consumed by an organism, such as detritus, phytoplankton, zooplankton, fish, etc.

**Longevity** - Average lifespan of a particular life stage, from 1 day to >20 years.

**Value**-
- *Recreational* - Often sought and harvested by sport anglers.
- *Commercial* - Harvested by commercial fishermen for market.
- *Ecological* - Of major importance in aquatic ecosystems as a predator or prey species, etc.
- *Indicator of stress* - Often used in studies of environmental stress.

**Table 7. Biological Attributes**

<u>Life stage</u>
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs

| Species / life stage | | Life Mode: Epibenthic | Benthic | Demersal | Nektonic | Planktonic | Spatial Strategy: Freshwater resident | Estuarine resident | Marine resident | Coastal migrant | Ocean migrant | Mobility: Nonmobile | Low mobility | High mobility | Feed*: Filter feeder | Non-filter feeder | Prey Items: Detritus | Phytoplankton | Zooplankton | Infauna | Epibenthos | Insects | Fish (eggs, larvae) | Fish (juveniles, adults) | Macroalgae | Vascular plants | Longevity: 1 day | 1-30 days | 1-12 months | 1-5 years | 5-20 years | >20 years | Value: Recreational | Commercial | Ecological | Indicator of stress |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bay scallop *Argopecten irradians* | A | ● | | | | | | ● | ● | | | | ● | | ● | | ● | ● | ● | | | | | | | | | | | ● | | | ● | ● | ● | ● |
| | S | ● | | | | | | ● | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | ● | | | | | | ● | ● | | | | ● | | ● | | ● | ● | ● | | | | | | | | | | ● | | | | | ● | ● | ● |
| | L | ● | | | | ● | | ● | ● | | | | ● | | ● | | | ● | ● | | | | | | | | | ● | | | | | | | ● | ● |
| | E | | | ● | | ● | | ● | ● | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | | |
| American oyster *Crassostrea virginica* | A | | ● | | | | | ● | | | | ● | | | ● | | ● | ● | ● | | | | | | | | | | | | ● | | ● | ● | ● | ● |
| | S | | ● | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | ● | | | | | ● | | | | ● | | | ● | | ● | ● | ● | | | | | | | | | | ● | | | | | | ● | ● |
| | L | | ● | | | ● | | ● | | | | ● | ● | | ● | | ● | ● | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | | | ● | | ● | | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | | |
| Atlantic rangia *Rangia cuneata* | A | | ● | | | | ● | ● | | | | ● | | | ● | | ● | ● | ● | | | | | | | | | | | | ● | | | ● | ● | ● |
| | S | | ● | | | | ● | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | ● | | | | ● | ● | | | | | ● | | ● | | ● | ● | ● | | | | | | | | | | | ● | | | | ● | ● | ● |
| | L | | | ● | | ● | ● | ● | | | | | ● | | | | ● | ● | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | ● | | ● | ● | ● | | | | | ● | | | | | | | | | | | | | | | ● | | | | | | | | |
| Hard clam *Mercenaria* species | A | | ● | | | | | ● | ● | | | ● | | | ● | | | ● | ● | | | | | | | | | | | | ● | | ● | ● | ● | ● |
| | S | | ● | | | | | ● | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | ● | | | | | ● | ● | | | | ● | | ● | | | ● | ● | | | | | | | | | | | ● | | | ● | ● | ● | ● |
| | L | ● | | | | ● | | ● | ● | | | | ● | | ● | | | ● | ● | | | | | | | | | | ● | | | | | | | |
| | E | | | | | ● | | ● | ● | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | | |
| Bay squid *Lolliguncula brevis* | A | | | | ● | | | ● | ● | | | | | ● | | ● | | | | | ● | | | ● | | ● | | | | ● | | | ● | ● | ● | |
| | S | | | | ● | | | ● | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | | ● | | | ● | ● | | | | | ● | | ● | | | | | ● | | | ● | | ● | | | ● | | | | ● | | ● | |
| | L | | | | ● | | | ● | ● | | | | | ● | | ● | | | ● | | | | ● | | | | | ● | | | | | | | | |
| | E | ● | | | | | | ● | ● | | | ● | | | | | | | | | | | | | | | | ● | | | | | | | | |
| Brown shrimp *Penaeus aztecus* | A | | | ● | | | | | ● | | | | | ● | | ● | ● | | | ● | ● | | | | ● | | | | | ● | | | ● | ● | ● | |
| | S | | | ● | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | | ● | | | | | | ● | | ● | ● | | ● | ● | ● | | ● | | ● | | | | ● | | | | ● | ● | ● | |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | ● | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | ● | | | | | ● | | | ● | | | | ● | | | | | | | | | | | ● | | | | | | | | | |

Table 7, continued. Biological Attributes

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs
M - Mating

| Species / life stage | | Epibenthic | Benthic | Demersal | Nektonic | Planktonic | Freshwater resident | Estuarine resident | Marine resident | Coastal migrant | Ocean migrant | Nonmobile | Low mobility | High mobility | Filter feeder | Non-filter feeder | Detritus | Phytoplankton | Zooplankton | Infauna | Epibenthos | Insects | Fish (eggs, larvae) | Fish (juveniles, adults) | Macroalgae | Vascular plants | 1 day | 1-30 days | 1-12 months | 1-5 years | 5-20 years | >20 years | Recreational | Commercial | Ecological | Indicator of stress |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **Biological Attributes** – Life Mode | | | | | Spatial Strategy | | | | | Mobility | | | Feed* | | Prey Items | | | | | | | | | | Longevity | | | | | | **Value** | | | |
| Pink shrimp *Penaeus duorarum* | A | | | ● | | | | ● | ● | | | | | ● | | ● | ● | | | ● | ● | | | | ● | | | | | ● | | | ● | ● | ● | |
| | S | | | ● | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | | ● | | | | | | ● | | ● | ● | | ● | ● | ● | | | | ● | | | | ● | | | | | ● | ● | |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | ● | ● | | | | ● | | | | | ● | | | | | | | | |
| | E | | | ● | | | | | ● | | | ● | | | | ● | | | | | | | | | | | ● | | | | | | | | | |
| White shrimp *Penaeus setiferus* | A | | | ● | | | | ● | ● | | | | | ● | | ● | ● | | | ● | ● | | | | ● | ● | | | | ● | | | ● | ● | ● | |
| | S | | | ● | | | | | ● | | | | | | | | | | | | | | | | ● | ● | | | | | | | | | | |
| | J | | | ● | | | | ● | | | | | | ● | | ● | ● | | | ● | ● | | | | | | | | ● | | | | ● | ● | ● | ● |
| | L | | | | ● | ● | | | ● | | | | | ● | | ● | | ● | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | ● | | | | | ● | | | ● | | | | | | | | | | | | | | | ● | | | | | | | | | |
| Grass shrimp *Palaemonetes pugio* | A | | | ● | | | ● | ● | | | | | | ● | | ● | ● | | | | ● | | ● | | ● | | | | ● | | | | | | ● | ● |
| | S | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | ● | ● | | | | | | ● | | ● | ● | | | | ● | | ● | | ● | | | | ● | | | | | | ● | ● |
| | L | | | | | ● | | ● | | | | | ● | | | ● | ● | | ● | | | | | | ● | | | ● | | | | | | | ● | ● |
| | E | | | ● | | | | ● | | | | ● | | | | | | | | | | | | | | | | ● | | | | | | | | |
| Spiny lobster *Panulirus argus* | A | | | ● | | | | ● | ● | | | | | ● | | ● | | | | | ● | | | | | | | | | | | ● | ● | ● | ● | |
| | M | | | ● | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | ● | | ● | ● | | | | | ● | | ● | | | | | ● | | | | | | | | | ● | | | | | | |
| | L | | | | | ● | | | ● | | | | ● | | | ● | | | ● | | | | ● | | | | | | ● | | | | | | | |
| | E | | | ● | | | | | ● | | | ● | | | | | | | | | | | | | | | | ● | | | | | | | | |
| Blue crab *Callinectes sapidus* | A | | | ● | | | | ● | | | | | | ● | | ● | ● | | | ● | ● | | | ● | | | | | | ● | | | ● | ● | ● | ● |
| | M | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | | ● | | | | | | ● | | ● | ● | | | ● | ● | | | ● | | | | | ● | | | | ● | ● | ● | ● |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | ● | ● | | | | | | | | | ● | | | | | | | | ● |
| | E | | | | | ● | | ● | | | | ● | | | | | | | | | | | | | | | | ● | | | | | | | | ● |
| Gulf stone crab *Menippe adina* | A | ● | | | | | | ● | ● | | | | ● | | | ● | | | | ● | ● | | | | | | | | | ● | | | ● | ● | ● | |
| | M | ● | | | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | ● | | | | | | ● | ● | | | | ● | | | ● | | | | ● | ● | | | | | | | | ● | | | | | | ● | |
| | L | | | | | ● | | | ● | | | | ● | | | ● | | ● | | | | | | | | | | ● | | | | | | | | |
| | E | ● | | | | | | | ● | | | ● | | | | | | | | | | | | | | | | ● | | | | | | | | |

Table 7, continued. Biological Attributes

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs
M - Mating
P - Parturition

| Species / life stage | | Biological Attributes: Life Mode | | | | | Spatial Strategy | | | | | Mobility | | | Feed* | | Prey Items | | | | | | | | | | Longevity | | | | | | Value | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Epibenthic | Benthic | Demersal | Nektonic | Planktonic | Freshwater resident | Estuarine resident | Marine resident | Coastal migrant | Ocean migrant | Nonmobile | Low mobility | High mobility | Filter feeder | Non-filter feeder | Detritus | Phytoplankton | Zooplankton | Infauna | Epibenthos | Insects | Fish (eggs, larvae) | Fish (juveniles, adults) | Macroalgae | Vascular plants | 1 day | 1-30 days | 1-12 months | 1-5 years | 5-20 years | >20 years | Recreational | Commercial | Ecological | Indicator of stress |
| Florida stone crab *Menippe mercenaria* | A | ● | | | | | | ● | ● | | | | ● | | | ● | | | | ● | ● | | | | | | | | | | ● | | ● | ● | ● | |
| | M | ● | | | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | ● | | | | | | ● | ● | | | | ● | | | ● | | | | ● | ● | | | | | | | | ● | | | | | | ● | |
| | L | | | | | ● | | | ● | | | | ● | | | ● | | | ● | | | | | | | | | ● | | | | | | | | |
| | E | ● | | | | | | | ● | | | ● | | | | | | | | | | | | | | | | ● | | | | | | | | |
| Bull shark *Carcharhinus leucas* | A | | | ● | | | | ● | ● | ● | | | | ● | | | | | | | | | | ● | | | | | | | ● | | ● | ● | ● | |
| | M | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | | ● | | ● | | | | ● | | | | | | | | | | ● | | | | | | | ● | | ● | | ● | |
| | P | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | ● | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Tarpon *Megalops atlanticus* | A | | | ● | | | ● | ● | ● | ● | | | | ● | | ● | | | | | ● | ● | | ● | | | | | | | | ● | ● | | | ● |
| | S | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | ● | ● | ● | | | | | ● | | ● | | | ● | | ● | ● | | ● | | | | | | | ● | | ● | | | ● |
| | L | | | | | ● | ● | ● | ● | | | | | ● | | ● | | | ● | | | ● | | | | | | | ● | | | | | | | |
| | E | | | | | ● | | | ● | | | | | | | | | | | | | | | | | | | ● | | | | | | | | |
| Alabama shad *Alosa alabamae* | A | | | ● | | | ● | ● | ● | | | | | ● | | ● | ● | | | | | ● | | ● | | ● | | | | ● | | | | | ● | |
| | S | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | ● | ● | ● | | | | | ● | | ● | ● | | | | | ● | ● | ● | | ● | | | ● | | | | | | ● | |
| | L | | | | | ● | ● | | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | |
| | E | | | | | ● | ● | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | |
| Gulf menhaden *Brevoortia patronus* | A | | | ● | | | | ● | ● | ● | | | | ● | ● | | ● | ● | ● | | | | ● | | | | | | | ● | | | | ● | ● | ● |
| | S | | | ● | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | | ● | ● | ● | | | | ● | ● | | ● | ● | ● | | | | ● | | | | | | | ● | | | | ● | ● | ● |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | | ● | | | | | | | | | | ● | | | | | | ● | ● |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | |
| Yellowfin menhaden *Brevoortia smithi* | A | | | ● | | | | ● | ● | ● | | | | ● | ● | | ● | ● | ● | | | | ● | | | | | | | | ● | | | | | |
| | S | | | ● | | | | ● | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | ● | ● | ● | ● | | | | ● | ● | | ● | ● | ● | | | | ● | | | | | | | ● | | | | | | |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | | | ● | | ● | ● | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | | |

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Table 7, continued. Biological Attributes

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs

| Species / life stage | | Biological Attributes: Life Mode | | | | | Spatial Strategy | | | | | Mobility | | | Feed* | | Prey Items | | | | | | | | | | Longevity | | | | | | Value | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Epibenthic | Benthic | Demersal | Nektonic | Planktonic | Freshwater resident | Estuarine resident | Marine resident | Coastal migrant | Ocean migrant | Nonmobile | Low mobility | High mobility | Filter feeder | Non-filter feeder | Detritus | Phytoplankton | Zooplankton | Infauna | Epibenthos | Insects | Fish (eggs, larvae) | Fish (juveniles, adults) | Macroalgae | Vascular plants | 1 day | 1-30 days | 1-12 months | 1-5 years | 5-20 years | >20 years | Recreational | Commercial | Ecological | Indicator of stress |
| Gizzard shad *Dorosoma cepedianum* | A | | | | ● | | ● | ● | | | | | | ● | ● | | ● | ● | | ● | ● | | | | ● | ● | | | | ● | | | | | ● | ● |
| | S | | | | ● | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | | ● | | ● | ● | | | | | | ● | ● | | ● | ● | | ● | ● | | | | ● | ● | | | | ● | | | | | ● | ● |
| | L | | | | | ● | ● | | | | | | | ● | | ● | | | ● | | | | | | | | | ● | | | | | | | ● | |
| | E | | | ● | | | ● | | | | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | |
| Bay anchovy *Anchoa mitchilli* | A | | | | ● | | | ● | | | | | | ● | ● | | ● | | ● | | ● | ● | ● | ● | | | | | | ● | | | | | ● | ● |
| | S | | | | ● | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | | ● | | | ● | | | | | | ● | ● | | ● | | ● | | ● | ● | ● | | | | | | ● | | | | | | ● | ● |
| | L | | | | ● | | | ● | | | | | | ● | ● | | ● | | ● | | | | | | | | ● | | | | | | | | ● | |
| | E | | | | | ● | | ● | | | | | | ● | | | | | | | | | | | | | ● | | | | | | | | | |
| Hardhead catfish *Arius felis* | A | | | ● | | | | ● | ● | | | | | ● | | ● | ● | | | ● | ● | ● | ● | ● | ● | ● | | | | ● | | | | | ● | ● |
| | S | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | | ● | ● | | | | | ● | | ● | ● | | ● | ● | ● | ● | ● | ● | ● | ● | | | ● | | | | | | ● | ● |
| | L | | | ● | | | | ● | | | | | ● | | | ● | | | | | | | | | | | | ● | | | | | | | | |
| | E | | | ● | | | | ● | | | | ● | | | | | | | | | | | | | | | | ● | | | | | | | | |
| Sheepshead minnow *Cyprinodon variegatus* | A | | | ● | | | | ● | | | | | | ● | | ● | ● | ● | ● | | ● | ● | ● | ● | ● | ● | | | | ● | | | ● | ● | ● | ● |
| | S | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | ● |
| | J | | | ● | | | | ● | | | | | | ● | | ● | ● | ● | ● | | ● | ● | ● | | ● | ● | | | ● | | | | ● | | ● | ● |
| | L | | | ● | | | | ● | | | | | ● | | | ● | | ● | ● | | | | | | | | | ● | | | | | | | | ● |
| | E | | | ● | | | | ● | | | | ● | | | | | | | | | | | | | | | | ● | | | | | | | | ● |
| Gulf killifish *Fundulus grandis* | A | | | | ● | | ● | | | | | | ● | | | ● | ● | | | | ● | ● | | ● | ● | ● | | | | ● | | | ● | ● | ● | ● |
| | S | | | ● | | | ● | | | | | | | | | | | | | | | | | | | | | | ● | | | | | | | |
| | J | | | | ● | | ● | | | | | | ● | | | ● | ● | | | | ● | ● | ● | ● | ● | ● | | | ● | | | | ● | ● | ● | ● |
| | L | | | | ● | | ● | | | | | ● | | | | ● | | | ● | | | | | | | | | | | | | | | | | |
| | E | | | ● | | | ● | | | | ● | | | | | ● | | | | | | | | | | | | ● | | | | | | | | |
| Silversides *Menidia* species | A | | | ● | | | | ● | | | | | | ● | | ● | ● | | | | ● | ● | ● | ● | ● | ● | | | | ● | | | | | ● | ● |
| | S | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | | ● | | | | | | ● | | ● | ● | | ● | | ● | ● | ● | | ● | ● | | | ● | | | | | | ● | ● |
| | L | | | ● | | | | ● | | | | | ● | | | ● | | | ● | | | | | | | | | ● | | | | | | | | ● |
| | E | | | ● | | | | ● | | | | ● | | | | | | | | | | | | | | | | ● | | | | | | | | ● |

Table 7, continued. Biological Attributes

<u>Life stage</u>
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs

| | | Biological Attributes | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Value | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Life Mode | | | | | Spatial Strategy | | | | | Mobility | | | Feed* | | Prey Items | | | | | | | | | | Longevity | | | | | | | | | |
| **Species / life stage** | | Epibenthic | Benthic | Demersal | Nektonic | Planktonic | Freshwater resident | Estuarine resident | Marine resident | Coastal migrant | Ocean migrant | Nonmobile | Low mobility | High mobility | Filter feeder | Non-filter feeder | Detritus | Phytoplankton | Zooplankton | Infauna | Epibenthos | Insects | Fish (eggs, larvae) | Fish (juveniles, adults) | Macroalgae | Vascular plants | 1 day | 1-30 days | 1-12 months | 1-5 years | 5-20 years | >20 years | Recreational | Commercial | Ecological | Indicator of stress |
| Snook | A | | | ● | | | | ● | ● | | | | | ● | | ● | | | | | ● | | | ● | | ● | | | | | ● | | ● | ● | | |
| *Centropomus* | S | | | | ● | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *undecimalis* | J | | | ● | | | ● | ● | | | | | | ● | | ● | | | ● | | ● | ● | ● | ● | | ● | | | | ● | | | ● | ● | | |
| | L | | | | | ● | | ● | | | | | | ● | | ● | | ● | ● | | | | | | | ● | | | ● | | | | | | | |
| | E | | | | | | | ● | | | | | | ● | | | | | | | | | | | | | ● | | | | | | | | | |
| Bluefish | A | | | | ● | | | | ● | ● | | | | ● | | ● | | | | | ● | | | ● | | | | | | | ● | | ● | ● | | |
| *Pomatomus* | S | | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *saltatrix* | J | | | | ● | | | ● | ● | ● | | | | ● | | ● | | | | | ● | | ● | ● | | | | | | ● | | | ● | ● | | |
| | L | | | | ● | ● | | | ● | | | | | ● | | ● | | | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | ● | | | | | | | | | |
| Blue runner | A | | | | ● | | | | ● | ● | | | | ● | | ● | | | | | ● | | | ● | | | | | | | ● | | ● | ● | | |
| *Caranx* | S | | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *crysos* | J | | | | ● | | | | ● | ● | | | | ● | | ● | | | ● | | | | ● | | | | | | | ● | | | | | | |
| | L | | | | | ● | | | ● | | | | | ● | | ● | | | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | ● | | | | | | | | | |
| Crevalle jack | A | | | | ● | | | ● | ● | ● | | | | ● | | ● | | | | | ● | | | ● | | | | | | | ● | | ● | ● | ● | |
| *Caranx* | S | | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *hippos* | J | | | | ● | | | ● | ● | ● | | | | ● | | ● | | | | | ● | | | ● | | ● | | | | ● | | | | | | |
| | L | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | ● | | | | | | | | | |
| Florida pompano | A | | | | ● | | | | ● | ● | | | | ● | | ● | | | | ● | ● | | | ● | | | | | | ● | | | ● | ● | ● | |
| *Trachinotus* | S | | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *carolinus* | J | | | | ● | | | ● | ● | ● | | | | ● | | ● | | | | ● | ● | ● | ● | | | | | | ● | | | | | | ● | |
| | L | | | | | ● | | | ● | | | | | ● | | ● | | | | | | | | | | | | ● | | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | ● | | | | | | | | | |
| Gray snapper | A | | | ● | | | ● | ● | ● | ● | | | | ● | | ● | | | | | ● | | | ● | | ● | | | | | ● | | ● | ● | | |
| *Lutjanus* | S | | | ● | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *griseus* | J | | | ● | | | ● | ● | ● | ● | | | | ● | | ● | | | | | ● | | ● | ● | | ● | | | | ● | | | ● | ● | | |
| | L | | | | | ● | | | ● | | | | | ● | | ● | | | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | ● | | | | | ● | | | | | ● | | | | | | | | | | | | | ● | | | | | | | | | |

Table 7, continued. Biological Attributes

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs

**Biological Attributes** / **Value**

| **Species / life stage** | | Life Mode | | | | | Spatial Strategy | | | | | Mobility | | | Feed* | | Prey Items | | | | | | | | | | Longevity | | | | | | Value | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Epibenthic | Benthic | Demersal | Nektonic | Planktonic | Freshwater resident | Estuarine resident | Marine resident | Coastal migrant | Ocean migrant | Nonmobile | Low mobility | High mobility | Filter feeder | Non-filter feeder | Detritus | Phytoplankton | Zooplankton | Infauna | Epibenthos | Insects | Fish (eggs, larvae) | Fish (juveniles, adults) | Macroalgae | Vascular plants | 1 day | 1-30 days | 1-12 months | 1-5 years | 5-20 years | >20 years | Recreational | Commercial | Ecological | Indicator of stress |
| Sheepshead | A | | | | ● | | | ● | ● | | | | | ● | | ● | | | | | ● | | | ● | | ● | | | | | ● | | ● | ● | ● | |
| *Archosargus probatocephalus* | S | | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | | ● | | | ● | | | | | | ● | | ● | | | ● | | ● | ● | | ● | | ● | | | | ● | | | ● | ● | ● | |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | | ● | | | | | | | | | | ● | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | |
| Pinfish | A | | | | ● | | ● | ● | ● | | | | | ● | | ● | | | | | ● | | | | | ● | | | | ● | | | ● | ● | ● | ● |
| *Lagodon rhomboides* | S | | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | | ● | | ● | ● | ● | | | | | ● | | ● | | | | | ● | | | | | | | | ● | | | | ● | ● | ● | ● |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | |
| Silver perch | A | | | ● | | | | ● | | | | | | ● | | ● | | | | | ● | | | ● | | | | | | | ● | | ● | | ● | ● |
| *Bairdiella chrysoura* | S | | | ● | | | | ● | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | | ● | | | | | | ● | | ● | | | ● | | ● | | ● | ● | | | | | | ● | | | | | ● | ● |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | ● | | ● | | ● | ● | | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | |
| Sand seatrout | A | | | ● | | | | ● | ● | ● | | | | ● | | ● | | | | | ● | | | ● | | | | | | ● | | | ● | ● | ● | |
| *Cynoscion arenarius* | S | | | ● | | | | ● | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | | ● | ● | ● | | | | ● | | ● | | | ● | | ● | | ● | ● | | | | | ● | | | | ● | ● | ● | |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | | | ● | | ● | ● | | | | | ● | | | | | | | | | | ● | | | ● | | | | | | | | | |
| Spotted seatrout | A | | | ● | | | | ● | | | | | | ● | | ● | | | | | ● | | | | | | | | | | ● | | ● | ● | ● | ● |
| *Cynoscion nebulosus* | S | | | ● | | | | ● | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | ● |
| | J | | | ● | | | | ● | | | | | | ● | | ● | | | | | ● | | | ● | | | | | ● | | | | ● | ● | ● | |
| | L | | | ● | | ● | | ● | ● | | | | | ● | | ● | | | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | ● | | ● | | ● | ● | | | | | ● | | | | | | | | | | | | | ● | | | | | | | | | |
| Spot | A | | | ● | | | ● | ● | ● | | | | | ● | | ● | | | | | ● | | | ● | | | | | | ● | | | ● | ● | ● | ● |
| *Leiostomus xanthurus* | S | | | ● | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | ● | ● | | | | | | ● | | ● | | | | | ● | | | | | | | | | ● | | | ● | ● | ● | ● |
| | L | | | | | ● | | | ● | | | | | ● | | ● | | | ● | | | | | | | | | | ● | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | |

Table 7, continued. Biological Attributes

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs

| Species / life stage | | Biological Attributes: Life Mode | | | | | Spatial Strategy | | | | | Mobility | | | Feed* | | Prey Items | | | | | | | | | | Longevity | | | | | | Value | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Epibenthic | Benthic | Demersal | Nektonic | Planktonic | Freshwater resident | Estuarine resident | Marine resident | Coastal migrant | Ocean migrant | Nonmobile | Low mobility | High mobility | Filter feeder | Non-filter feeder | Detritus | Phytoplankton | Zooplankton | Infauna | Epibenthos | Insects | Fish (eggs, larvae) | Fish (juveniles, adults) | Macroalgae | Vascular plants | 1 day | 1-30 days | 1-12 months | 1-5 years | 5-20 years | >20 years | Recreational | Commercial | Ecological | Indicator of stress |
| Atlantic croaker *Micropogonias undulatus* | A | | | ● | | | | ● | ● | | | | | ● | | ● | | | | ● | ● | | | ● | | | | | | ● | | | ● | ● | ● | ● |
| | S | | | ● | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | ● | ● | | | | | | ● | | ● | | | ● | ● | ● | | | ● | | | | | | ● | | | ● | ● | ● | ● |
| | L | | | ● | | ● | | ● | ● | | | | | ● | | ● | | | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | |
| Black drum *Pogonias cromis* | A | | | | ● | | | ● | ● | | | | | ● | | ● | | | | ● | ● | | | ● | | ● | | | | | | ● | ● | ● | ● | |
| | S | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | | ● | | ● | ● | ● | | | | | ● | | ● | | | | ● | ● | | | ● | | ● | | | | ● | | | ● | ● | ● | |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | | | ● | | ● | ● | | | | | ● | | | | | | | | | | | | | ● | | | | | | | | | |
| Red drum *Sciaenops ocellatus* | A | | | | ● | | | | ● | | | | | ● | | ● | | | | | ● | | | ● | ● | ● | | | | | | ● | ● | ● | | ● |
| | S | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | | ● | ● | | ● | ● | | | | | ● | | ● | | | | | ● | | ● | ● | ● | ● | | | | ● | | | ● | ● | | |
| | L | | | | | ● | | | ● | | | | | ● | | ● | | | ● | | | | | | | | | ● | | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | ● | | | | | | | | | |
| Striped mullet *Mugil cephalus* | A | | | | ● | | | ● | ● | | | | | ● | | ● | ● | ● | ● | | ● | | ● | | ● | | ● | | | | ● | | ● | ● | ● | ● |
| | S | | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | | ● | | | ● | | | | | | ● | | ● | ● | ● | ● | | ● | | ● | | ● | | ● | | | ● | | | ● | ● | ● | ● |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | ● | ● | | | ● | ● | | | ● | | | ● | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | | ● | | | | | | ● | | |
| Code goby *Gobiosoma robustum* | A | | | ● | | | | ● | | | | | | ● | | ● | ● | ● | | | ● | ● | | | | | | | | ● | | | | | ● | |
| | S | | | ● | | | | ● | | | | | ● | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | | ● | | | | | ● | | | ● | ● | ● | ● | | ● | ● | | | ● | | | | ● | | | | | | ● | |
| | L | | | ● | | | | ● | | | | | ● | | | ● | | ● | ● | | | | | | | | | | | | | | | | | |
| | E | ● | | | | | | ● | | | | ● | | | | | | | | | | | | | | | | ● | | | | | | | | |
| Spanish mackerel *Scomberomorus maculatus* | A | | | | ● | | | | ● | ● | ● | | | ● | | ● | | | | | ● | | | ● | | | | | | | ● | | ● | ● | | ● |
| | S | | | | ● | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | | | | | | |
| | J | | | | ● | | | ● | ● | ● | ● | | | ● | | ● | | | | | ● | | | | | | | | | ● | | | | | | ● |
| | L | | | | | ● | | | ● | | | | | ● | | ● | | | ● | | ● | | ● | | | | | ● | | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | |

Table 7, continued. Biological Attributes

Life stage
A - Adults
S - Spawning
J - Juveniles
L - Larvae
E - Eggs

| Species / life stage | | Biological Attributes: Life Mode | | | | | Spatial Strategy | | | | | Mobility | | | Feed* | | Prey Items | | | | | | | | | | Longevity | | | | | | Value | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Epibenthic | Benthic | Demersal | Nektonic | Planktonic | Freshwater resident | Estuarine resident | Marine resident | Coastal migrant | Ocean migrant | Nonmobile | Low mobility | High mobility | Filter feeder | Non-filter feeder | Detritus | Phytoplankton | Zooplankton | Infauna | Epibenthos | Insects | Fish (eggs, larvae) | Fish (juveniles, adults) | Macroalgae | Vascular plants | 1 day | 1-30 days | 1-12 months | 1-5 years | 5-20 years | >20 years | Recreational | Commercial | Ecological | Indicator of stress |
| Gulf flounder | A | | | ● | | | | ● | ● | | | | | ● | | ● | | | | | ● | | | ● | | | | | | ● | | | ● | ● | | |
| *Paralichthys albigutta* | S | | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | | ● | ● | | | | | ● | | ● | | | | | ● | | | ● | | | | | | ● | | | ● | ● | | |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | | ● | | | | | | | | | | ● | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | |
| Southern flounder | A | | | ● | | | ● | ● | ● | | | | | ● | | ● | | | | | ● | | | ● | | | | | | | ● | | ● | ● | ● | |
| *Paralichthys lethostigma* | S | | | | ● | | | | ● | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | J | | | ● | | | ● | ● | ● | | | | | ● | | ● | | | | | ● | | | ● | | | | | | ● | | | ● | ● | ● | |
| | L | | | | | ● | | ● | ● | | | | | ● | | ● | | | ● | | | | | | | | | | ● | | | | | | | |
| | E | | | | | ● | | | ● | | | | | ● | | | | | | | | | | | | | | ● | | | | | | | | |

## Table 8. Reproduction

**Terms used in Table 8, Reproduction:**

**Fertilization/development** - Method of egg fertilization and development.
- *External* - Egg fertilization occurs after eggs and sperm are shed into the water.
- *Internal* - Egg fertilization occurs when a male inseminates an egg within a female.
- *Oviparous* - Eggs are laid and fertilized externally.
- *Ovoviviparous* - Eggs are fertilized and incubated internally, and usually released as larvae. Little or no maternal nourishment is provided.
- *Viviparous* - Eggs are fertilized, incubated, and develop internally until birth. Maternal nourishment is provided.

**Mating Type** - Mate selection strategy.
- *Monogamous* - A single male and a single female pair for a prolonged and exclusive relationship.
- *Polygamous* - A male mates with numerous females or vice-versa.
- *Broadcast spawner* - Numerous males and females release gametes during mass spawning.

**Spawning strategy** - Spawning mode.
- *Anadromous* - Species spends most of its life at sea but migrates to fresh water to spawn.
- *Catadromous* - Species spends most of its life in fresh water but migrates to salt water to spawn.
- *Iteroparous* - Species reproduces repeatedly during a lifetime.
- *Semelparous* - Species reproduces only once during a lifetime.
- *Batch* - Species spawns (releases gametes) several times during a reproductive period.

**Parental Care** - Type of egg protection.
- *Protected* - Eggs are protected by parent(s); eggs are buoyant or attached to substrates, or eggs develop in the shelter of a nest.
- *Non-protected* - Eggs are not protected by parent(s).

**Domain** - Location of spawning.
- *Riverine* - Spawning occurs primarily in fresh water, above head of tide.
- *Estuarine* - Spawning occurs primarily in estuarine waters (to head of tide).
- *Marine* - Spawning occurs primarily in open marine waters.

**Temporal Schedule** - Months when spawning typically occurs.

**Periodicity** - Frequency of spawning events.
- *Annual spawning* - Spawning once each year, usually during a restricted season.
- *2 or more per year* - Spawning more than once each year (more than one spawning season).
- *2 or more years* - Spawning events separated by at least two years.
- *Undescribed* - Spawning frequency not documented.

**Fecundity** - Number of eggs typically produced by a mature female, from <100 to >10 million.

**Maturation age** - The typical length of time for an individual to reach sexual maturity, from < 6 months to > 5 years.

## Table 8. Reproduction

**Reproduction**

| Species | Fertilization/ development | | | | | Mating type | | | Spawning strategy | | | | | Parntl. care | | Domain | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | External | Internal | Oviparous | Ovoviviparous | Viviparous | Monogamous | Polygamous | Broadcast spawner | Andromous | Catadromous | Iteroparous | Semelparous | Batch | Protected | Non-protected | Riverine | Estuarine | Marine |
| Bay scallop *Argopecten irradians* | ● | | ● | | | | | ● | | | | ● | ● | | ● | | ● | ● |
| American oyster *Crassostrea virginica* | ● | | ● | | | | | ● | | | ● | | ● | | ● | | ● | ● |
| Atlantic rangia *Rangia cuneata* | ● | | ● | | | | | ● | | | ● | | | | ● | ● | ● | |
| Hard clam *Mercenaria* species | ● | | ● | | | | | ● | | | ● | | ● | | ● | | ● | ● |
| Bay squid *Lolliguncula brevis* | ● | | ● | | | ● | | ● | | | ● | | | | ● | | ● | ● |
| Brown shrimp *Peneaus aztecus* | ● | | ● | | | | ● | | | | ● | | | ● | | | | ● |
| Pink shrimp *Peneaus duorarum* | ● | | ● | | | | ● | | | | ● | | | ● | | | | ● |
| White shrimp *Penaeus setiferus* | ● | | ● | | | | ● | | | | ● | | | ● | | | ● | ● |
| Grass shrimp *Palaemonetes pugio* | ● | | ● | | | | ● | | | | ● | | | ● | | | ● | |
| Spiny lobster *Panulirus argus* | ● | | ● | | | | ● | | | | ● | | | ● | | | | ● |
| Blue crab *Callinectes sapidus* | | ● | ● | | | | ● | | | | ● | | | ● | | ● | ● | |
| Gulf stone crab *Menippe adina* | | ● | ● | | | | ● | | | | ● | | | ● | | | ● | ● |
| Florida stone crab *Menippe mercenaria* | | ● | ● | | | | ● | | | | ● | | | ● | | | ● | ● |
| Bull shark *Carcharhinus leucas* | | ● | | | ● | | ● | | | | ● | | | | ● | | | ● |
| Tarpon *Megalops atlanticus* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● |
| Alabama shad *Alosa alabamae* | ● | | ● | | | | ● | ● | ● | | ● | | ● | | ● | ● | | |
| Gulf menhaden *Brevoortia patronus* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● |
| Yellowfin menhaden *Brevoortia smithi* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● |
| Gizzard shad *Dorosoma cepedianum* | ● | | ● | | | | ● | ● | ● | | ● | | | | ● | ● | | |
| Bay anchovy *Anchoa mitchilli* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | ● | ● |
| Hardhead catfish *Arius felis* | ● | | ● | | | | ● | ● | | | ● | | | ● | | | ● | ● |
| Sheepshead minnow *Cyprinodon variegatus* | ● | | ● | | | | ● | ● | | | ● | | | ● | | | ● | |

| Species | Temporal Schedule | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | January | February | March | April | May | June | July | August | September | October | November | December |
| Bay scallop *Argopecten irradians* | | | | | | | | ● | ● | ● | | |
| American oyster *Crassostrea virginica* | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| Atlantic rangia *Rangia cuneata* | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | |
| Hard clam *Mercenaria* species | | | ● | ● | ● | ● | ● | ● | ● | ● | | |
| Bay squid *Lolliguncula brevis* | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| Brown shrimp *Peneaus aztecus* | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| Pink shrimp *Peneaus duorarum* | | | | ● | ● | ● | ● | | | | | |
| White shrimp *Penaeus setiferus* | | | ● | ● | ● | ● | ● | ● | ● | ● | | |
| Grass shrimp *Palaemonetes pugio* | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | |
| Spiny lobster *Panulirus argus* | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| Blue crab *Callinectes sapidus* | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | |
| Gulf stone crab *Menippe adina* | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | |
| Florida stone crab *Menippe mercenaria* | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | |
| Bull shark *Carcharhinus leucas* | | | | | | ● | ● | | | | | |
| Tarpon *Megalops atlanticus* | | | | | ● | ● | ● | ● | ● | | | |
| Alabama shad *Alosa alabamae* | | | ● | ● | | | | | | | | |
| Gulf menhaden *Brevoortia patronus* | ● | ● | ● | ● | ● | | | ● | ● | ● | ● | ● |
| Yellowfin menhaden *Brevoortia smithi* | ● | ● | ● | | | | | | | | | ● |
| Gizzard shad *Dorosoma cepedianum* | | | ● | ● | ● | ● | ● | ● | | | | |
| Bay anchovy *Anchoa mitchilli* | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| Hardhead catfish *Arius felis* | | | | | ● | ● | ● | ● | ● | | | |
| Sheepshead minnow *Cyprinodon variegatus* | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | |

| Species | Periodicity | | | | Fecundity | | | | | | | | Maturation age | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Annual spawning | 2 or more per year | 2 or more years | Undescribed | <100 | 100-1,000 | 1,000-10,000 | 10,000-100,000 | 100,000-1 million | 1-10 million | >10 million | Undescribed | ≤6 months | 0.5 to 1 Year | 1 to 3 Years | 3 to 5 Years | > 5 Years | Undescribed |
| Bay scallop *Argopecten irradians* | | ● | | | | | | | ● | | | | | ● | | | | |
| American oyster *Crassostrea virginica* | | ● | | | | | | | | | ● | | ● | | | | | |
| Atlantic rangia *Rangia cuneata* | | ● | | | | | | | | | | ● | | | ● | | | |
| Hard clam *Mercenaria* species | | ● | | | | | | | | | ● | | | | ● | | | |
| Bay squid *Lolliguncula brevis* | | ● | | | | | ● | | | | | | | ● | | | | |
| Brown shrimp *Peneaus aztecus* | | ● | | | | | | | ● | | | | ● | | | | | |
| Pink shrimp *Peneaus duorarum* | | ● | | | | | | | ● | | | | ● | | | | | |
| White shrimp *Penaeus setiferus* | | ● | | | | | | | ● | | | | ● | | | | | |
| Grass shrimp *Palaemonetes pugio* | | ● | | | | ● | | | | | | | ● | | | | | |
| Spiny lobster *Panulirus argus* | | ● | | | | | | | | ● | | | | | ● | | | |
| Blue crab *Callinectes sapidus* | | ● | | | | | | | | ● | | | | | ● | | | |
| Gulf stone crab *Menippe adina* | | ● | | | | | | | ● | | | | | | ● | | | |
| Florida stone crab *Menippe mercenaria* | | ● | | | | | | | ● | | | | | | ● | | | |
| Bull shark *Carcharhinus leucas* | ● | | | | ● | | | | | | | | | | | | ● | |
| Tarpon *Megalops atlanticus* | ● | | | | | | | | | | ● | | | | | | ● | |
| Alabama shad *Alosa alabamae* | | ● | | | | | | | ● | | | | | ● | | | | |
| Gulf menhaden *Brevoortia patronus* | | ● | | | | | | ● | | | | | | | ● | | | |
| Yellowfin menhaden *Brevoortia smithi* | | | | ● | | | | | | | | ● | | | ● | | | |
| Gizzard shad *Dorosoma cepedianum* | | ● | | | | | | | ● | | | | | | ● | | | |
| Bay anchovy *Anchoa mitchilli* | | ● | | | | | ● | | | | | | ● | | | | | |
| Hardhead catfish *Arius felis* | | ● | | | ● | | | | | | | | | | ● | | | |
| Sheepshead minnow *Cyprinodon variegatus* | | ● | | | ● | | | | | | | | ● | | | | | |

Table 8, continued. Reproduction

| | Reproduction | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Fertilization/ development | | | | | Mating type | | | Spawning strategy | | | | | Parntl. care | | Domain | | | Temporal Schedule | | | | | | | | | | | | Periodicity | | | | Fecundity | | | | | | | | Maturation age | | | | | |
| | External | Internal | Oviparous | Ovoviviparous | Viviparous | Monogamous | Polygamous | Broadcast spawner | Andromous | Catadromous | Iteroparous | Semelparous | Batch | Protected | Non-protected | Riverine | Estuarine | Marine | January | February | March | April | May | June | July | August | September | October | November | December | Annual spawning | 2 or more per year | 2 or more years | Undescribed | <100 | 100-1,000 | 1,000-10,000 | 10,000-100,000 | 100,000-1 million | 1-10 million | >10 million | Undescribed | <6 months | 0.5 to 1 Year | 1 to 3 Years | 3 to 5 Years | > 5 Years | Undescribed |
| Gulf killifish *Fundulus grandis* | ● | | ● | | | | ● | ● | | | ● | | | | ● | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | | ● | | | | | | | | | | ● | | | |
| Silversides *Menidia* species | ● | | ● | | | | ● | ● | | | ● | | | | ● | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | | | ● | | | | | | | | ● | | | | |
| Snook *Centropomus undecimalis* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | | | | | | | ● | | | | | | ● | | |
| Bluefish *Pomatomus saltatrix* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | | | ● | ● | ● | | | | ● | ● | ● | | | ● | | | | | | | ● | | | | | | ● | | | |
| Blue runner *Caranx crysos* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | | | | | | ● | | | | | | ● | | | |
| Crevalle jack *Caranx hippos* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | | | ● | ● | ● | ● | ● | ● | ● | | | | | ● | | | | | | | | | | ● | | | | | | ● |
| Florida pompano *Trachinotus carolinus* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | | | | | | ● | | | | | | ● | | | |
| Gray snapper *Lutjanus griseus* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | | | | | | ● | ● | ● | ● | | | | | ● | | | | | | | ● | | | | | | ● | | | |
| Sheepshead *Archosargus probatocephalus* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | | | ● | ● | | | | | | | | | | ● | | | | | | | | | | ● | | | ● | | | |
| Pinfish *Lagodon rhomboides* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | ● | ● | ● | | | | | | | ● | ● | ● | | ● | | | | | | ● | | | | | | | ● | | | |
| Silver perch *Bairdiella chrysoura* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | ● | ● | | | | | ● | ● | ● | ● | ● | | | | | ● | | | | | | ● | | | | | | | ● | | | |
| Sand seatrout *Cynoscion arenarius* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | | | ● | ● | ● | ● | ● | ● | ● | | | | | ● | | | | | | | ● | | | | | ● | | | | |
| Spotted seatrout *Cynoscion nebulosus* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | | | | ● | | | | | | | | ● | | | | | ● | | | |
| Spot *Leiostomus xanthurus* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | ● | ● | ● | ● | | | | | | | ● | ● | | ● | | | | | | | ● | | | | | | ● | | | |
| Atlantic croaker *Micropogonias undulatus* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | ● | ● | ● | ● | ● | | | | ● | ● | ● | ● | | ● | | | | | | | | ● | | | | | ● | | | |
| Black drum *Pogonias cromis* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | ● | ● | ● | ● | ● | ● | ● | | | | | | ● | ● | | ● | | | | | | | | ● | | | | | ● | | | |
| Red drum *Sciaenops ocellatus* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | ● | ● | ● | | | | | | | ● | ● | ● | ● | ● | | ● | | | | | | | | ● | | | | | | ● | | |
| Striped mullet *Mugil cephalus* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | ● | ● | ● | | | | | | | ● | ● | ● | | ● | | | | | | | | ● | | | | | | ● | | |
| Code goby *Gobiosoma robustum* | ● | | ● | | | ● | | | | | ● | | | ● | | | ● | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | | ● | | | | ● | | | | | | | ● | | | | | |
| Spanish mackerel *Scomberomorus maculatus* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | | | | ● | ● | ● | ● | ● | ● | ● | | | | ● | | | | | | | | ● | | | | | ● | | | |
| Gulf flounder *Paralichthys albigutta* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | ● | ● | | | | | | | | | ● | ● | | ● | | | | | | | | | | ● | | | ● | | | |
| Southern flounder *Paralicthys lethostigma* | ● | | ● | | | | ● | ● | | | ● | | ● | | ● | | | ● | ● | ● | | | | | | | | | ● | ● | | ● | | | | | ● | | | | | | | | ● | | | |