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RIVERINE DISCHARGE AND ESTUARINE FISH NURSERIES:

FIRST ANNUAL REPORT FOR THE ICHTHYOPLANKTON SURVEY OF THE LITTLE MANATEE RIVER, FLORIDA

Ernst B. Peebles and Susan E. Davis

Department of Marine Science
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November 15, 1989

Funds for this project were provided by the Florida Department of Environmental Regulation, Office of Coastal Management using funds made available through the National Oceanic and Atmospheric Administration under the Coastal Zone Management Act of 1972, as ammended. Local administration of this work was conducted through contracts with the Southwest Florida Water Management District. Project manager: Michael S. Flannery.

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EXECUTIVE SUMMARY

The abundance of fish eggs and young fishes in the tidal portion of the Little Manatee River was monitored on a regular basis during 1988. Collections with fine-meshed (0.5 mm) nets were made twice each month at six locations ranging between fresh water and the open waters of Tampa Bay.

Approximately 74,000 fish representing 68 species were collected. Fish eggs and newly-hatched fishes (larvae) were concentrated in the higher salinities at the mouth of the river and in Tampa Bay. The status of bone development in the tail region of the larval fishes was used as index of relative age. The different species were ranked according to the abundance of their various larval age classes. Species which were most abundant during their youngest stages were considered to have been spawned in closer proximity to the study area than species which were most abundant as older stages. This analysis indicated that species such as spotted seatrout (speckled trout), sand seatrout (silver trout), silver perch, kingfishes (whitings) and anchovies (glass minnows) spawned nearby, probably near the the mouth of the Little Manatee River. Although this general area may provide suitable spawning conditions for a wide variety of fishes, it is not considered to be an exclusive spawning location for Tampa Bay fishes. Previous surveys indicate that the aforementioned fishes also spawn in similar habitats outside of the study area. The spawning seasons were different for the different fish species, but spawning activity was generally highest during the period from March through August.

Within specific age classes, correlations between fish length (age) and salinity of capture were tested for statistical significance. This analysis indicated that the young of several species migrated upstream to low salinity areas of the river during the first few weeks of life. Percentages of total abundance concentrated in low salinity (<18 $^{o}/oo$) areas were calculated. More than 75% of the total abundance of young menhaden, anchovies, spot, sand seatrout, and several other fishes was found to be concentrated in these low salinity areas. One or more of these species was found to be occupying low salinity areas of the river at any time of year. In addition to simple documentation of the low-salinity concentration phenomenon, abundances in low salinity areas were tested for statistical difference from abundances in higher salinity areas. This test proved significant for several species, most notably young anchovies and menhaden. Previous research has indicated that snook and red drum (redfish) also concentrate in low salinity areas during the first few weeks of life.

Increased freshwater discharge had variable effects on the distribution of young fishes. Some persisted in the upper river during strong discharge periods, while others moved closer to the mouth of the river. Correlations between young fish abundance and flow rate of the river were not found. However, most of the "concentrating" species increased in abundance in the river channel during periods of rapid salinity reduction. This could reflect either migration into or out of the river. Likely causes of migration are local shifts in food resources and limits on the physiological adjustment capabilities of the young fishes during periods of rapid salinity reduction.

Since small, suspended organisms (such as copepods) were not abundant in low salinity areas, it is probable that the concentrations of young fishes

were feeding on organisms associated with the bottom and edges of the river and its backwaters. In these areas, particulate organic matter, such as decaying leaves, may be the foundation of the food web. A significant correlation was found between flow rate of the river and the importation of particulate organic matter into nursery areas.

INTRODUCTION

This report represents one component of a comprehensive study of the estuarine portion of the Little Manatee River in west-central Florida. In regard to municipal development, the Little Manatee River is the least impacted of the rivers which empty into Tampa Bay. Documentation of the river's biological and water quality characteristics is presently being conducted in the form of a multifaceted database collection effort. This report and reports on fisheries habitat (Haddad et al. 1989), phytoplankton (Vargo 1989) and zooplankton (Rast and Hopkins 1989) represent the biological portion of the study during 1988.

Tampa Bay is part of a nearly continuous coastal estuarine system ranging from Chesapeake Bay to the western Gulf of Mexico. Species which are associated with estuaries comprise the vast majority of the fisheries yields in most, if not all, of this region (Skud and Wilson 1960, Gunter 1967). General degradation of the estuarine environment and reductions in the productivity of important estuarine-based fisheries have increased the demand for estuarine management (Mansueti 1961, Copeland 1970, Odum 1970, Fischer 1970).

The use of estuaries as nursery grounds is a principal characteristic of estuarine dependence, yet the relationship between freshwater discharge and the abundance of young estuarine-dependent fishes is incompletely understood. Some researchers have associated increased freshwater discharge with enhanced fish nursery production (Gunter and Hall 1963), while others have not (Kobylinski and Sheridan 1979, Weinstein et al. 1980, Rogers et al. 1984). In extreme cases, such as in the case of the totoaba (Cynoscion macdonaldi) of the Colorado River estuary, reductions in freshwater discharge have resulted in population collapse.

Because of the Little Manatee River study area's position on the salinity gradient, the data provided by the present survey are well-suited to the study of nursery grounds used by estuarine-dependent fishes. Analyses in this report are directed toward assessment of the potential impacts of freshwater discharge on these nursery grounds.

OBJECTIVES

1. To provide a record of the use of the tidal portion of the Little Manatee River by the early stages of coastal fishes.

2. To identify the fishes whose spawning and nursery grounds are most likely to be impacted by changes in the quantity and/or quality of riverine discharge.

3. To identify the seasons when impact on spawning and nursery habitat would be greatest.

4. To initiate an investigation into the relationship between the quantity and/or quality of riverine discharge and short-term changes in the distribution of the early stages of estuarine-dependent fishes.

METHODS

Sampling Procedure

Plankton collections were made at six fixed locations at approximately two-week intervals from January 1988 through January 1989 (total of 24 collections). The six stations covered an 11-mile (17.7 km) transect between a very low salinity area and the open waters of Tampa Bay (Fig. 1). Some characteristics of these stations are given below (depth and salinity are presented as means with ranges in parentheses).

Sta.	Mile	Depth (m)	Salinity (^{o}/oo)	Description
1	8.8	1.9 (1.0-2.5)	0.8 (0.0-4.5)	Braided channel, sloughs, marsh, hammocks Dominant vegetation: Juncus, Typha, Acrostichum, Serinoa, Myrica, Juniperus, Pinus, Sabal, Alternanthera
2	6.4	2.3 (1.5-3.0)	2.9 (0.0-11.5)	Channel bordered by low bluffs on left bank; marsh-rimmed embayment on right. Dominant vegetation: Juncus, Serinoa, Sabal, Pinus, Quercus, Casuarina
3	4.4	1.7 (1.3-2.0)	6.7 (0.0-19.0)	Channel bordered by low bluffs on right bank; low, marshy ground on left. Dominant vegetation: Juncus, Schinus, Serinoa, Sabal, Pinus, Rhizophora, Phragmites
4	2.2	2.3 (1.5-3.3)	10.8 (0.0-22.5)	Channel bordered by municipal development on right bank, mangrove swamp on left. Dominant vegetation: Rhizophora, Avicennia, Quercus
5	0.0	1.8 (1.3-3.0)	16.6 (1.0-30.0)	Braided channel bordered by municipal development on right bank; mangrove swamp on left - oyster growth near shoreline. Dominant vegetation: Rhizophora, Halodule,
6	-2.2	2.9 (2.0-3.5)	25.0 (13.0-34.0)	Open bay with sand bottom.

All collections were made at night on an incoming tide. The plankton samples were taken sequentially, rather than simultaneously (a single boat was used). In order to keep tidal phase as similar as possible during the collections, the upper (1-3) and lower (4-6) stations were sampled on consecutive nights. There was no established order in which the two groups of stations (upper and lower) were sampled, except that each night's sampling progressed upstream, in the direction of tide travel.

Sampling gear consisted of a 0.5 meter mouth diameter, 505 um mesh, conical (3:1) plankton net equipped with a digital flowmeter. Two three-step oblique tows (bottom-midwater-surface), one surface tow and one bottom tow were made at each station (24 samples per collection, total of 576 samples). Fishing depth of the weighted net was controlled by adjusting the length of the tow line while keeping line angle as constant as possible. The position of the winch on the gunnel caused a controlled "crabbing" by the boat, which directed propeller turbulence away from the towed net. The net was towed at approximately 2 m/s for five minutes, resulting in a tow length of about 500 m and an average volume-filtered of about 75 m^3. Samples were fixed in sodium borate-buffered 6-10% formalin in saline.

Immediately preceding net deployment, water column samples taken with a Niskin bottle were filtered through 35 um mesh. The analysis of the zooplankton from these samples is found in the report by Rast and Hopkins (1989). Before and after net deployment, salinity, temperature, and dissolved oxygen were determined electronically at surface, bottom, and at one-meter intervals between surface and bottom.

Laboratory Procedure

After allowing a few days for tissue fixation, the oblique samples were rinsed with water and transferred to 70% ethanol in de-ionized water. At this step it was discovered that one of the oblique samples had not been properly preserved, so it was replaced with one surface and one bottom sample taken at the same location and time (the remainder of the surface and bottom samples were stored, and there are presently no plans for processing them). Dissecting microscopes were used to separate fishes from invertebrates for later identification, measurement, and enumeration.

Identifications were based on descriptions found in: Fahay (1983), Lippson and Moran (1974), the U.S. Fish and Wildlife Service's series on fish development in the Mid-Atlantic Bight (e.g., Fritzsche 1978), Moser (1983), Houde and Fore (1973), Hettler (1984), Hogue et al. (1976), Peters (1981, 1983, 1985), Watson (1983), Fable et al. (1978), Houde et al. (1970), Carr (1942) and Fuiman et al. (1983). The taxonomic nomenclature used follows Robins et al. (1980). Each identified taxonomic group (species, in most cases) was subdivided by stage of development. The divisions were based primarily on the status of bone development in the caudal region of the young fish (Fig. 2), specifically:

preflexion stage - period between hatching and notochord flexion; tip of notochord is most distal osteological feature.

flexion stage - period during notochord flexion; upturned

notochord or urostyle is most distal osteological feature.

postflexion stage - = postlarval stage; period between completion of flexion and juvenile stage; hypural bones are most distal osteological feature.

juvenile stage - period beginning with the approximate size at which median fin meristic characters are complete, or in some cases, when dense pigment fields appear (such as the development of silver pigmentation in clupeiform fishes); ends with attainment of sizes known to be sexually mature.

The abundance of fish eggs and dominant invertebrate groups (mysids, amphipods, cumaceans, ostracods, etc.) were estimated after subsampling, if neccesary, with a box-type plankton splitter. This re-examination of the sample provided a means for quality control for the fish/invertebrate sorting process. Although the fishes in the vast majority of samples were counted directly, the plankton splitter was used on a few occasions when anchovy catches were very high. In these samples, all other fishes were removed and counted directly, rather than splitting them along with the anchovies. The data were recorded using an electronic spreadsheet and were then sorted into taxonomic subfiles to facilitate analysis with a microcomputer.

Statistical Treatment of Fish Abundance, Length, and Seasonality

The three principal biological variables associated with the ichthyoplankton collections are fish abundance, fish length, and season of collection. In regard to fish abundance, each plankton sample has a total catch (number of individuals) and an estimated density (number of individuals per filtered volume) associated with it. The analyses included within this report require descriptions of various combinations of abundance data from individual plankton samples. The frequency distributions for these combinations tend to be kurtose and positively skewed (Fig. 3).

Cumulative catch, average density and median density were evaluated as descriptive parameters for fish abundances that were based on combinations of samples. As a particular taxon is encountered more frequently during sampling, the first-order trend in the cumulative catch tends to be linear. However, a stepwise second-order trend was often found to be superimposed upon this, and sometimes had a large impact on apparent abundance, particularly at small sample sizes. Similarly, the strong influences of values in the tails of combined density distributions often caused average densities to be much more variable than median densities at small sample sizes. Since different taxa are found in different abundances in the estuary, sampling resolution cannot be equal for all taxa. Therefore, the potential for sample-size dependence of cumulative catch and average density, along with the discussions of Steel and Torrie (1980) and Sokal and Rohlf (1981), argue against the use of these parameters in describing abundances with skewed frequency distributions. The remaining parameter, median density, is generally less variable at low sample sizes, but loses sensitivity when zero densities are more numerous than nonzero densities. In such cases the median is zero regardless of the magnitude of the nonzero values. To overcome this problem, the median from nonzero densities was weighted by the proportion of zero

densities in the collections. In other words, just as a nonzero average density can be corrected to include zero values by multiplying the nonzero average by the ratio of nonzero sample size to total sample size, the nonzero median can be corrected to produce a positive number even when zero densities dominate. This is expressed as

$$A = D_m \frac{f}{n}$$

where D_m is the median density from the nonzero samples, f is the number of nonzero samples, and n is total number of samples. The value A is referred to as an abundance "index" rather than a median. Single sample (instantaneous) densities are also reported in several cases.

The exponential nature of larval mortality results in length-frequency distributions that are often similar in shape to those for abundance frequency, although an ascending limb, which represents escapement through the mesh or an absence of small larvae, is sometimes present (Fig. 4). Gear selectivity and migration into or out of the study area may affect both ends of the collected length range. For each sample, an estimate of median standard length (using an ocular micrometer for specimens <10 mm standard length) was made for each developmental stage of each fish taxon collected. This number was based on a maximum of 20 specimens from each stage.

The spawning seasons of estuarine and estuarine-dependent fishes are variable on both an interspecific and interannual basis. Instantaneous densities were plotted over time as an indication of spawning season (Appendix I). Assuming that spawning activity is directly reflected by the abundance of newly-hatched larvae, then Appendix I indicates that spawning intensity often undergoes a rapid increase during the first part of the season, and then diminishes gradually. A more concise representation of spawning season was included in a catch table (Table 1) as seasonal ranges and modal values of f. Modes were used to locate peak spawning months since median determinations would not apply to year-round spawners and would be sensitive to the disjunction in the ordination of the months (e.g., when a species spawned between November (month 11) and March (month 3)). Seasonal trends in abundance (as A) were also plotted for some taxa.

Analyses

Analysis 1: Assessment of spawning ground vulnerability

Spawning locations which were closest to riverine discharge were assumed to be the most sensitive to changes in the quantity and/or quality of discharge. The relative abundance (as A) of the different developmental stages was used as a means of gauging the proximity of spawning locations. The collected taxa were divided into categories based on the relative abundance of their preflexion, flexion and postflexion stages. For example, species which were most abundant at the preflexion stage were presumed to have spawned in greater proximity to the study area than those which were only present as postlarvae. Within each of these categories, taxa which otherwise had similar stage distributions were ranked by the abundance of their dominant stages. The interpretation of this secondary ranking is somewhat limited by the variability in the total egg productions of the different species. In this procedure, is also possible that mesh extrusion of species with very small preflexion stages could result in an underestimation of spawning ground proximity.

In addition to spawning ground proximity, the season when the greatest number of species were spawning was identified (species-specific information on spawning season is included in Table 1). In this procedure, the most abundant larval stage of each species was assigned a single month of peak occurrence (from Table 1). The frequency distribution for these months was plotted for the inshore-spawning (discharge-sensitive) and offshore-spawning (discharge-insensitive) assemblages in order to identify the seasons with the highest number of spawning peaks. This was supported by a seasonal plot of the number of species collected.

Analysis 2: Assessment of nursery ground vulnerability

Nursery habitat vulnerability was assumed to be proportional to degree of dependence on low salinity habitats. A systematic design for categorizing this dependence is diagramed by Figure 5. The principle classification factor used in this categorization is the salinity occupied by different developmental stages. In order to identify trends in salinity occupation, instantaneous densities were plotted against salinities at capture for the various collected stages (Appendix II). These density-salinity distributions were represented numerically by density-weighted average salinities at capture (Table 3). Among the frequently collected taxa, trends in salinity occupation allowed identification of those which were dependent on low salinity habitats.

The higher part of the salinity range was not always sampled. It is therefore possible that the weighted salinitied at capture for species which spawn in high salinities (e.g., >30 $^{o}/oo$) are underestimates of the true salinity where the earliest stages of these species were concentrated. At the other end of the length range, the abundances of certain postlarvae and small juveniles may be underestimated due to gear avoidance or microhabitat specializations which would make them unavailable to the gear.

Spearman's rank correlations between salinity at capture and fish length

were also used as indicators of upstream migration against the salinity gradient. The significance of negative correlations between salinity and length is limited to adequately sampled, slowly migrating stages (as opposed to fast-moving juveniles), since growth during the migration is neccesary for statistical significance. Therefore, although significance in these tests was considered to be evidence of migration, lack of significance was not interpreted as lack of migration.

The concentration of young estuarine-dependent fishes in low salinity waters was identified by ranking the ratios of abundance (A) in 0-18 $^{o}/oo$ to abundance (A) in 18-36 $^{o}/oo$. The abundance index takes the difference in sampling intensity between the two salinity ranges (186 vs. 102 samples) into consideration. Density differences in the two salinity ranges were tested for significance by using Mann-Whitney U-tests. An adequate sample size from both salinity categories is neccesary for significance; therefore, as with the correlations, lack of significance was not interpreted as lack of concentration.

Analysis 3: Impacts of riverine discharge on nursery grounds

As a preliminary investigation into this relationship, the abundance data for species which are most dependent on low salinity habitats (as determined by Analysis 2) were compared with trends in salinity and freshwater discharge. The relationship between discharge and the availabilty of food resources, including river-borne organic matter and crustacean zooplankton, was examined. The data for flow rate and water chemistry used in this analysis were provided by the Southwest Florida Water Management District.

RESULTS AND DISCUSSION

Over 74,000 fish representing approximately 68 species were collected by the plankton gear during 1988. Catch statistics are provided in Table 1. As is typical of many estuaries in southeastern North America, the ichthyoplankton community was dominated by anchovies (Engraulidae), gobies (Gobiidae), and drums and seatrout (Sciaenidae).

Spawning Vulnerability

Spawning location

Fish eggs were concentrated in the higher salinities near the mouth of the river and in Tampa Bay. The most commonly collected egg type (50 collections, approx. 48,000 eggs) was identified as belonging to either the Order Perciformes and/or the Order Pleuronectiformes (Fahay 1983), but could not be reliably identified beyond this level. This egg type is spherical, ranging in diameter from 0.6-0.9 mm, and had a density-weighted salinity of capture of 29 $^{o}/oo$. The Gobiid and Blenniid eggs expected to occur in the study area have adhesive filaments and adhesive discs, respectively, and are not likely to be collected by plankton nets (Fritzsche 1978, Peters 1981, 1983). The remaining taxa which have eggs that are similar to those collected and which were concurrently abundant in the study area at the earliest larval stages include: Menticirrhus spp., Cynoscion nebulosus, Oligoplites saurus, Trinectes maculatus, Bairdiella chrysoura, Cynoscion arenarius, and Achirus lineatus.

A second unidentified egg type (22 collections, approx. 1100 eggs) is also spherical, but ranges in diameter between 1.0 and 1.5 mm, and sometimes has segmented yolk. The density-weighted salinity at capture was 26 $^{o}/oo$ for this type. Based on the concurrent abundance of small larvae of species with eggs matching this description, identities may have included: Pogonias cromis, Opisthonema oglinum, and Chaetodipterus faber.

The eggs of Anchoa mitchilli, Anchoa hepsetus, Gobiesox strumosus, and an unidentified Tetraodontiform fish had density-weighted average salinities ranging from 22 to 26 $^{o}/oo$. The eggs of Anchoa mitchilli were far more abundant than all other types of identified eggs (20 collections, approx. 2100 eggs). The eggs of Menidia beryllina were associated with vegetation collected from fresh water at station 1.

The results of spawning ground proximity analysis (Analysis 1) are given in Table 2. Comparison of the ranking in Table 2 with existing literature shows that the species in the first three categories tend to be considered inshore spawners (within Tampa Bay and/or the Little Manatee River), while the species in the fourth and fifth categories tend to be considered bay-mouth or offshore spawners.

Most, if not all, of the species indicated by minus signs in Table 2 are included within one of the larger taxonomic divisions indicated by plus signs. Therefore, the position of the more inclusive taxa is a better indication of the status of these species in Table 2. Assuming that species compositions are proportionally similar in the preflexion and later larval stages, then:

the taxon Anchoa spp. is dominated by A. mitchilli; the taxon Gobiidae is dominated by Gobiosoma spp. and Microgbius gulosus; the taxon Blenniidae is dominated by Chasmodes saburrae; and the taxon Prionotus spp. is dominated by Prionotus tribulus. All but one of the preflexion and flexion-stage larvae included in the taxon Clupeidae were associated with catches of Opisthonema oglinum and Harengula jaguana, and are assumed to be one or both of these species.

The advanced development of the newly-born young of the live-bearers Syngnathus louisianae and S. scovelli resulted in their classification as juveniles, yet the occurence of very small individuals was considered evidence of "spawning" in intermediate-to-high salinity areas.

Fundulus spp. fell into the offshore spawner group because this genus, like the offshore spawners, invaded the study area at the postflexion stage. However, the majority of Fundulus were collected from the upstream end of the study area after heavy rains, and it is likely that they were invading from fresh water rather than from a seaward direction. As adults, Fundulus seminolis was particularly abundant near station 1.

Lepisosteus platyrhincus (the probable identity of Lepisosteus sp.), Notemigonis crysoleucas, Ictalurus catus, Elassoma okefenokee, Lepomis auritus, L. macrochirus, and Micropterus salmoides are freshwater fishes, most of which occasionally invade brackish or tidal fresh water at the juvenile and adult stages. Richmond (1940) reported spawning by Lepomis auritus in brackish water. The live-bearers Gambusia affinis, Heterandria formosa and Poecilia latipinna are freshwater fishes with a high degree of salt tolerance, and undoubtedly give birth within the study area.

NOTE:

The evidence provided by egg distribution and by Table 2 indicates that many species spawn close to or within the study area, but does not indicate the proportion of total spawning that is taking place there. Total spawning effort varies from species to species. For example, the impact of riverine discharge on a large clupeid stock which spawns intensively off of the mouth of Tampa Bay and farther offshore, but has a small percentage of eggs washing into Tampa Bay, is going to be less than the impact on a particular gobiid stock which spawns locally among the oyster beds at the mouth of the Little Manatee River.

The spawning grounds of estuarine-dependents are sometimes widely displaced from the low salinity areas used later as nursery habitat. However, a rigorous definition of estuaries as places where salinity falls below that of seawater would include the spawning locations of a large percentage of coastal marine fishes. Within this percentage, most fishes, such as seatrout, make an effort to spawn in intermediate-to-high salinity areas that are relatively stable in a physicochemical sense (Peebles and Tolley 1988). Others, such as many species of killifish and silversides, spawn locally in unstable, low-salinity backwaters. Members of the former group tend to be highly motile, usually belong to families composed mostly of marine species, and often occupy higher salinities after they leave their low-salinity nursery grounds. These fishes are included in the estuarine-dependent category of Figure 5. Members of latter group, categorized as estuarine in Figure 5, tend to belong to families with many freshwater representatives, and may undergo most or all of their life histories in low salinity habitats.

Spawning Season

Figure 6A indicates the period from March through August as having the greatest number of species undergoing peak spawning activity in or near the spawning area. This period coincides with temporal peaks in egg abundance and total number of species collected (Fig. 7). The abundance of eggs and small larvae in the study area during this period suggests that there is relatively high potential for riverine discharge impact on the spawning activity of the following fishes:

bay anchovy (Anchoa mitchilli)
skilletfish (Gobiesox strumosus)
silversides (Menidia spp.)
kingfishes (Menticirrhus spp.)
spotted seatrout (Cynoscion nebulosus)
sand seatrout (Cynoscion arenarius)
silver perch (Bairdiella chrysoura)
Florida blenny (Chasmodes saburrae)
highfin blenny (Lupinoblennius nicholsi)
frillfin goby (Bathygobius soporator)
naked goby (Gobiosoma bosci)
code goby (Gobiosoma robustum)
clown goby (Microgobius gulosus)
wormfish (Microdesmis sp.)
bighead searobin (Prionotus tribulus)
hogchoker (Trinectes maculatus)
lined sole (Achirus lineatus)

Peak activity for bay-mouth and offshore spawners was distributed throughout the year (Fig. 6B). Fishes which utilize the study area as a nursery ground, but whose spawning activity is not likely to be impacted by riverine discharge include:

menhaden (Brevoortia spp.)
snook (Centropomus undecimalis)
pigfish (Orthopristis chrysoptera)
sheepshead (Archosargus probatocephalus)
pinfish (Lagodon rhomboides)
spot (Leiostomus xanthurus)
red drum (Sciaenops ocellatus)
striped mullet (Mugil cephalus)

Nursery Habitat Vulnerability

Figure 8 illustrates the decreasing salinity of capture for several fishes as they migrate toward low salinities. Generally, migration upstream was first detected at the flexion stage, but appeared to be stronger at the postflexion stage (Table 3). Table 4 provides abundance values for comparisons between 0-18 and 18-36 $^{o}/oo$. In Figures 9 and 10, the percentage of overall abundance found in the lower salinities is used as a gauge for identifying some of the species which not only disperse into, but congregate in low salinities at the postlarval or early juvenile stage. Figures 9 and 10 also show that for most species, concentration occurs during the early juvenile, rather than postlarval, stage.

"Concentrating" species have life history stages where most or all of the individuals in a particular stage occupy or, in the case of diadromous fishes, pass through low salinity habitats. Snook and red drum are concentrating species which are locally abundant in the upper estuary as juveniles. Snook migrate toward low salinity areas at the postlarval stage (Tolley et al. 1987) and concentrate as early juveniles in freshwater and oligohaline areas, usually in association with emergent or shoreline vegetation (Gilmore et al. 1983). In the Tampa Bay area, over 90% of the juvenile red drum in the 15-59 mm length range collected by Peters and McMichael (1987) were found in backwaters with mean surface salinities ranging from 7-21 $^{o}/oo$. During the two years prior to the onset of plankton sampling for the present study, the first author (EBP) participated in the FDNR Marine Research Institute's seine and stop-net surveys of the Little Manatee and Alafia rivers. It is clear from these surveys that species such as snook, red drum and striped mullet are abundant in the study area as very small juveniles. The absence of these species in the plankton collections could be attributed to net avoidance, insufficient sampling resolution during peak ingress periods, or failure to sample specialized habitats used by postlarvae and early juveniles.

Young estuarine-dependent fishes are usually present in low salinity habitats for at least several months after arrival from the spawning grounds, resulting in year-round use of these nursery areas: young red drum arrive in autumn; peak arrivals of postlarval menhaden occur in winter; young spot and black drum arrive from late winter to early spring; and most of the remaining fishes arrive from late spring through early summer. Peak spawning by the bay anchovy is in late spring and early summer, but juveniles are abundant in low salinity areas throughout the year. Many of the young gobies and hogchokers remain in low salinity habitats until maturity, and then return to higher salinities for spawning.

Riverine Discharge and Nursery Grounds

Two principal features of the discharge regime for 1988 were a spring/early summer drought and a late summer/early fall rainy season, which included a period of exceptionally heavy rain in early September (Fig. 11). Three cycles of salinity reduction and increase were evident: the first was caused by the passage of cold fronts in January, February and March; the second by the late summer thunderstorm season, and the third by the passage of

a cold front and tropical storm Keith through the area in November (Fig.12).

For taxa which had an affinity for low salinity areas, simple correlations between seasonal abundance and seasonal salinity or flow rate were not evident. There was evidence that the rate of change of salinity and flow influenced abundances, however. Juvenile bay anchovies (Anchoa mitchilli) were collected year-round, but were most abundant during the three periods when salinities were falling the fastest, and were least abundant during the drought and during periods of extremely high discharge (Fig. 15). Postlarval menhaden (Brevoortia spp.) were not present during the second salinity cycle, but were most abundant during salinity reductions of the first and, to a lesser extent, the third cycles (Fig. 16). Juvenile hogchokers (Trinectes maculatus) were not collected during the first salinity cycle, but appeared to be most abundant during or soon after the salinity reductions in the second and third cycles (Fig. 17). Juvenile sand seatrout (Cynoscion arenarius) were collected during the second salinity cycle only, and also appeared to be most abundant during a period of rapid salinity reduction (Fig. 18). These fluctuations in abundance may simply represent salinity-related migrations superimposed on the seasonal spawning activity of the adult stocks. Both emigration from and immigration to the upper river could result in increased abundance in the channel where the nets were towed. Most of the captures of burrowing fishes, such as juvenile speckled worm eels (Myrophis punctatus) and adult pink wormfish (Microdesmis longipinnis), were associated with freshets in 1988 and 1989.

In regard to spatial distribution and short-term salinity fluctuation, postlarval and juvenile menhaden and juvenile hogchokers persisted in the upper river during freshets (Figs. 19, 20, 22). Postlarval and juvenile spot were somewhat less persistent, but remained in the river during freshets (Figs. 23, 24). Juvenile bay anchovies, sand seatrout, and gobies (Gobiosoma) were found closer to the mouth of the river during freshets (Figs. 26, 28, 30). This displacement was even more pronounced during the postlarval stages of these species (Figs. 21, 25, 27, 29). As suggested by Rogers et al. (1984), the advection associated with freshets probably inhibits the upstream migration and retention of small, relatively weak-swimming seatrout, hogchoker, and goby postlarvae, while having a lesser effect on larger, more robust forms, such as postlarval menhaden. However, variable physical impacts would not explain why juvenile bay anchovies move farther downstream while postlarval menhaden persist in the upper river. It therefore appears that biological factors play a role in displacement. Likely biological influences include differences in osmoregulatory capability and differences in the response of unique food resources to freshwater discharge.

It is clear that many fish species concentrate in low salinity areas of the river (Tables 3 and 4; Figs. 8-10, Appendix II). In euryhaline species, the energetic cost of enduring rapidly-fluctuating, reduced salinities is compensated through reduced interspecific competition for the abundant food resources found in low salinity areas, and possibly through exposure to a reduced number of predatory species.

In general, organisms which might serve as potential food for young fishes were removed from the water column during high discharge periods. This was particularly true for copepod nauplii and copepodites (primarily Acartia and Oithona, Rast and Hopkins 1989), although these organisms primarily serve as food for the younger stages found outside of the river. Among estuarine-dependent fishes, it is common for principal food sources to shift from

copepods to mysids, amphipods, polychaetes, and organic detritus as the young fishes grow larger (Darnell 1961, Carr and Adams 1973, Chao and Musick 1977, Peters and McMichael 1987). Mysids (Neomysis) and gammarid amphipods were widely distributed along the salinity gradient (Figs. 31, 32). Although mysids were often very abundant in low salinities, abundance was generally correlated with salinity (abundance, A, vs. salinity at station 3: $r=0.59$, $d.f.=22$, $p=0.003$), and was reduced during peak discharge periods (Fig. 33). Amphipods were fairly abundant in the water column during the drought, and peaked at the start of the rainy season. However, during and after the period of sustained high discharge, water column amphipod abundance dropped to very low levels and did not return to pre-rain concentrations (Fig. 34). Other small crustaceans which might serve as food for young fish (cumaceans, decapod zoeae, ostracods, cladocerans, and isopods) tended to be most abundant in higher salinities.

Organisms in the water column of low salinity areas of the river do not appear to be reliable sources of food for young fishes. When food is abundant in the water column, it is probably exploited in an opportunistic manner. Benthic food resources, which were not monitored during this study (except as vertically migrating benthos and tychoplankton), are a more likely source of food, particularly for demersal species.

The sedimentary accumulation of organic detritus is a distinctive characteristic of the area of the Little Manatee River where many young estuarine-dependents congregate. Imported organic matter is often a dominant energy source for streams and even large rivers (Berner 1951, Fisher and Likens 1972). Teal (1962) estimated that 45 percent of the net production of a temperate salt marsh is exported to estuarine waters. The importance of allochthonous organic matter as a seasonally-buffered source of nutrition for young estuarine-dependent fishes was discussed by Darnell (1961, 1967). The microbial protein content of decomposing, naturally-shed vegetable matter (leaves and sticks) may increase for months, but a variety of factors, such as species of plant, determine the rate of decomposition and the quality of the material as food (Kaushik and Hynes 1971). The distribution of many benthic animals is correlated with detritus distribution (Egglishaw 1964). Some invertebrates, such as copepods and amphipods (and probably mysids and polychaetes), are able to assimilate much of the microbial protein ingested as detritus, which allows these organisms to function as trophic intermediates between detritus and those fishes which do not eat detritus directly (Hargrave 1970, Heinle et al., 1977). An intermediate trophic position may also be held by protozoans such as flagellates or tintinnids (Robertson 1983).

The discharge-associated peaks in particulate organic carbon is evidence of the importation of energy into low salinity nursery habitats (Fig. 35). Levels of both particulate and dissolved organic carbon were correlated with the flow rate of the river (POC: $r=0.70$, $d.f.= 22$, $p<0.001$; DOC: $r=0.73$, $d.f.=9$, $p=0.02$). In addition to flow rate, cycles in the accumulation of organic matter on land (such as leaf litter) undoubtedly play a role in the importation of organic carbon into the Little Manatee River. Much of the organic carbon in freshwater streams is dissolved leaf leachate which may contribute to particulate deposition through precipitation as solids (Fig. 36). The sources of allochthonous particulate and dissolved organic carbon in the Little Manatee River range from riparian vegetation to the terrestrial communities of the entire watershed, depending on the extent and intensity of freshwater runoff.

The impact of organic matter importation on eutrophication is dependent on the type of organic matter being imported. Naturally-shed plant material is often rich in organic carbon, but very poor in nutrients (Fenchel and Harrison 1975). Bacterial decomposition of leaf litter is dependent on nitrogen and phosphorus concentrations in the water, such that heterotrophic bacteria actually remove nutrients from the water column during decomposition (Kaushik and Hines 1971, Fenchel and Harrison 1975). On the other hand, remineralization of nutrient-rich organic matter, such as sewage, releases nutrients into the water column, thereby enhancing eutrophication.

The watershed encompasses an area that is comparable in size to Tampa Bay, and most of the runoff from this region is funneled through the study area (Fig. 37), so there is great potential for terrestrial and wetland subsidization of nursery ground productivity. Backwaters and deep holes in the channel collect organic debris in a manner analogous to that of ponding areas in freshwater streams. Many of these areas were scoured out by the September flood, leaving sand where detrital bottoms once were. Under most flow conditions, however, only fine particulate organic matter is exported farther downstream, so that downstream areas depend increasingly on autochthonous sources of organic matter, and the influence of freshwater discharge on organic matter availability becomes less noticeable. In these higher salinity areas, cycles in mangrove, seagrass, macroalgae and phytoplankton growth play a greater role in the availability of secondary, as well as primary, production.

There is no reason not to assume that upper estuarine nursery areas benefit from energy importation in the same manner as freshwater ecosystems. Two seasonal cycles are immediately evident as regulators of this process: organic matter accumulation in the watershed and physical flushing of organic matter into the upper estuary. Reduction in either capacity could result in decreased food resources for important fish nursery grounds. However, the two factors are interdependent in the sense that the timing of the two cycles relative to each other may be as important as their magnitude. It is likely that, in some cases, sustained flushing is excessive in relation to the watershed's finite supply of organic matter.

CONCLUSIONS

1. The spawning activities of fishes which were present as eggs or newly-hatched young in the Little Manatee River study area are considered to be the most likely to be impacted by changes in the quantity or quality of freshwater discharge. The following fishes are in this category:

FISH	PERIOD OF SPAWNING VULNERABILITY
bay anchovy (Anchoa mitchilli)	April-December
striped anchovy (Anchoa hepsetus)	May-June
skilletfish (Gobiesox strumosus)	January-December
tidewater silverside (Menidia beryllina)	January-December
Gulf pipefish (Syngnathus scovelli)	January-December
chain pipefish (Syngnathus louisianae)	January-December
Atlantic bumper (Chloroscombrus chrysurus)	July-September
leatherjacket (Oligoplites saurus)	May-August
kingfishes (Menticirrhus spp.)	April-October
spotted seatrout (Cynoscion nebulosus)	April-August
sand seatrout (Cynoscion arenarius)	March-September
silver perch (Bairdiella chrysoura)	April-September
black drum (Pogonias cromis)	March-April
Atlantic spadefish (Chaetodipterus faber)	May-July
Florida blenny (Chasmodes saburrae)	January-December
feather blenny (Hypsoblennius hentzi)	April-July
highfin blenny (Lupinoblennius nicholsi)	April-November
frillfin goby (Bathygobius soporator)	April-October
naked goby (Gobiosoma bosci)	March-December
code goby (Gobiosoma robustum)	May-August
clown goby (Microgobius gulosus)	May-January
wormfish (Microdesmis sp.)	April-August
bighead searobin (Prionotus tribulus)	April-August
hogchoker (Trinectes maculatus)	April-November
lined sole (Achirus lineatus)	April-November
blackcheek tonguefish (Symphurus plagiusa)	May-August

A wide variety of fishes undergo peak spawning activity during the period from March through August.

2. Migration from moderate-to-high salinity spawning grounds into low salinity areas of the Little Manatee River occurred during the postlarval and early juvenile stages.

3. During the survey, the majority of the estuarine-dependent fishes which concentrate in low salinity areas (>75% abundance in <18 °/oo) did so during the early juvenile stage. The young of fishes which concentrate in low salinity areas are likely to be impacted by changes in the quantity or quality of riverine discharge. The following fishes are in this category:

FISH	PERIOD OF INGRESS/INITIAL CONCENTRATION
menhaden (Brevoortia spp.)	November-August
bay anchovy (Anchoa mitchilli)	January-December
skilletfish (Gobiesox strumosus)	January-December
rainwater killifish (Lucania parva)	May-October
tidewater silverside (Menidia beryllina)	March-December
snook (Centropomus undecimalis)	May-September
mojarras (Eucinostomus spp.)	January-December
sand seatrout (Cynoscion arenarius)	March-September
spot (Leiostomus xanthurus)	December-April
red drum (Sciaenops ocellatus)	September-November
naked goby (Gobiosoma bosci)	March-December
lined sole (Achirus lineatus)	April-November
hogchoker (Trinectes maculatus)	April-November

Most of these fishes remain in low salinity areas for at least several months following ingress and initial concentration.

4. Concentrations of dissolved organic carbon, amphipods, and the young of several species of fish increased at the beginning of high discharge periods, but fell to relatively low levels during periods of sustained high discharge.

5. The distributional response of young fishes to increased freshwater discharge depended on developmental stage and species. During high discharge periods, postlarval menhaden and juvenile hogchokers persisted in the upper river, postlarval and juvenile spot were widely distributed in the river, and juvenile bay anchovies, sand seatrout, and gobies (Gobiosoma) were most abundant in the lower river. The postlarvae of the latter group were concentrated in higher salinities than the early juveniles during high discharge periods.

6. Postlarval and early juvenile food sources (copepods, mysids, and amphipods) were inconsistently present in the water column of low salinity nursery areas, and are strongly reduced in the water column during periods of sustained discharge (see also: Rast and Hopkins 1989, Vargo 1989). Benthic food resources probably play a greater role as food for young fishes than do water column resources.

7. Energy in the form of dissolved and particulate organic carbon is imported into low salinity nursery habitats. The quantity of energy that is imported is largely dependent on cycles in both freshwater runoff and terrestrial accumulation of organic matter.

LITERATURE CITED

Berner, L.M. 1951. Limnology of the lower Missouri river. Ecology 32(1):1-12.

Carr, M.H. 1942. The breeding habits, embryology and larval development of the largemouth black bass in Florida. Proceedings New Engl. Zool. Club. 20:43-77.

Carr, W.E. and C.A. Adams. 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. Trans. Amer. Fish. Soc. 102(3):511-540.

Chao, L.N. and J.A. Musick. 1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull. 75(4)657-702.

Copeland, B.J. 1970. Estuarine classification and response to disturbances. Trans. Amer. Fish. Soc. 4:826-835.

Darnell, R.M. 1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. Ecology 42(3):553-568.

Darnell, R.M. 1967. Organic detritus in relation to the estuarine ecosystem. Pages 376-382 in G.H. Lauff, ed., Estuaries. Amer. Assn. Advancement Sci., Washington, D.C.

Egglishaw, H.J. 1964. The distributional relationships between the bottom fauna and plant detritus in streams. J. Anim. Ecol. 33:463-476.

Fable, W.A., Jr., T.D. Williams and C.R. Arnold. 1978. Description of reared eggs and young larvae of the spotted seatrout, Cynoscion nebulosus. Fish. Bull. 76(1):65-71

Fahay, M.P. 1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. J. Northwest Atl. Fish. Sci., vol. 4, 423 p.

Fenchel, T. and P. Harrison. 1975. The significance of bacterial grazing and mineral cycling for the decomposition of particulate detritus. Pages 285-299 in: J.M. Anderson and A. Macfadyen, eds., The Role of Terrestrial and Aquatic Organisms in Decomposition Processes, Blackwell Scientific Publications, Oxford.

Fisher, S.G. and G.E. Likens. 1972. Stream ecosystems: organic energy budget. BioSci. 22:33-35.

Fischer, D.W. 1970. An economic addendum. Trans. Amer. Fish. Soc. 4:849-850.

Fritzsche, R.A. 1978. Development of fishes of the Mid-Atlantic Bight, vol. 5. U.S. Dept. Interior, Fish and Wildl. Service. 340 p.

Fuiman, L.A., J.V. Conner, B.F. Lathrop, G.L. Buynak, D.E. Snyder, and J.J. Loos. 1983. State of the art of identification for cyprinid fish larvae from eastern North America. Trans. Am. Fish. Soc. 112:319-332.

Gilmore, R.G., C.J. Donohoe, and D.C. Cooke. 1983. Observations on the distribution and biology of east-central Florida populations of the common snook, Centropomus undecimalis (Bloch). Fla. Scientist 46(3/4):313-336.

Gunter, G. 1967. Some relationships of estuaries to the fisheries of the Gulf of Mexico. Pages 621-638 in G.H. Lauff, ed., Estuaries. Amer. Assn. Advancement Sci., Washington, D.C.

Gunter, G. and G.E. Hall. 1963. Biological investigations of the St. Lucie Estuary (Florida) in connection with Lake Okeechobee discharges through the St. Lucie Canal. Gulf Res. Rept. 1(5):189-307.

Haddad, K.D., G.A. McGarry, R.E. Matheson, W.J. Conley, P.R. Carlson, R.H. McMichael, J.L. Serino, and K.A. Killam. 1989. Assessment of fisheries habitat final report for tasks 1, 2, 3, 4, and 5. Submitted to the Fla. Dept. Environ. Reg.

Hargrave, B.T. 1970. The utilization of benthic microflora by Hyalella azteca (Amphipoda). J. Anim. Ecol. 39:427-437.

Hettler, W.F. 1984. Description of eggs, larvae, and early juveniles of Gulf menhaden, Brevoortia patronus, and comparisons with Atlantic menhaden, B. tyrannus, and yellowfin menhaden, B. smithi. Fish. Bull. 82(1):85-95.

Hogue, J.J., Jr., R. Wallus, and L.K. Kay. 1976. Preliminary guide to the identification of larval fishes in the Tennessee River. Tenn. Valley Auth. Div. Forestry, Fish., Wildl. Development Tech. Note B19.

Houde, E.D., and P.L. Fore. 1973. Guide to the identity of eggs and larvae of some Gulf of Mexico clupeid fishes. Fla. Dept. Nat. Resources Mar. Res. Lab. Leaflet Series. 4(1) No. 23. 14 p.

Houde, E.D., C.R. Futch, and R. Detwyler. 1970. Development of the lined sole, Achirus lineatus, described from laboratory-reared and Tampa Bay specimens. Fla. Dept. Nat. Resources Tech. Series No. 62. 43 p.

Kaushik, N.K. and H.B.N. Hynes. 1971. The fate of the dead leaves that fall into streams. Arch. Hydrobiol. 68(4):465-515.

Kobylinski, G.J. and P.F. Sheridan. 1979. Distribution, abundance, feeding, and long-term fluctuations of spot, Leiostomus xanthurus, and croaker Micropogonias undulatus, in Apalachicola Bay, Florida, 1972-1977. Contr. Mar. Sci. 22:149-161.

Lippson, A.J. and R.L. Moran. 1974. Manual for the identification of early developmental stages of fishes of the Potomac River estuary. Power Plant Citing Program of the Maryland Dept. Nat. Resources. 282 p.

Lush, D.L. 1970. Dissolved organic matter in streams. M.S. thesis. Univ. Waterloo. 78 p.

Mansueti, R.J. 1961. Effects of civilization on striped bass and other estuarine biota in Chesapeake Bay and tributaries. Univ. Miami Inst. Mar. Sci. Gulf and Carib. Fish. Inst. Proceed. 14th Ann. Sess., Miami Beach, November 1961: 111-136.

Moser, H.G. (ed.) 1983. Ontogeny and systematics of fishes. Am. Soc. Ichthyologists and Herpetologists Spec. Publ. No. 1.

Odum, W.E. 1970. Insidious alteration of the estuarine environment. Trans. Amer. Fish. Soc. 4:836-847.

Peebles, E.B. 1987. Early life history of the sand seatrout (Cynoscion arenarius) in southwest Florida. M.S. thesis, Univ. South Fla. 70 p.

Peebles, E.B. and S.G. Tolley. 1988. Distribution, growth and mortality of larval spotted seatrout, Cynoscion nebulosus: a comparison between two adjacent estuarine areas of southwest Florida. Bull. Mar. Sci. 42(3):397-410.

Peters, K.M. 1981. Reproductive biology and developmental osteology of the Florida blenny, Chasmodes saburrae (Perciformes: Blenniidae). Northeast Gulf Sci. 4(2):79-98.

Peters, K.M. 1983. Larval and early juvenile development of the frillfin goby, Bathygobius soporator (Perciformes: Gobiidae). Northeast Gulf Sci. 6(2):137-153.

Peters, K.M. 1985. Larval development of Lupinoblennius nicholsi with comments on larval blenniini identification in Tampa Bay, Florida. Bull. Mar. Sci. 36(3):445-453.

Peters, K.M. and R.H. McMichael. 1987. Early life history of the red drum, Sciaenops ocellatus (Pisces: Sciaenidae), in Tampa Bay, Florida. Estuaries 10(2):92-107.

Rast, J. and T.L. Hopkins. 1989. The zooplankton of the Little Manatee River Estuary, Florida. First Yearly Report.: 1988. Submitted to the Southwest Florida Water Management District. 48 p.

Richmond, N.D. 1940. Nesting of the sunfish, Lepomis auritus (Linnaeus), in tidal water. Zoologica (N.Y.) 25(3):329-330.

Robertson, J.R. 1983. Predation by estuarine zooplankton on tintinnid ciliates. Estuarine, Coastal and Shelf Sci. 16:27-36.

Robins, C.R., R.M. Bailey, C.E. Bond, J.R. Brooker, E.A. Lachner, R.N. Lea, and W.B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada (4th ed.). Amer. Fish. Soc. Spec. Publ. 12, 174 p.

Rogers, S.G., T.E. Targett, and S.B. Van Sant. 1984. Fish-nursery use in Georgia salt-marsh estuaries: the influence of springtime freshwater conditions. Trans. Amer. Fish. Soc. 113:595-606.

Skud, B.E. and W.B. Wilson. 1960. Role of estuarine waters in Gulf fisheries. Trans. 25th N. amer. Wildl. Conf. 1960: 320-326.

Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43(4):387-397.

Tolley, S.G., E.T. Dohner, and E.B. Peebles. 1987. Occurrence of larval snook, Centropomus undecimalis (Bloch), in Naples Bay, Florida. Fla. Scientist 50(1):34-38.

Vargo, G. 1989. Phytoplankton studies in the Little Manatee River: species composition, biomass, and nutrient effects on primary production. First annual report submitted to the Southwest Florida Water Management District. 211 p.

Watson, W. 1983. Redescription of larvae of the pigfish, Orthopristis chrysoptera Linnaeus (Pisces, Haemulidae). Fish. Bull. 81(4):847-854.

Weinstein, M.P., S.L. Weiss and M.F. Walters. 1980. Multiple determinants of community structure in shallow marsh habitats, Cape Fear River estuary, North Carolina, USA. Marine Biology (Berlin) 58:227-243.