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Pathways of Energy Flow in a South Florida Estuary

William E. Odum

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PREFACE

The Sea Grant Colleges Program was created in 1966 to stimulate research, instruction, and extension of knowledge of marine resources of the United States. In 1969 the Sea Grant Program was established at the University of Miami.

The outstanding success of the Land Grant Colleges Program, which in 100 years has brought the United States to its current superior position in agricultural production, was the basis for the Sea Grant concept. This concept has three objectives: to promote excellence in education and training, research, and information services in the University's disciplines that relate to the sea. The successful accomplishment of these objectives will result in material contributions to marine oriented industries and will, in addition, protect and preserve the environment for the enjoyment of all people.

With these objectives, this series of Sea Grant Technical Bulletins is intended to convey useful research information to the marine communities interested in resource development quickly, without the delay involved in formal publication.

While the responsibility for administration of the Sea Grant Program rests with the Department of Commerce, the responsibility for financing the program is shared equally by federal, industrial, and University of Miami contributions. This study, Pathways of Energy Flow in a South Florida Estuary, is published as a part of the Sea Grant Program. Graduate research support was provided by grants from the National Park Service and the National Institutes of Health.

A complementary investigation of certain aspects of the production of organic detritus in a sub-tropical estuary was performed concurrently by Dr. Eric J. Heald whose research report, The Production of Organic Detritus in a South Florida Estuary, is available as Sea Grant Technical Bulletin #6.

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INTRODUCTION

Shallow estuaries, particularly at lower latitudes, exhibit features intermediate between those of terrestrial and aquatic ecosystems. Although the communities of animals in such systems are typically aquatic, much of the energy fixed in primary production comes from vegetation of terrestrial origin such as seagrasses, marsh grasses and mangroves which have become adapted to the aquatic environment. In the process of adaptation these plant communities have not lost the three principal characteristics of a mature terrestrial community ------ (1) a high standing crop of resistant vegetation, (2) low grazing rates by herbivores and (3) the resulting plant detritus-based food webs. Estuaries with such characteristics may present a confusing picture to the aquatic ecologist who is accustomed to the study of phytoplankton-based communities with low standing crops of unicellular primary producers, with rapid reproduction rates, high grazing rates by herbivores and food webs based predominantly upon herbivores, rather than detritus consumers.

The Mangrove Ecosystem

The mangrove swamp is an example of a detritus-based ecosystem which has been poorly understood by many traditionally trained marine biologists. Dr. Harold Humm of the University of South Florida has stated (1969), "It is my opinion that most of this mangrove-covered land [refering to the western shore of south Biscayne Bay, Florida] is in fact a form of waste land. It does not make a significant contribution to the productivity of Biscayne Bay or associated waters. ..... There are no biological research results that indicate that mangrove swamps contribute to the productivity of the adjacent waters. They certainly are far less important in this respect than an equal area of sea grass, if for no other reason than the fact that they do not provide refuge for the young of economically valuable fish and other forms of sea food. The bottom or ground on which mangroves grow is anaerobic, toxic from hydrogen sulfide, and unsuitable for all but a few burrowing organisms in contrast to the great population of burrowers found on seagrass flats."

This pronouncement was accepted as expert testimony by officials of the state of Florida in determining the future of mangrove areas. Undoubtedly, it was made with little or no experimental evidence. Evidence is presented here that mangrove swamps are valuable, productive regions.

In truth, there is no way to ascertain from the published literature whether mangrove systems contribute significantly to the productivity of surrounding waters. Although the mangrove environment has been studied from many different aspects (summarized by Kuenzler, 1969), there has only been one brief study concerned with their primary productivity (Golley et al, 1962) and no mention of energy transfer to consumer trophic levels.

With this lack of information in mind, a program was initiated by Eric Heald and myself at the urging of Dr. Durbin Tabb to determine the importance of organic detritus in the energy scheme of a south Florida mangrove community. We selected the North River estuary of the

Everglades National Park for investigation. This area presented a situation where it was possible to correlate the production of mangrove debris and detritus within the drainage basin of the river with export of particulate matter out of the river into Whitewater Bay. Moreover, due to extreme seasonal salinity fluctuations, the fauna of the North River is composed of relatively few species, a feature which simplifies the task of understanding trophic relationships.

The first objective was to estimate the annual production of organic detritus by the plants of the estuary along with a detailed study of the detritus ------- whether it remained in the system or was exported, whether it lost or gained nutritional value as it disintegrated, and how long it took to decompose sufficiently to be available as food for detritus consumers. These aspects of the study were reported by Heald (1969).

The second portion of the joint project is conveyed in this dissertation, and concerns the importance of organic detritus as a nutritional source to the heterotrophic community. Does detritus provide a broad base for most of the food webs associated with the mangrove ecosystem or are phytoplankton, benthic algae and their associated herbivorous food chains more important?

To answer this question a detailed investigation was made of the links in the major food webs of the mangrove environment. This required food studies of organisms at all trophic levels, but with special emphasis upon primary consumers. Over 7,000 stomach content analyses were made of over 80 species which included fishes, elasmobranchs, caridean and penaeid shrimp, mysids, amphipods, isopods, crabs, cumaceans, bivalve molluscs, copepods, and insect larvae. From these analyses it is possible to reconstruct the biological pathways of energy exchange in the mangrove community and, ultimately, to assess the value of mangrove detritus to the associated animal community.

Description of the North River Region

The southwest coast of Florida is fringed by a contiguous series of mangrove forests which form a band 10 - 20 kilometers wide and over 100 kilometers in length. Intersecting this belt are numerous small drainage basins which channel the surface flow of the freshwater Everglades through the mangrove region into a series of shallow coastal embayments.

Typical of these basins is the North River, a drainage system constituting an area of 21.7 square kilometers of which approximately two thirds is covered by vegetation and one third by open water. The open water is comprised of the river channel itself of 14 kilometers length and up to several hundred meters width and a series of shallow ponds which are interconnected by small winding streams ultimately emptying into the river proper. These ponds are usually less than a meter deep and range in size from a few square meters to 10 hectares. Although the pond bottoms are composed of flocculent organic mud, most of the streams and the river have exposed limestone beds and undercut mangrove peat banks.

In the upper reaches of the North River the ponds are replaced to a great extent by scattered marsh areas composed of the needlerush, *Juncus roemerianus*. These marshes are isolated from the river by a 0.2 - 0.4 meter levee which is broken at intervals by small drainage creeks.

The headwaters of the North River is a poorly defined region ranging from the open, seasonally flooded sawgrass prairies to the enchanneled mangrove belt. Generally, it is characterized by mangrove lined fingers intruding into the sawgrass prairie.

Because the North River area is a flooded basin, the usual zonation pattern of mangroves (Davis, 1940; Golley et al, 1962) is absent. The vegetation of the river basin is dominated by the red mangrove, Rhizophora mangle. The white mangrove, Laguncularia racemosa, is present as scattered individuals, but the black mangrove, Avicennia nitida, and the buttonwood, Conocarpus erectus, are rare. Sawgrass, Mariscus jamaicensis, is present in the system in the headwaters, but only in scattered clumps. This grass is characteristic of the open freshwater Everglades and not of the mangrove-dominated river system.

Parameters of the Physical Environment

Because south Florida is subject to pronounced wet and dry seasons, there is a great seasonal variation in the salinities of the rivers draining the Everglades (shown for the North River in Fig. 1). During a year of normal rainfall patterns, the months from December to May are characterized by little rain, low water levels in the Everglades and reduced runoff through the drainage rivers. As a result the rivers become tidal streams with most water movement dependent upon tide and wind. Saline water intrudes far up the rivers so that by April or May salinities reach 27 to 29 ppt in the mouth of the North River and may be as high as 25 ppt in the headwaters. In late May the rainy season usually begins and by the middle of June salinities in the entire river are uniformly "fresh" (from 100 to 300 ppm) and ramain so until late fall.

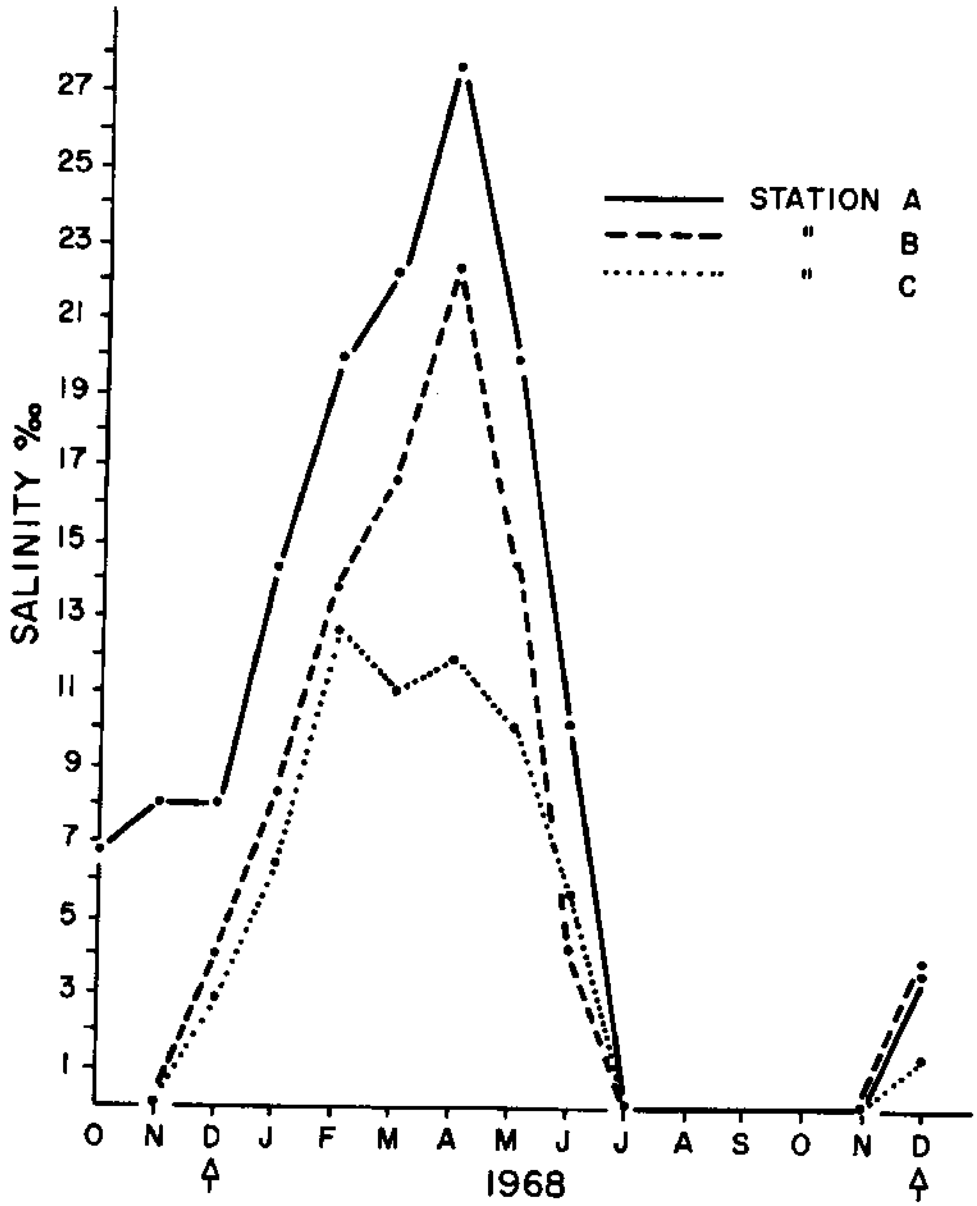


Figure 1. Ambient salinities during the sampling period.

Not all years are normal, however; in 1965, a year of prolonged drought, the rainy season did not arrive in May and salinities remained uniformly high in the North River during most of the summer. Tabb (pers. commun.) recorded salinities in the North River headwaters consistently above 20 ppt through August. These conditions might have continued unchanged until the following spring except for the arrival of hurricaine Betsy in early September; within a few days after the storm the salinity had dropped to 2 - 6 ppt throughout the North River.

With the exception of two periods of the year, the diurnal dissolved oxygen content of the North River water ranges from 3 to 7 ppt (Tabb, pers. commun.). There is often a drop to 2 ppt or lower in June or October, the two periods of the year when heavy rainfall is most likely. These oxygen depletions or "bad water" periods appear to be the result of increased BOD caused by temporarily suspended organic detritus particles with their associated microfauna along with hydrotroilite resulting from H_2S production by Desulphovibrio. This suspended detritus and debris is either flushed out of marsh areas along the river or is stirred up from the river bottom when a great deal of cold rainwater falls in a short period of time, sinks because of its greater density and causes a turnover of the bottom water. It is interesting to note that the lowest oxygen values reported by Tabb (pers. comm.) ranging from 0 to 1 ppt occurred during the month following the visit of hurricane Betsy with her torrential rains (rainfall amounts in this area were in excess of 25 cm. in 24 hours).

Invertebrates and Plant Communities

Invertebrates and aquatic plants are limited in the North River both by the great variation in salinity and by a scarcity of suitable habitats. In the upstream section of the river the bottom is composed to a great extent of scoured limestone rock, while downstream and in the ponds the bottom is soft, shifting, organic mud with the reducing layer almost at the sediment-water interface. As a result there are few burrowing organisms in the center of the river and, although attached animals are easily established on the rock bottom upstream, they are vulnerable to grazing and do not reach a large size. The greatest concentrations of small animals and plants occur within a few meters of the shore where the combination of a firm peat-mud bottom with fallen trees and other debris along with oyster shells provides suitable habitat.

The North River possesses a small permanent population of invertebrates which is supplemented by seasonal invasions of fresh or salt water organisms. Characteristic residents of the high salinity coastal mangrove swamps such as the tree crab, Aratus pisonii, and the pulmonate snail, Melampus coffeus, are absent or rare in the North River Basin.

Most abundant of the permanent community are the crab, Rhithropanopeus harrisii, the caridean shrimp, Palaemonetes intermedius, the snapping shrimp, Alpheus heterochaelis, and the scorched mussel, Brachidontes exustus. Numerous, but not as common are the pink shrimp, Penaeus duorarum, and the blue crab, Callinectes sapidus. Also found year round are the alga, Batophora oerstedi, and the grass, Ruppia maritina. Neither is ever abundant and are found only in scattered patches near the river mouth.

The late spring, summer and fall low salinity period is characterized by an explosive increase in numbers of the false mussel, Congeria leucophaeata. The crayfish, Procambarus alleni, moves downstream from the headwaters region and becomes relatively abundant in all parts of the river. Another downstream migrant is Palaemonetes paludosus, although it never becomes as abundant as P. intermedius. The alga, Chara hornemannii, is found during this period.

The rise of salinity in the late fall is shortly followed by the arrival of both Acetabularia crenulata and Udotea wilsonii in the plant community. The oyster, Crassostrea virginica becomes established on mangrove roots and large pieces of debris along the shore. The intrusion of saline water is characterized by indicator organisms in the plankton such as the chaetognath, Sagitta hispida.

Fish Populations

Tabb (1966) recorded 39 species of teleosts and two elasmobranchs during a survey of the North River. In the present study I collected all but three of these in addition to 14 other teleost species. The total collected in these two surveys of the North River is 53 species of teleosts and two elasmobranchs (Table 1).

Lepomis punctatus, L. microlophis, Lepomis gulosus, Micropterus salmoides, Lepisosteus platyrhincus, Heterandria formosa and Lucania goodei are all fishes which move downstream from the freshwater Everglades when salinities in the North River drop below 5 ppt. At such times certain marine fishes such as Sphyraena barracuda, Lagodon rhomboides and Bairdiella chrysura are much scarcer in the North River than during high salinity months. Tabb (pers. commun.) has suggested, however, that the actual standing crop of fishes is about the same at all times of the year with the exception of certain periods when low dissolved oxygen drive fishes out of the river into Whitewater Bay.

Table 1.

Fishes collected in the North River. Unless otherwise noted each species was collected both in this survey and that of Tabb (1966). (*) = collected in this survey only. (T) = collected in Tabb's survey only. Abundance estimates are based upon underwater observations, observations from above water and gear catches. Characteristic habitat refers to the area of greatest abundance and does not imply that the species is not found elsewhere in the river system at times.

Species	Abundance	Characteristic habitat
Marsh killifish *Fundulus confluentus*	Abundant	Throughout river system
Sheepshead *Archosargus probatocephalus*	Abundant	Throughout river system
Snook *Centropomus undecimalis*	Abundant	Throughout river system
Tarpon snook *C. pectinatus*	Abundant	Headwaters and marsh pools
Tarpon *Megalops atlantica*	Abundant	Throughout river system
(*)Ladyfish *Elops saurus*	Abundant	Throughout river system
Gray snapper *Lutjanus griseus*	Abundant	Throughout river system
Striped mojarra *Diapterus plumieri*	Abundant	Throughout river system
Silver jenny *Eucinostomus gula*	Abundant	Throughout river system
Spotfin mojarra *E. argenteus*	Abundant	Throughout river system
Gulf toadfish *Opsanus beta*	Abundant	Throughout river system
Sea catfish *Arius felis*	Abundant	Throughout river system
Redfin needlefish *Strongylura marina*	Abundant	Throughout river system
(*)Striped mullet *Mugil cephalus*	Abundant	Throughout river system
Bay anchovy *Anchoa mitchilli*	Abundant	Lower river and ponds
Crested goby *Lophogobius cyprinoides*	Abundant	Throughout river system
Clown goby *Microgobius gulosus*	Abundant	Throughout river system
Rainwater killifish *Lucania parva*	Abundant	Headwaters and marsh pools
Bluefin killifish *Chriopeops goodei*	Abundant	Headwaters region
Mosquitofish *Gambusia affinis*	Abundant	Throughout river system
Sailfin molly *Poecilia latipinna*	Abundant	Marsh pools
(*)Goldspotted killi *Floridichthyes carpio*	Abundant	Marsh pools and river edges
Tidewater silversides *Menidia beryllina*	Abundant	Throughout river system
(*)Spotted sunfish *Lepomis punctatus*	Abundant	Headwaters region

Table 1. (cont)

Species	Abundance	Characteristic habitat
Barracuda _Sphyraena barracuda_	Common	Lower river near mouth
Crevalle jack _Caranx hippos_	Common	River, larger creeks and ponds
Spotted seatrout _Cynoscion nebulosus_	Common	River, larger creeks and ponds
Red drum _Sciaenops ocellata_	Common	River, larger creeks and ponds
Scaled sardine _Harengula pensacolae_	Common	Lower river near mouth
Timucu _Strongylura notata_	Common	Throughout river system
Hogchoker _Trinectes maculatus_	Common	Lower river and ponds
Silver perch _Bairdiella chrysura_	Common	Lower river near mouth
Leatherjacket _Oligoplites saurus_	Common	Lower river and ponds
Bull shark _Carcharhinus leucas_	Common	River channel and ponds
(*)Clingfish _Gobiesox strumosus_	Common	Lower river near mouth
(*)Least killifish _Heterandria formosa_	Common	Headwaters region
Lined sole _Achirus lineatus_	Common	Lower river and ponds
Code goby _Gobiosoma robustum_	Common	Lower river and ponds
(*)Gafftopsail catfish _Bagre marinus_	Common	Lower river and ponds
(*)Pinfish _Lagodon rhomboides_	Common	Lower river and ponds
(*)Common eel _Anguilla rostrata_	Common	Throughout river system
(*)Diamond killifish _Adinia xenica_	Common	Marsh pools
(*)Gulf killifish _Fundulus grandis_	Common	River edges and marsh pools
Sheepshead minnow _Cyprinodon variegatus_	Common	River edges and marsh pools
(*)Emerald goby _Gobionellus smaragdus_	Rarely taken	Lower river and ponds
(*)Frillfin goby _Bathygobius soporator_	Rarely taken	Throughout river system
(*)Rivulus _Rivulus marmoratus_	Rarely taken	Throughout river system
Jewfish _Epinephelus itajara_	Rarely taken	River and larger streams
Bighead searobin _Prionotus tribulus_	Rarely taken	Lower river near mouth
Largemouth bass _Micropterus salmoides_	Rarely taken	Headwaters
Florida gar _Lepisosteus platyrhincus_	Rarely taken	Headwaters
Atlantic stingray _Dasyatis sabina_	Rarely taken	Lower river and ponds
(T)Warmouth _Chaenobryttus gulosus_	Not taken in this survey	
(T)Redear sunfish _Lepomis microlophis_	Not taken in this survey	
Thread herring _Ophisthonema oglinum_	Not taken in this survey	

My catches and observations tend to support this since any depletion in marine species is offset by the invasion of freshwater fishes.

Movement of Saltwater Organisms into Freshwater Areas

In addition to the truly euryhaline fishes present in the North River (e.g. Megalops atlantica, Mugil cephalus and Menidia beryllina), there are many strictly marine species which are able to remain in the river even when the water is apparently "fresh". This phenomenon of marine fishes and crustaceans penetrating great distances into the freshwater regions of Florida has been reported by Carr (1937) and Gunter (1942). Sixteen species of marine fishes have been recorded from Homosassa Springs (Herald and Strickland, 1949).

This ability to invade freshwaters is probably due to two factors: (1) most Florida freshwaters are not strictly freshwater (less than 25 ppm chlorinity), but may range from 100 to 1000 ppm chlorinity due to NaCl deposited in the sediments during the last submergence of the land under seawater during the Pamlico of the Pleistocene. It has been suggested (H. T. Odum, 1953) that the successful invaders of such waters are able to use these low NaCl concentrations to osmoregulate, (2) Breder (1934) and Hulet, Mased, Jodry and Wehr (1967) have suggested that the relatively high calcium content of these waters inhibits the inward diffusion of water across biological membranes allowing the organisms to successfully osmoregulate. Hulet et al further concluded that marine species which lack a distal renal tubule and the ability to excrete a dilute urine are unable to survive in these "fresh" waters.

Whatever the reasons, there are a number of marine species which are normally found in the North River in large numbers even at times of lowest salinities. Tabb (1966) lists 18 species; the most important of these in terms of standing biomass are Lutjanus griseus, Archosargus probatocephalus, Centropomus undecimalis, C. pectinatus, Sciaenops ocellata, Strongylura marina, Eucinostomus gula and E. argentius, Lophogobius cyprinoides and Microgobius gulosus. The presence or absence of these fish is determined by suitable temperature and oxygen conditions. During periods of extremely low water temperatures (below 17.5) or low dissolved oxygen concentrations there is a large scale movement of fish out of the river into Whitewater Bay. At other times there is a tendency for fishes such as Lutjanus griseus and Archosargus probatocephalus to remain in the river for long periods, while others such as Sciaenops ocellata and Elops saurus are on the move daily and are likely to be found in some other river system or Whitewater Bay in a few days time.

PRIOR RESEARCH IN THE REGION

Since the brackish water belt of southwest Florida is one of the most extensive mangrove areas of the world, it is surprising to note that prior to 1960 almost no scientific publications existed concerning the region. Exceptions were John H. Davis's comprehensive paper (1940) dealing with the ecology and geologic role of mangroves, Charles C. Davis's account (1950) of the brackish water plankton and a description of coastal vegetation zonation by Egler (1952). Other works (summarized by Tabb, 1963) either were concerned solely with the freshwater sections of the Everglades or were of a vaguely descriptive nature.

Fortunately, a group of recent publications have appeared which are most useful in an attempt to understand the Everglades estuarine environment from an ecosystem energy-flow standpoint. Fundamental among these works are Tabb and Manning (1961) and Tabb, Dubrow and Manning (1962) which deal with the occurrence and distribution of macro-organisms of the region. Tabb and Jones (1962) described the effects of a large hurricane on the biological communities, while Kahl (1962) delt with the bioenergetics of nesting woodstorks of the Everglades.

Pink shrimp, *Penaeus duorarum*, constitute the most valuable commercial resource of the Everglades estuary; aspects of their ecology are given in Tabb, Dubrow and Jones (1962), Yokel, Roessler and Iversen (1967), and by Idyll, Tabb and Yokel (1968). The biology of sport fish stocks are treated by Rosen and Dobkin (1959), Higman and Stewart (1961), Higman and Yokel (1962A), Higman and Yokel (1962B), Higman and Roessler (1963), Rouse and Higman (1964), Dooley and Higman (1965), and Higman (1967). Tabb (1967) has reported data dealing with fish stocks of the North River estuary. Roessler (1968) investigated the seasonal occurrence and life history of fishes passing through Buttonwood Canal near Flamingo. Croker (1962) studied grey snapper, Lutjanus griseus, populations of the Everglades estuary, while Eidman (1968) concentrated on the needlefish, Strongylura marina and Waldinger (1968) on the family Gerridae.

Finally, Spackman et al (1966) give an extensive description of the recent biological history of the Everglades estuary.

PROCEDURES

Sampling Stations

Five major sampling stations were established, four in each of the subsystems of the North River drainage (Fig. 2) and one in Whitewater Bay. Sporadic collections were made elsewhere in the river and bay. The major stations were visited monthly from December 1967 through May 1969, with the exception of October 1968 when a hurricane intervened. Each of these monthly trips consisted of from three to five days consecutive sampling of organisms along with measurements of water temperature, salinity and water level. These stations were also used by E.J. Heald for measurements of suspended loads of detritus, leaf fall, sedimentation rates and decomposition rates of leaf material.

The locations of the sampling stations on the North River as shown in Fig. 2 are:

Station "C" or Headwaters Station

This area is characterized by a limestone bedded stream channel several meters in width, lined with mangroves, which penetrates an area of scattered *Juncus* marshes interspersed with clumps of sawgrass. This is as far upstream as a small boat can penetrate and is the closest to a freshwater "sawgrass" environment as the defined river channel reaches.

Station "B" or the Juncus Marsh Station

Station "B" lies several kilometers downstream from Station "C"

Figure 2. Aerial photograph of the North River, showing sampling locations.

Since this region is a few centimeters lower in elevation than the area around Station "C", the *Juncus* marshes contain many small shallow pools. These pools are connected to small creeks which eventually empty into the North River which is 30 meters wide at this point. All sampling at this station was done in the pools and drainage creeks. The bottoms of the pools are composed of *Juncus* and mangrove peat while the creek bottoms are either hard packed mud or limestone rock.

Station "D" or the Mangrove Pond Station

This collecting station consisted of one of the ponds lying near the mouth of the river and connected to it by a winding stream. This pond is ten hectares in area, a meter deep, extremely turbid and has a bottom consisting principally of mangrove detritus mud mixed with broken shell. All collecting was done in the pond itself and not in the associated drainage stream.

Station "A" or the Main River Channel Station

Station "A" was selected in an area which most typified the environment of the main river channel. It consists of the shoreline and shallow waters bordering a mangrove island in addition to the river channel passing the island. Along the shore the bottom was eroded peat which graded into fine mud mixed with shell toward the center of the river and culminated in scoured limestone rock in the main channel where the current was the strongest. At this point the North River is 80 meters in width.

Stations 5 and 6 or the Whitewater Bay Stations

The area chosen for this station is typical of northeast Whitewater Bay, the region into which the North River empties. The bottom, which lies at a depth of about 1.5 meters, is composed of fine mud mixed with shell fragments. The benthos is dominated by Udotea englemani, which flourishes during periods of higher salinites. This area rarely becomes completely fresh and usually remains between 10 and 30 ppt. This station is identical to stations 5 and 6 for the juvenile shrimp project. All samples from this station originated from this project and were obtained through the generosity of Bernie Yokel and Steve Clark.

Collection of Organisms

As with most ecological field investigations adequate sampling proved to be a difficult problem. Although several dozen different sampling devices were tried, and 15 of these were used routinely, none were completely satisfactory for quantitative sampling, especially for the fishes. This mangrove region with its rocky stream beds, undercut banks, and its dark, sometimes turbid water presented such a variable environment that quantitative sampling was impossible. For these reasons the sampling procedures were designed simply to procure as many different organisms as possible for stomach examination rather than to obtain accurate quantitative standing crop data.

Collection of the small fishes was relatively easy. Near the mouth of the river it was possible to use a 30 foot bag seine with three quarter inch stretched mesh. A 12 foot three quarter inch throw net was used where it was not feasible to seine. A fine mesh dip net was used at all stations to collect top minnows and caridean shrimp. Plastic "Breder Traps" were used primarily in the marsh pools and along the banks of the river. These proved very effective as did the "Beamish Trap Net" designed and built by R. Beamish of the University of Toronto. The latter device is a pound net constructed from mosquito netting and designed to fish in depths up to a meter, while the former is a plexiglass funnel trap. The Beamish Trap Net is effective for most organisms ranging in size from mysids to small sharks. One-gallon glass jars fitted with fiber glass screen funnels were suspended at each station to collect crabs, gobies and caridean shrimp. It was necessary with all of the trap devices to empty them frequently; even with these precautions the carnivores caught in traps were not usually used for food studies since their stomachs may have contained organisms obtained inside the trap.

A fish poison, ProNox Fish, was used several times in the small streams draining the upstream Juncus marshes, but was only successful for some species. Even when a small stretch of stream was blocked off with nets, treated with ProNox Fish and systematically collected for dead and dying fish, even with the utmost thoroughness, recovery rates were probably no higher than 40 percent of the standing crop actually present. Many individuals buried themselves in pockets of mud or underneath overhanging banks. This sampling problem was made more complex by the presence of large loads of suspended material which quickly adsorbed much of the ProNox Fish and effectively neutralized it.

Capture of the larger fishes proved to be the most difficult sampling problem. Certain highly mobile species such as snook, mullet and tarpon were never sampled adequately. The most satisfactory method of collection for the larger fishes was rod and reel; several hundred were taken in this manner. A 300 foot trammel net (inside mesh two inches, outside mesh 10 inches) was used successfully at the pond station and with limited success in the river channel. Set lines baited with squid strips took both species of marine catfishes consistently.

Initial samples from Whitewater Bay were taken with a ten foot otter trawl. Eventually this was discontinued as much better samples were available from the juvenile shrimp project which utilized a one meter roller beam trawl.

Planktonic animals were sampled routinely with a standard 12 inch 135 micron plankton net. Larger organisms such as mysids and amphipods were taken at the mud-water interface with an Ockleman Dredge with a one tenth meter Van Veen Grab or a piece of core tubing. Due to the rocky nature of most of the river bottom, the grab was of little use.

Quantitative samples of mysids, amphipods, small crabs and chironomids were taken with a piece of core tubing of 6 cm diameter. Penaeid and caridean shrimp along with crabs, amphipods, isopods and small fishes were captured successfully in a fine mesh lift net which was left covered with leaves and branches on the stream bed for 12 hours before being lifted. Many amphipods and other small organisms were removed from the river bottom while diving with a face mask and snorkel.

Routine sampling with this heterogeneous assemblage of methods resulted in a reasonably accurate inventory of the animals present and what they consume.

Preservation

Smaller organisms were preserved in buffered 10 percent formalin. The larger fishes and elasmobranchs were dissected in the field and only the digestive tract retained and preserved for later examination. Selected samples of small organisms and fishes were preserved in a chilled brine solution at -4°C and transported to the laboratory for analyses within 12 hours.

Digestive Tract Contents Analyses

Routine food analyses were performed in the laboratory on previously collected material. Ideally, only the stomach contents were examined; however, if the stomach was empty or only partially filled, the intestinal contents were also inspected. Because of differential digestive rates, these intestinal examinations were considered to have value only in a qualitative way and no quantitative estimates were made.

For caridean and penaeid shrimp, crabs, and mysids, material for examination was taken from the buccal cavity. For insect larvae, amphipods, cumaceans and isopods the method of Croker (1967) was used. This involves first removing the animal's head and then applying pressure to the body so that the gut contents are squeezed out onto a microscope slide.

The following estimates were made during the examination of each organism's stomach contents.

Percent composition of stomach contents

Estimates of the relative occurrence of materials in stomach contents are admittedly subjective and unique to the individual investigator. For this reason it is essential that the same procedure be used consistently by one individual throughout a project to obtain good comparative data. For this project I used either of two methods depending upon the size of the stomach content particles. The first method, for larger particles, consisted of the standard practice of immersing the individual food items either in a graduated cylinder or a small diameter calibrated glass tube. Stomach contents of small animals containing fine particles (less than one millimeter) required a second approach. A known volume of stomach contents were pipeted onto a glass slide etched with a fine grid. With the aid of an eyepiece micrometer and the marked slide, an estimate was made of the volumetric composition of the stomach contents. This method is similar to attempts to quantify the gut contents of insects made by Jones (1950), Brown (1961), and Chapman and Deomory (1963). The same technique was used for the examination of stomach contents of Mugil cephalus by W. E. Odum (1969); in that paper there is a discussion of the merits and drawbacks of the method.

A third method (Mecom and Cummins, 1964) was tried, but discarded. This involved filtering known volumes of stomach contents through a 0.45 micron gridded millipore, clearing the filter and estimating the percent composition of the material retained on the filter. Although basically a good method, it proved impractical for this study because the structure of delicate detritus particles was often altered beyond recognition on the surface of the filter during filtration.

Percent fullness of the digestive tract

An estimate of the percent fullness of the stomach or buccal cavity was based upon experience and comparisons with previously encountered filled stomachs. Although this is a subjective value, I feel that it is a suitable indicator of feeding intensity.

Identification of food organisms

With the use of a reference collection of the common organisms of the North River it was possible to identify stomach contents accurately, even when only stray parts were present. Most food organisms were identified to species; adult and larval insects, copepods and hydrozoans were more broadly classified.

Identification of organic detritus particles

At the beginning of the study a photographic atlas was compiled which included color microphotographs of 12 different types of detritus particles at various magnifications. These photographs were made from material of known origin taken from E.J. Heald's decomposition bags and included such tissues as mangrove leaf parenchema, sawgrass stem and roots of *Juncus*. With the aid of the atlas it was possible to identify most detritus particles above 30 to 40 microns from their characertistic cell structure.

Measurement of particle size

All stomach content particles were measured whether they were diatoms, small copepods, detritus particles or entire fish. These measurements were made with an eyepiece micrometer for the smaller particles and a pair of calipers or small ruler for the larger organisms. Measurements of fish throughout this study whether predator or prey were standard length (i.e. from the tip of the snout with the mouth closed to the tip of the vertebral column or hypural plate). Crustacean measurements were usually of the carapace length (shrimp) or width (crabs), but were total body lengths for mysids, amphipods, cumaceans and copepods.

Measurement of Physical Parameters

Salinities were determined with a hydrometer and were corrected for temperature. Extremely low salinities were measured by the conductivity bridge method. Oxygen determinations were by the Winkler method. Eh and pH measurements were made with the Coleman model 37A portable pH meter.

Measurement of Chemical Characteristics

Caloric, fat and nitrogen determinations of detritus particles were done under the direction of Mrs. Shirley Marshall of the Ecological Institute of the University of Georgia. Additional protein, fat, carbohydrate, crude fiber and ash determinations were conducted by Law and Company of Atlanta, Georgia. These results were shared jointly with E. J. Heald and most have already been reported by Heald (1969).

Caloric determinations were made with the Paar Adiabatic Bomb Calorimeter. Nitrogen determinations were by the conventional Kjeldahl method as outlined in the handbook of the Association of Official Argicultural Chemists. A few values were obtained using the Coleman Nitrogen analyzer. Protein content was then estimated by multiplying the nitrogen value by 6.25.

Fat content was derived by the direct "anhydrous ether" method. This gives a crude fat value which includes sterols, fatty acids, chlorophylls, fat and glycerol esters of fatty acids. Crude fiber represented what remained after the particles had been boiled in dilute sulphuric acid followed by dilute sodium hydroxide. It was composed mainly of cellulose and other insoluble carbohydrates.

TROPHIC ANALYSES

CARCHARHINIDAE

Carcharhinus leucas (Müller and Henle)

Bull Shark

Carcharhinus leucas is well known for its ability to penetrate freshwater rivers and lakes. It occurs in Central American lakes (summarized by Thorson et al, 1966), and in North American rivers where it may be found as far as 160 miles from the sea (Gunter, 1938). Juvenile bull sharks are found in brackish estuaries (Springer, 1967). Which provide both protection from larger sharks and a plentiful food supply.

Young bull sharks were observed in the upper reaches of the North River in October, 1967, May, and June, 1968, but none were captured. An individual measuring 102 centimeters, total length, was caught in the trammel net at the pond station in November, 1968. In February, 1969, twelve individuals ranging in length from 110 to 162 centimeters were taken in three days in the same manner at the same station. Since C. leucas are born in Florida in April, May and June and are about 74 - 75 centimeters total length at birth (Clark and von Schmidt, 1965), these were probably all yearlings. Seven of the 13 sharks were females.

Baughman and Springer (1950) reviewed the work of earlier authors and concluded that the bull shark is a carnivore which feeds on sting rays, other sharks, shad and mackerel. Schwarts (1960) mentioned a number of species of fish eaten by adult C. leucas from Chesapeake Bay. Clark and von Schmidt (1965) while examining the stomach contents of large bull sharks found remains of Archosargus probatocephalus, Caranx sp., Centropomus undecimalis, Euthynnus alletteratus, Galeichthys felis, Lactophrys tricornis, Megalops atlanticus, Mugil sp., Prionotus sp., crustaceans, molluscs and parts of other sharks. Miles (1949) examined five juveniles caught in Texas bays which ranged from 100 to 150 centimeters and found remains of Cynoscion arenarius, Alosa pseudoharengus, and Penaeus setiferus in their stomachs. Darnell (1958) examined three juveniles of the same size range from Lake Ponchartrain, Louisiana, and found a large Mugil cephalus (255 mm), a number of small Brevoortia patronus (66 - 103 mm), a Micropogon undulatus (67 mm), Penaeus setiferus and a small crab (probably Callinectes sapidus). Fishes made up 90 per cent of the ingested food.

Only six of the 13 sharks from the North River pond contained food. Four contained Galeichthys felis which ranged in size from 200 to 250 mm. Two of these G. felis had been bitten in two pieces just behind the dorsal and pectoral spines and only the posterior portion of the fish ingested. Of the two remaining sharks containing food, one had ingested a Penaeus duorarum (10 mm carapace) and one a Lophogobius cyprinoides of 42 mm.

Thus, from the literature and North River examples it appears that juvenile C. leucas are predators at the top of the food web with fish consituting the greatest portion of their diet. They have the ability to catch and devour large elusive fishes such as Mugil cephalus which may be a quarter of their own length.

LEPISOSTEIDAE

Lepisosteus platyrhincus DeKay

Florida Gar

An occasional gar moves into the North River from the freshwater Everglades during the rainy summer months. Although uncommon in the North River, at least during the time of this survey, the species becomes abundant in other basins of the Everglades mangrove belt during the rainy season.

Hunt (1953) has written a complete and definitive account of the food chain which supports the Florida gar in the freshwater Everglades. He examined 448 gar, 106 of which contained food. This food was made up of 76.4 per cent fishes and 23.6 per cent invertebrates by volume. *Gambusia affinis* was the most commonly encountered fish in the stomachs; others included *Lucania goodei*, *Jordanella floridae*, *Heterandria formosa*, *Poecilia latipina*, and small centrarchids. The most important invertebrate (16.5 per cent of total stomach contents) was *Palaemonetes paludosus*. Chironomid and chaoborus larvae and dragonfly and damselfly nymphs were also ingested by gars.

No gars were examined from the North River. Several were observed during July and August and one was caught in a trammel net, but subsequently lost.

The Florida gar can therefore be considered a carnivore which feeds upon small fishes and invertebrates. In turn it serves as an important food for the alligator. Although unimportant in the North River, it may be influential in other sections of the Everglades mangrove belt.

ELOPIDAE

Megalops atlantica Valenciennes

Tarpon

A moderately large population of juvenile tarpon is present in the North River basin. A limited amount of suitable habitat in the form of shallow, dark-colored, brackish ponds as described by Wade (1962) prevents larger populations as found in the nearby Roberts River headwaters. In general, the brackish mangrove belt should be regarded as an important habitat for young tarpon.

No tarpon were taken in this survey. From the recent summary of Rickards (1968) young tarpon appear to be strictly carnivorous and predominantly piscivorous. He found that in Georgia marshes *Gambusia* predominated in the stomach contents of tarpon in the size range 19 to 273 mm; ostracods and *Palaemonetes* were of some importance. Tarpon of larger sizes also consumed *Fundulus heteroclitus* and *Mugil cephalus*. Harrington and Harrington (1960, 1961) examined 214 tarpon between 16 and 45 mm SL and found cyclopoid copepods dominant in the diet indicating that the very young fish are plankton feeders. Adults prey upon a wide variety of fishes, crabs, shrimp, and even ctenophores (Randall, 1967).

From published reports it can be concluded that very young tarpon (less than 45 mm) are primarily plankton feeders while also eating small fishes, ostracods and aquatic insects. The older juveniles concentrate upon fishes and caridean shrimp.

Elops saurus Linnaeus

Ladyfish

Juvenile ladyfish are found abundantly throughout the brackish mangrove belt. In the North River basin they first appear at a length of about 20 mm; the largest specimen collected was 346 mm. Larger fish are found in the deeper sections of Florida Bay and the mouth of the Shark River (Tabb and Manning, 1961).

Darnell (1958) reviewed the papers of Linton (1904), Gunter (1945), Hiatt (1947), Knapp (1949), and Reid (1954) and concluded that *Elops saurus* feeds on penaeid shrimp and fishes. Springer and Woodburn (1962) agree for fish from Tampa Bay, Florida, as does Cervigon (1966) for Venezuelan *E. saurus*. From the data of Harrington and Harrington (1961) it can be concluded that the diet of young ladyfish in marsh communities is based upon copepods until the fish reach a size of about 45 mm. At this point they begin feeding upon small fishes and *Palaemonetes*.

My analyses of the food of North River *E. saurus* agree with the quoted literature. Five of six fish ranging from 19 to 38 mm were filled with copepods and a few crab zoea; the sixth was empty. Of twenty eight fish measuring between 223 and 346 mm only nine contained food; this food by volume was composed of 44 per cent caridean shrimp and 56 per cent small fishes (*Poecilia latipinna*, *Eucinostomus gula*, *Menidia beryllina* and *Anchoa hepsetus*). These larger *E. saurus* appeared to feed primarily from dusk to dawn.

The North River system serves as an important nursery ground for *E. saurus*. Ladyfish of less than about 45 mm are zooplankton feeders; above this size they consume caridean and penaeid shrimp and various small fishes.

CLUPEIDAE

Harengula pensacolae Goode and Bean

Scaled Sardine

Small schools of *Harengula pensacolae*, juveniles, 60 - 100 mm, visit the lower North River and mangrove ponds during the winter months when salinities are above 15 ppt. This is a lower tolerance than the 25 ppt. limit noted by Springer and Woodburn (1960) for this species in Tampa Bay, Florida.

Reid (1954) listed planktonic crustaceans as the food of *H. pensacolae* near Cedar Key, Florida. Mysids, amphipods, copepods, ostracods and small molluscs were removed from a large number of fish taken from Tampa Bay by Springer and Woodburn (op. cit.).

In the North River I observed schools of scaled sardines which remained in the same locality for two or three days feeding upon shallow water benthic invertebrates. Scrutiny of 45 stomachs of fish from 64 - 96 mm revealed 32 which contained food (Fig. 3). Amphipods were the chief food and probably made up most of the "unidentified residue" category. 22 smaller fish (16 - 30 mm) collected in the Little Shark River contained planktonic copepods, zoea, nauplii and a few fish larvae.

Although *Harengula pensacolae* is not a permanent part of the North River fauna, it does visit the region during higher salinity periods and feeds upon benthic crustaceans and insect larvae. Post-larvae were not taken from the North River, but are found nearer the Gulf of Mexico feeding upon zooplankton.

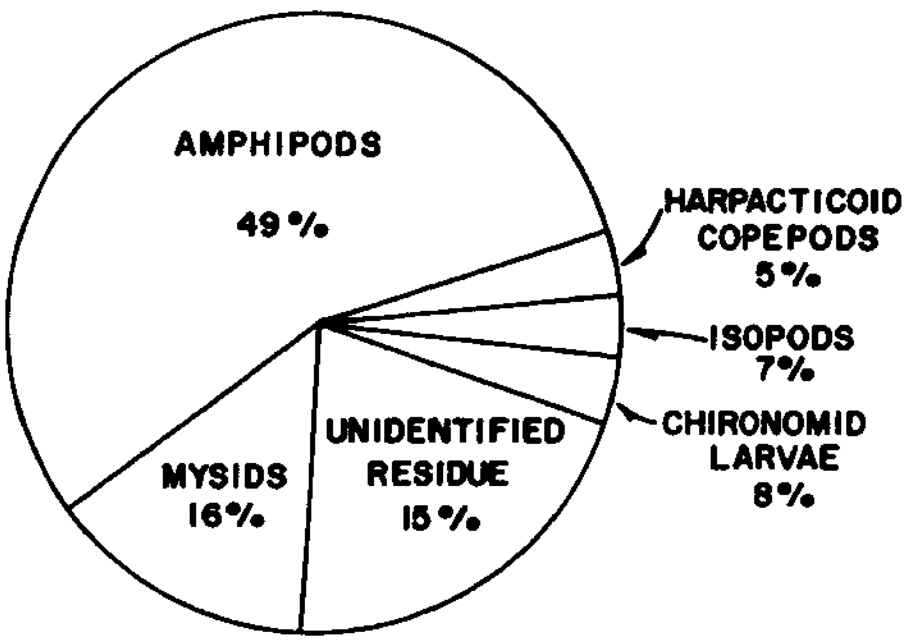


Figure 3. The volumetric per cent composition of the stomach contents of 32 scaled sardines, *Harengula pensacolae*, 64-96mm, collected between December, 1967, and March, 1968, at station A.

ENGRAULIDAE

Anchoa mitchilli (Valenciennes)

Bay Anchovy

The bay anchovy is the most abundant fish in the brackish bays of the Everglades estuary (Tabb and Manning, 1961; Roessler, 1967). It is not, however, particularly numerous in the North River system indicating that this fish may prefer to remain in more open waters.

The food of *A. mitchilli* was described by Hildebrand and Schroeder (1928) as mysids and copepods. Springer and Woodburn (1960) concluded from the stomachs of 42 *A. mitchilli* from Tampa Bay, Florida, that the principal foods are copepods, ostracods, mysids, pelecypods, gastropods, small fish and crustacean larvae. From his work in Lake Pontchartrain, Louisiana, Darnell (1958) suggested that this anchovy passed through two ontogenetic feeding stages. Young individuals (no size specified) are plankton strainers consuming large quantities of micro-zooplankton and suspended detritus. At larger sizes the fish are more selective and prey upon planktonic mysids, post-larval shrimp and larval fishes in addition to mysids, amphipods, isopods, ostracods, harpacticoid copepods, small snails and clams obtained from the benthos.

Examination of *A. mitchilli* from the North River did not completely support Darnell's conclusions about the Lake Pontchartrain population of *A. mitchilli*. Seventeen larval and young juveniles of less than 25 mm had fed solely upon microzooplankton (copepods, copepodites, nauplii) which did not appear to be the result of simple straining of the water but rather the product of selective capture of the appropriate sized organisms. Further evidence against simple filtration was provided by the complete absence in the fish's stomachs of detritus particles of the same size as the microzooplankton. Charles Mayo (personal communication) has observed larvae of A. mitchilli for many hours in the laboratory and is convinced that feeding is a process of intentional, visually aided capture of individual zooplankters.

Twenty seven larger bay anchovies, 31 - 62 mm were dissected and found to have consumed material similar to that described by Darnell for anchovies of this size (Fig. 4); little of this food originated from the plankton. Seventy five A. mitchilli were collected in July from the Turkey Point shrimp rearing ponds, a system in which planktonic copepods are very numerous. All of these anchovies had fed upon planktonic copepods (Acartia sp.) to the exclusion of benthic organisms. The predominantly benthic feeding in the North River is probably encouraged by the abundance of benthic organisms and the meager supply of zooplankton; this scarcity could explain the relatively low populations of anchovies in the North River system.

Anchoa hepsetus which is most abundant in Florida Bay (Tabb and Manning, 1961) and other higher salinity areas, was encountered so infrequently in the North River that I considered it unimportant to the system.

A. mitchilli are of limited importance in the North River compared to its role in the open waters of Whitewater Bay. Anchovies smaller than 25 mm selected copepods and other small zooplankton. Larger fish continue to feed upon zooplankton and include amphipods, mysids, harpacticoid copepods, chironomid larvae, ostracods and small molluscs. Detritus is of little importance in the diet. A. hepsetus only occassionally strays into the North River.

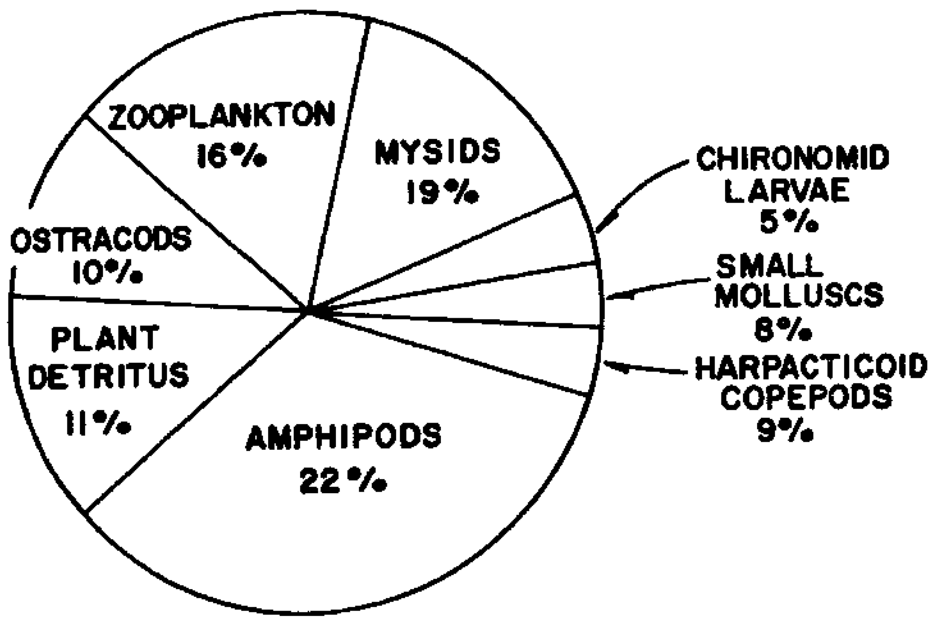


Figure 4. The volumetric per cent composition of the stomach contents of 27 bay anchovies, *Anchoa mitchilli*, 31-62mm. The fish were collected throughout the year at stations A and B.

SYNODONTIDAE

Synodus foetens (Linnaeus)

Inshore Lizardfish

Synodus foetens occasionally enter the lower portion of the North River and associated mangrove ponds during late winter and early spring when salinities exceed 15 ppt. Only two (189,112 mm) were taken during this survey and neither contained food. Smith's (1907) description of *S. foetens* ably characterizes its feeding: "it is a voracious feeder; small fish constitute its principal food, but crabs, shrimp, worms and other animals are eaten". This description is supported by the data of Hildebrand and Schroeder (1928), Reid (1954), and Springer and Woodburn (1960).

Synodus foetens is not an important factor in the North River ecosystem. Nothing new can be stated concerning its feeding habits from my data.

ARIIDAE

Arius felis (Linnaeus)

Sea Catfish

Arius felis is abundant at all times of the year throughout the North River including the mangrove lined ponds and small creeks which drain the *Juncus* marshes in the headwaters region.

Darnell (1958) has summarized the extensive literature on *A. felis* and concluded, from this and from examination of Lake Pontchartrain, Louisiana catfish, that three feeding stages exist. For fish of less than 100 mm copepods and other zooplankton appeared to be most important. Above this size benthic invertebrates become more important until finally, catfish above 200 mm eat larger crabs and fishes (this final stage is not completely correct for North River catfish). Although other authors have not emphasized it, "bottom detritus" was noted by Darnell in a large proportion of the Louisiana catfish stomachs. He suggested that the presence of only the hard parts of fishes in the catfish stomachs was traceable to straining of bottom sediments and not actual capture of live fish (this also is not true for A. felis in the North River, as fresh fishes were observed in their stomachs).

Both Knapp (1949) and Harris and Rose (1968) have emphasized the ability of A. felis to consume large quantities of commercial penaeid shrimp. Of 468 catfish examined by Knapp in Texas, 87 per cent had eaten shrimp. Harris and Rose present data which estimates a potentially significant loss to the shrimp fishing industry from catfish predation.

The stomach contents of 14 young A. felis, 52 - 74 mm, from Whitewater Bay were dominated by amphipods; other foods were mysids, chironomid larvae, isopods, and small crabs. Fig. 5 summarizes the food of 62 catfish, 205 to 331 mm, from the North River. Included in the miscellaneous category are 11 types of food which each made up less than five per cent of the fish's diet: nematodes, crayfish, dragonfly larvae, tarpon and other fish scales, adult insects, Brachidontes exustus, isopods, algal strands, Penaeus duorarum, Palaemonetes sp. and Alpheus heterochaelis. There was a tendency for chironomid and dragonfly larvae and crayfish to be more important in feeding by catfish in the low salinity headwaters region than is

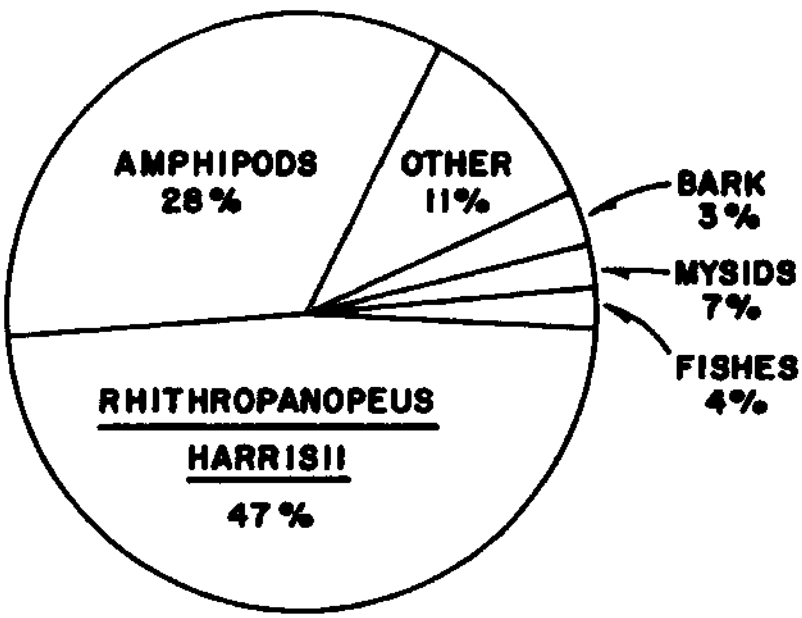


Figure 5. The volumetric per cent composition of the stomach contents of 62 sea catfish, _Arius felis_, 205-331mm, collected throughout the year at all stations.

shown in Fig. 5.

A. felis is an abundant and important carnivore in the North River system. Although the crab Rhithropanopeus harrisii and two species of amphipods made up almost 70 per cent of the stomach contents, the catfish is able to feed upon a variety of small animals. It is this capacity to utilize a number of food sources which probably explains the ability of A. felis to adapt successfully to different habitats.

Bagre marinus (Mitchill)

Gafftopsail Catfish

Bagre marinus was outnumbered eight to one by Arius felis in catches from the North River. These data agree closely with the ratio of ten to one found by Tabb and Manning (1969) after a large fish kill in Whitewater Bay.

There is a hint in the literature that the diet of B. marinus may be different from that of A. felis. Gudger (1910) states that the blue crab, Callinectes sapidus, is the staple food of B. marinus in North Carolina waters (quoted from Gunter, 1945). Gunter examined five gafftopsails from Texas and found blue crabs in all five. Miles (1949) looked at 85 fish from Texas and found six species of crabs, 11 species of fishes and penaeid shrimp in their stomachs. Cervigon (1966) states that B. marinus in Venezuela feed on crabs, shrimp and small fishes.

Of eight gafftopsail catfish, 262 - 445 mm, collected in the North River, five contained food. Three had eaten small Callinectes sapidus of a carapace width of about 40 - 50 mm; the remaining two contained remains of unidentified fish. In contrast to A. felis no amphipods or mysids were found in their stomachs. Although this is an extremely small sample, it does indicate a possible difference in diet compared to *A. felis*. The latter species from the same samples as *B. marinus* rarely was found without amphipods or with fishes in its stomach.

B. marinus is common in the North River, but much less numerous than *A. felis*. From a small sample size of fish in the range 262 - 445 mm, the diet appears to be dominated by *Callinectes sapidus* and small fishes, a situation somewhat different than that for *A. felis* of the same size.

ANGUILLIDAE

Anguilla rostrata (LeSueur)

American Eel

During rotenone sampling *Anguilla rostrata* was commonly collected from beneath the undercut banks of the river channel and small streams. Although eels taken in my survey ranged from 181 to 472 mm, Tabb and Manning (1969) reported several of 1000 mm from the Everglades estuary.

Hildebrand and Schroeder (1928) regarded large eels as omnivorous consumers of crustaceans, annelids, fish, echinoderms, molluscs, and eelgrass. Small eels of the size 50 - 200 mm feed on amphipods and isopods. De Sylva et al (1962) list a number of food items removed from the stomachs of 47 *A. rostrata* from the Delaware River estuary. Included were polychaetes, mysids, *Limulus* larvae and eggs, *Menidia* sp. and insect remains.

All eight eels, 181 - 472 mm, examined from North River daytime samples were empty indicating nocturnal feeding. Four of the same size range taken at night contained *Rhithropanopeus harrisii*, *Palaemonetes intermedius*, *Alpheus heterochaelis*, and *Lophogobius cyprinoides*.

From limited data it appears that *Anguilla rostrata* is common in the North River channel and small streams and is an omnivorous consumer of available crustaceans and probably fishes, mollusks and polychaete worms.

CYPRINODONTIDAE

Fundulus confluentus Goode and Bean

Marsh Killifish

The marsh killifish is one of the most common fishes from the brackish marsh areas (Tabb and Manning, 1961), although its abundance evidently fluctuates. In 1965-66, *Fundulus confluentus* was listed by Tabb (1966) as the fifth most common fish taken in the entire North River basin with more than 500 collected. Sampling at the same stations with the same gear in 1968-69 I captured only 16 marsh killifish.

Harrington and Harrington (1961) analyzed the stomach contents of 88 *F. confluentus* from a Florida salt marsh and found mosquito instars and pupae when available dominating the diet. Other foods included *Palaemonetes*, isopods, amphipods, fishes, insects, nematodes, gastropods, ostracods and a small amount of plant material. In a Sapelo Island, Georgia, marsh pool, detritus and algae composed 30 per cent of the stomach contents of three marsh killifish (Kawanabe et al., unpublished manuscript).

Since so few individuals of *F. confluentus* were taken in my survey the data collected by Billy Drummond in 1965-66 is most useful. He looked at the stomach contents of 77 fish ranging from 29 to 88 mm, but did not measure stomach content volume. These fish were obtained from the marsh pool station (Station B). Most often recorded in his data are chironomid larvae, adult insects, amphipods, small bivalves and a few isopods. Fish (primarily Gambusia affinis) occurred in stomachs of killifish above 55 mm, but most often in those longer than 70 mm.

I examined four fish, 15 - 18 mm, which were taken in December. They had fed upon small chironomid larvae and small amphipods.

Fundulus confluentus is an important fish in the marsh areas of the North River, although its abundance may fluctuate. It has a diverse diet which includes Palaemonetes, small fishes, amphipods, isopods, adult and larval insects, copepods, mysids, ostracods, and algal filaments.

Fundulus grandis Baird and Girard
Gulf Killifish

Fundulus grandis was collected more frequently in my survey of the North River than F. confluentus. Judging from the data of Tabb and Manning (1961) and Tabb (1961) this probably does not properly reflect the normal abundance ratio between the two species.

Springer and Woodburn (1960) reported a varied diet for F. grandis from the Tampa Bay, Florida, region which included hermit crabs, pelecypods, unidentified arthropods, and small fishes such as Poecilia latipinna. Harrington and Harrington (1961) found the stomach contents of the gulf killifish to be composed of Palaemonetes, mosquitoes, and small fishes.

I collected 27 gulf killifish, 29 - 98 mm, all of which contained some food in their digestive tracts. Fish between 29 and 45 mm had eaten amphipods, isopods, small Rhithropanopeus harrisii (two to four mm carapace width), chironomid larvae, terrestrial insects, small snails and filaments of algae. Above this length they included fishes and larger R. harrisii (up to 12 mm carapace width) to the gradual exclusion of the smaller components of the diet. One killifish of 68 mm had managed to swallow a Gambusia affinis of 25 mm.

Fundulus grandis is a small predator in the marsh pools, small streams, and shoreline areas of the North River. Its diet is primarily carnivorous, but diverse.

Cyprinodon variegatus Lacépède

Sheepshead Minnow

Although Cyprinodon variegatus may at times be abundant in the Juncus lined pools and along the shallow edges of the North River, the population size evidently fluctuates. During 1965-66 this was by far the most common species collected by Tabb (1966) composing 40.9 per cent of 10,509 fishes. However, during the period of my survey relatively few individuals of C. variegatus were caputred and those were outnumbered by Floridicthys carpio.

C. variegatus is generally regarded as a herbivore which ingests algae, plant detritus and sand particles (Hildebrand and Schroeder, 1928; Reid, 1954; Springer and Woodburn, 1960), although Harrington and Harrington (1961) found that they fed upon mosquito instars and pupae when available.

The food of 44 Cyprinodon variegatus, 15 - 53 mm, taken from the Juncus marsh pools of the North River system is shown in Fig. 6. There

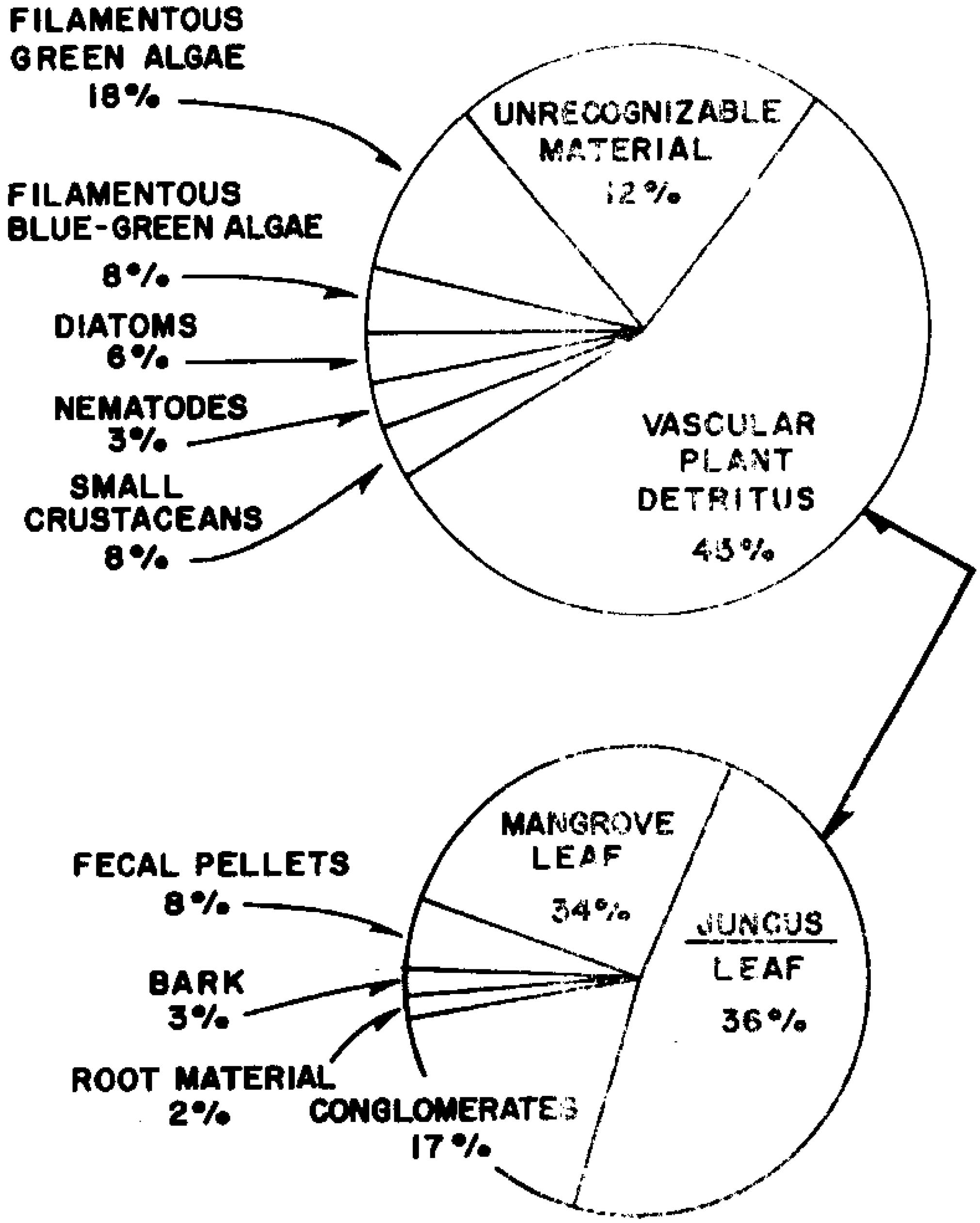


Figure 6. The volumetric per cent composition of the digestive tract contents of 44 sheepshead minnows, *Cyprinodon variegatus*, 15-53 mm, collected throughout the year at station B.

was little variation from a predominantly detritus-algal diet, although fish rangind from ten to 15 mm had eaten a few harpacticoid copepods and small amphipods.

Cyprinodon variegatus is one of the few fishes in the North River system which consumes vascular plant detritus and algae directly. In some years it is one of the most abundant species in the shallow water areas of the river system, but at other times it is less numerous and may be outnumbered by *F. carpio*.

Floridichthys carpio (Günther)

Goldspotted Killifish

This species was considered by Tabb and Manning (1969) to be rare in the Everglades estuary. Tabb (1966) did not record it from the North River. During the present survey *F. carpio* was collected routinely throughout the year in water which ranged from less than one to 26.5 ppt. In the *Juncus* marsh pools it was taken in approximately equal numbers as *C. variegatus*, but outnumbered the latter 20 to one in samples from the shallow waters adjacent to the shore of the North River.

Little information exists concerning the food of *F. carpio*. Springer and Woodburn's data (1960) from Tampa Bay, Florida, indicates a diet of tiny crustaceans, molluscs, and annelids. This indication of a more carnivorous diet than that of *C. variegatus* is supported by my data from the North River (Fig. 7). At least 45 per cent of the food material was of an animal origin compared to 11 per cent of *C. variegatus* (Fig. 6).

Floridichthys carpio is abundant the year round in the small marsh pools and shallow edges of the North River. Its diet, although omnivorous,

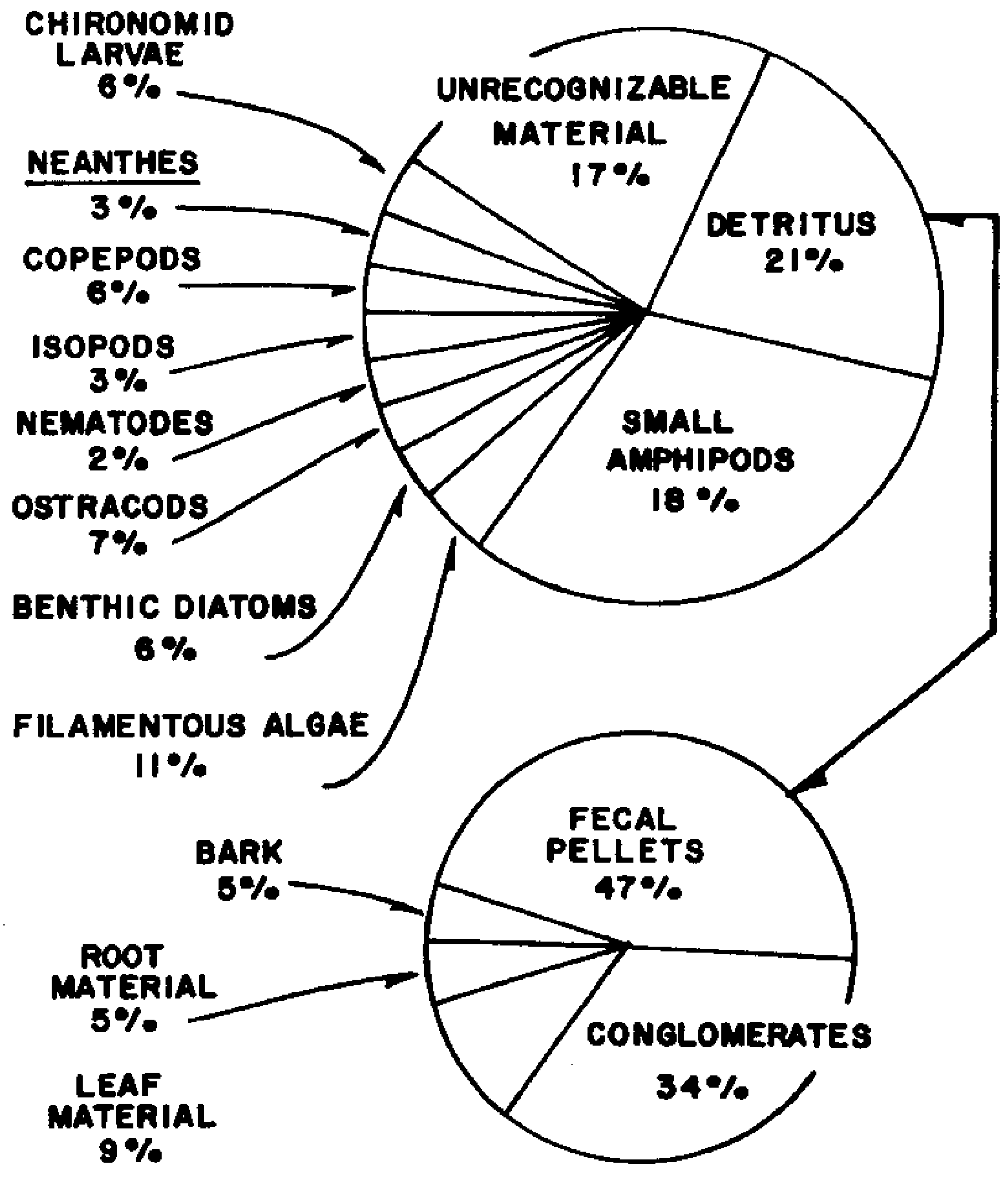


Figure 7. The volumetric per cent composition of the digestive tract contents of 81 gold spotted killifish, *Floridichthyes carpio*, 14-59 mm, collected throughout the year at station B.

contains much more animal material than that of Cyprinodon variegatus.

Adinia xenica (Jordan and Gilbert)

Diamond Killifish

This little fish was collected in every season from the Juncus marsh pools, but never were more than two or three taken in the same sample. I could find no information in past literature which referred to its food. Examination of 28 fish, 26 - 35 mm, from the Juncus marsh station indicated a diet (Fig. 8) which was based primarily upon plants, both living and detrital. Almost all of this plant material was very fine, either tiny detrital particles or diatoms. When animal material was consumed it was eaten almost exclusively.

Adinia xenica was commonly collected in marsh pools, but was never abundant. It feeds primarily upon vascular plant detritus and diatoms, with only an occasional digression to consume small amphipods, harpacticoid copepods and small insects.

Lucania parva (Baird and Girard)

Rainwater Killifish

Along with Gambusia affinis and Menidia beryllina, this is one of the most abundant small, carinvorous forage fishes present in the North River system. It is most numerous in the Juncus marsh pools and along the banks of the river wherever mangrove proproots or other cover afford some protection.

Hildebrand and Schroeder (1928) considered the diet of L. parva to be small crustaceans. Harrington and Harrington (1969) found cyclopoid and harpacticoid copepods dominant in the diet except during

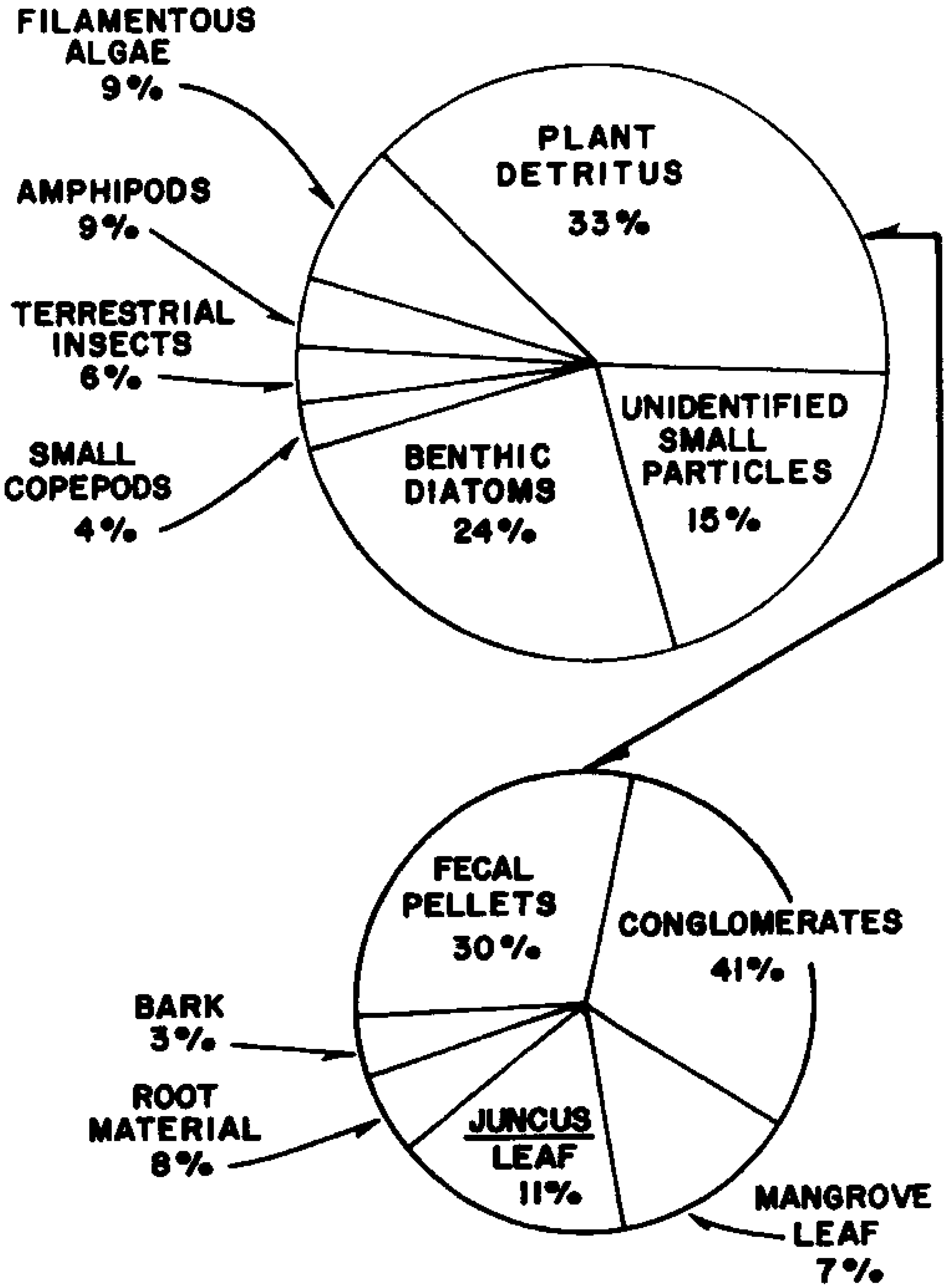


Figure 8. The volumetric per cent composition of the digestive tract contents of 28 diamond killifish, Adinia xenica, 26-33 mm, collected throughout the year at station B.

periods when mosquito instars and pupae were present in the environment and were consumed in large numbers by this fish. Plant material was found infrequently.

Forty eight L. parva of less than 20 mm from the North River had eaten planktonic copepods almost exclusively. The diet of fish measuring 21 to 37 mm is shown in Fig. 9.

Lucania parva is an abundant forage fish which serves as an intermediate step between detritus-algal feeders and top carnivores. Chironomid larvae, amphipods, ostracods, and mysids are most important in the diet of fish over 20 mm, while planktonic copepods are eaten by smaller fish.

Lucania goodei Jordan

Bluefin Killifish

This little fish exhibits little tolerance for saline water and moves into the mangrove belt of the Everglades estuary only during the period of freshwater influx. As Tabb and Manning 1961 have pointed out, it is common at such times, but never abundant.

Hunt (1953) studied the diet of the bluefin killifish in the Tamiami canal and found that 95 per cent of the stomach content volume was composed of animal matter (chironomid larvae, ostracods, copepods, cladocerans, mayfly nymphs, Hydracarina and snails). I dissected 12 L. goodei, 18 to 23 mm, from the North River; eight contained food which included copepods, cladocerans, ostracods and chironomid larvae.

Lucania goodei strays into the headwaters of the North River during the freshwater period, but only in limited numbers. These fish are carnivores, which feed on small crustaceans and insect larvae.

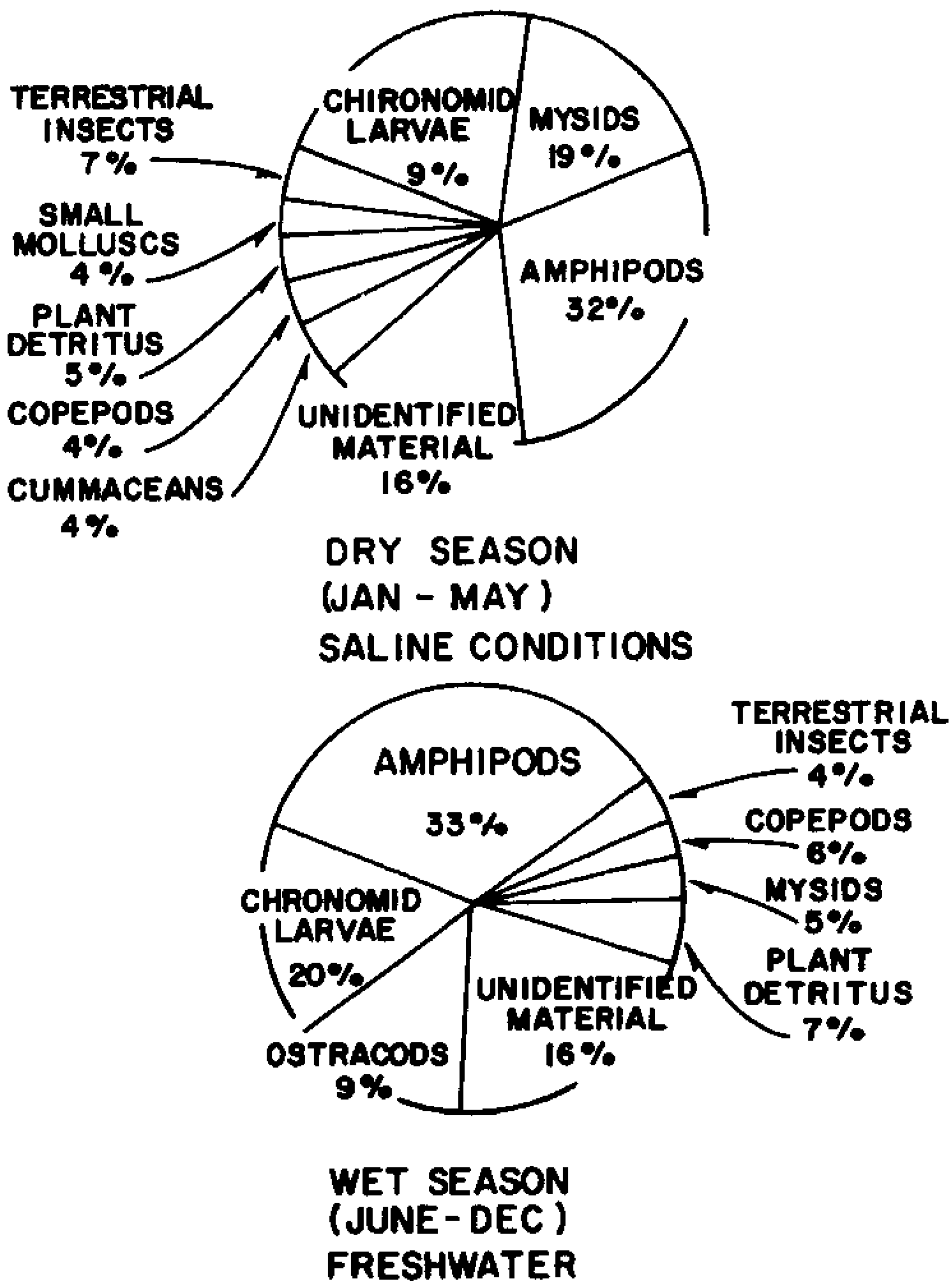


Figure 9. The volumetric per cent composition of the stomach contents of 74 rainwater killifish, Lucania parva, 21-37 mm, collected throughout the year at all stations.

POECILIIDAE

Gambusia affinis (Baird and Girard)

Mosquitofish

Gambusia affinis is an ubiquitous fish found in every type of aquatic habitat in the North River basin; it reaches its greatest abundance in the headwater creeks and *Juncus* marsh pools. Tabb (1966) listed *Gambusia* as the eighth most common fish from the North River system, comprising two and a half per cent of his catch of 10,509 fishes.

Hunt's (1953) review of the literature demonstrates that although *G. affinis* is considered a surface feeder with a predilection for insects and insect larvae, it is quite capable of switching to an almost completely herbivorous diet based on benthic and epiphytic algae. For instance, Harrington and Harrington (1961) found over 70 per cent of the stomach contents of mosquitofish from a south Florida salt marsh to be composed of mosquito larvae and pupae, along with other arthropods and only eight per cent of the volume made up of plant material On the other hand, Barney and Anson (1920), Ward (1931) and Hiatt (1947) have mentioned the importance of algae in the diet. Hunt (1953) estimated that 174 *Gambusia* from the Tamiami Canal in the Florida Everglades had fed upon 60 per cent algal material and 40 per cent animal material. The algae originated from the periphyton and was not phytoplankton; the animals which had been consumed included chironomid larvae, entomostraca, ants, and many insects and small crustaceans. Mosquito larvae were found in only two stomachs.

Of 107 *G. affinis*, 14 to 41 mm, examined from the North River, 87 contained food (Fig. 10). In contrast to Hunt's data from the freshwater Everglades, algal material was of little importance occurring in only 22 per cent of the stomachs examined. This may be explained, in part, by the scarcity of algae as compared to the periphyton encrusted canal in which Hunt collected his fish. The "other" category in Fig. 10 includes harpacticoid copepods, small snails, ants, adult insects, Neanthes, ostracods and mosquito pupae. The latter were found in only three fish. There were no discernible seasonal trends in change of diet or were there differences in the fish's diet between the sampling stations. Any changes in food ingested from one sample to the next reflected the opportunistic nature of Gambusia affinis.

In the North River Gambusia affinis exists primarily as a carnivore feeding upon small crustaceans and insects; during the sampling period algal material was not important in the diet. As Hunt (1953) has concluded the versatility of this fish, as expressed in its ability to switch its diet to conform with the environment, probably explains to a great extent its abundance in a wide variety of aquatic habitats.

Poecilia latipinna (Leseur)
Sailfin Molly

Mollies are extremely abundant throughout the year in the flooded Juncus marshes and associated pools. The greatest numbers were taken between February and April, but this was because water levels are lowest at this time and the fish are concentrated in the least amount of water.

The food of P. latipinna has been investigated by several authors. Hiatt (1947) found mollies feeding upon periphyton and plant debris in

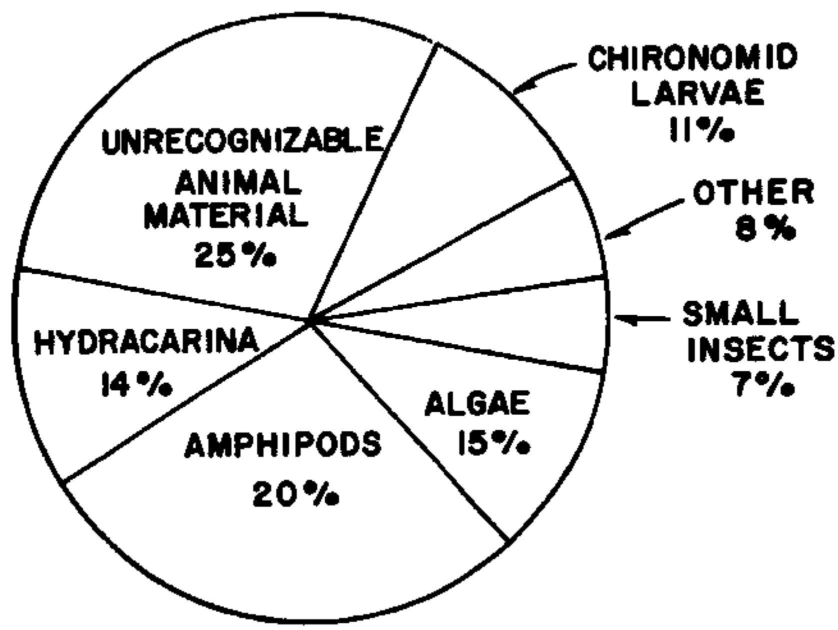


Figure 10. The volumetric per cent composition of the stomach contents of 87 mosquito fish, *Gambusia affinis*, 14-41 mm, collected throughout the year at all stations.

Hawaiian fish ponds. Hunt's data (1953) from Florida's Tamiami Canal indicate a similar diet although a few small ostracods and rotifers were consumed. Harrington and Harrington (1969) stated that vascular plant detritus was the item ingested in the greatest quantities by mollies in a high tidal marsh. They also noted feeding upon mosquito instars and pupae when they were available.

Two hundred and twenty four *P. latipinna*, 29 - 54 mm, from the North River had fed almost exclusively upon fine particles most of which were of vascular plant origin (Fig. 11). Particles larger than 800 microns were seldom ingested. Filamentous algae was rarely eaten and fecal pellets and animal material were not found in the digestive tract.

Poecilia latipinna is an abundant fish of the *Juncus* marshes which feeds upon fine particles of vascular plant detritus and algae.

Heterandria formosa Agassiz

Least Killifish

The least killifish is common, but not abundant in the headwaters of the North River. Surprisingly, it was collected there all year, even when salinities were as high as 23 ppt.

Seal (1910), Mellen (1927) and Hunt (1953) all considered *Heterandria formosa* to be omnivorous, although the first two authors regarded the fish as primarily carnivorous. Hunt's investigations in the Tamiami Canal revealed a diet of 80 per cent plant material (green algae, diatoms, and detritus) and 20 per cent of animal origin (rotifers, copepods, cladocerans, chironomids, and Hydracarina).

The stomach contents of 22 least killifish, 11 to 18 mm, from the North River are summarized in Fig. 12. The fish were observed feeding

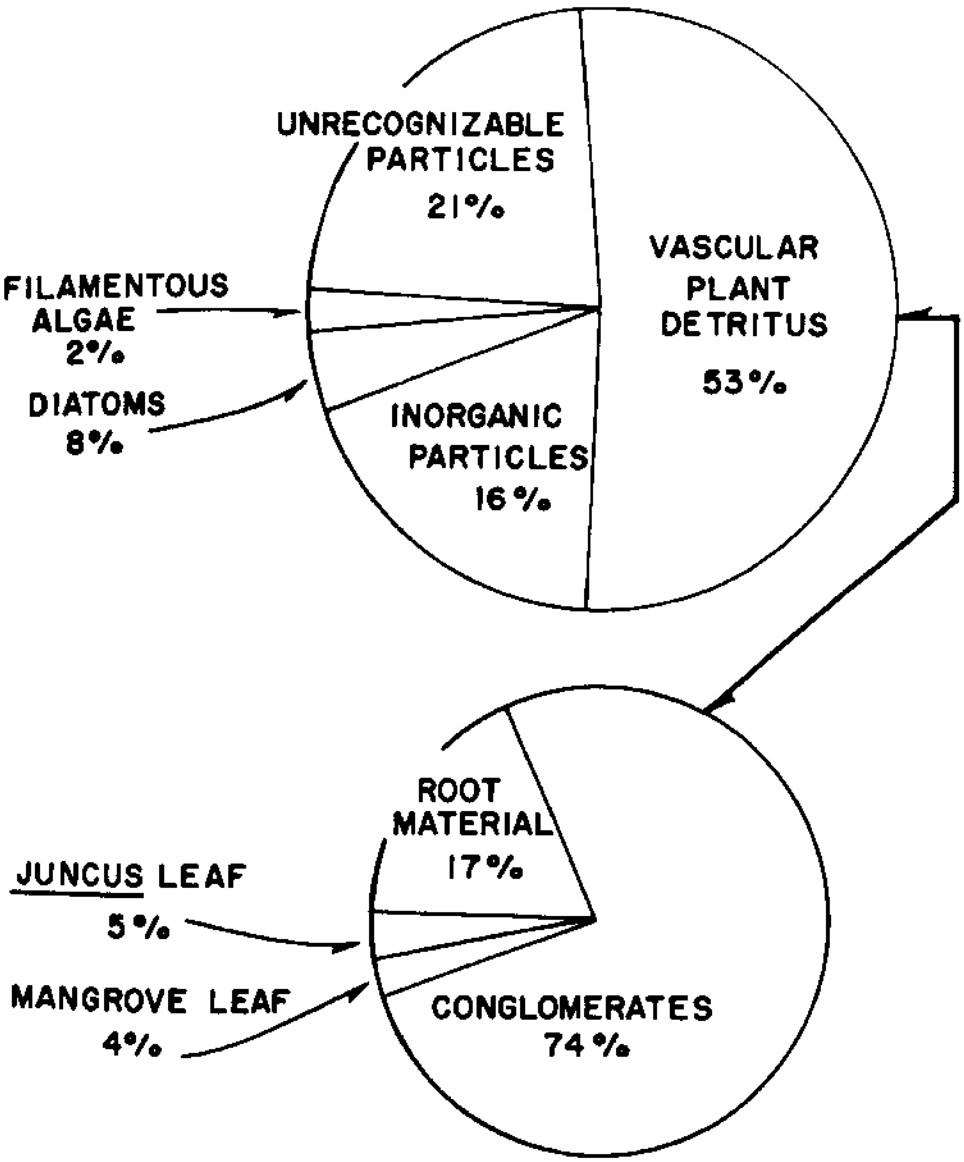


Figure 11. The volumetric per cent composition of the digestive tract contents of 224 sailfin mollies, *Poecilia latipinna*, 29-54 mm, collected at stations B and C throughout the year.

upon epiphyte encrusted surfaces of mangrove roots and drooping limbs.

Heterandria formosa, which is common but not abundant in the North River, grazes submerged surfaces and feeds primarily upon animal material (79 per cent) and to a lesser degree upon filamentous green algae and epiphytic diatoms.

CENTROPOMIDAE

Centropomus undecimalis (Bloch)

Snook

Although they occur elsewhere in Florida, snook are found principally in the brackish water mangrove habitat. During the years when commercial snook fishing was legal, the greatest catches came from the mangrove belt of southwest Florida (Marshall, 1958). Centropomus sp. were often observed in the North River during the course of this survey, but none was captured. Small specimens occur in the Juncus marsh pools and small drainage streams in the headwaters; older fish are found in the main river channel and in the mangrove lined ponds near the mouth.

Since I do not have data on snook stomach contents, it is necessary to base the analysis of their trophic position upon other sources. Marshall (1958) obtained 128 fish ranging from 230 - 851 mm from the nearby Ten Thousand Islands and found food in 61. Fish were the most important food (57.3 per cent by volume); they included Eucinostomus sp., Mugil cephalus, Lagodon rhomboides, Anchoa sp., Poecilia latipinna, and Gambusia affinis. Other foods were caridean and penaeid shrimp (41.0 per cent), crabs (18.0 per cent) and crayfish (8.2 per cent). Thomas H. Fraser (personal communication) has suggested that crayfish and

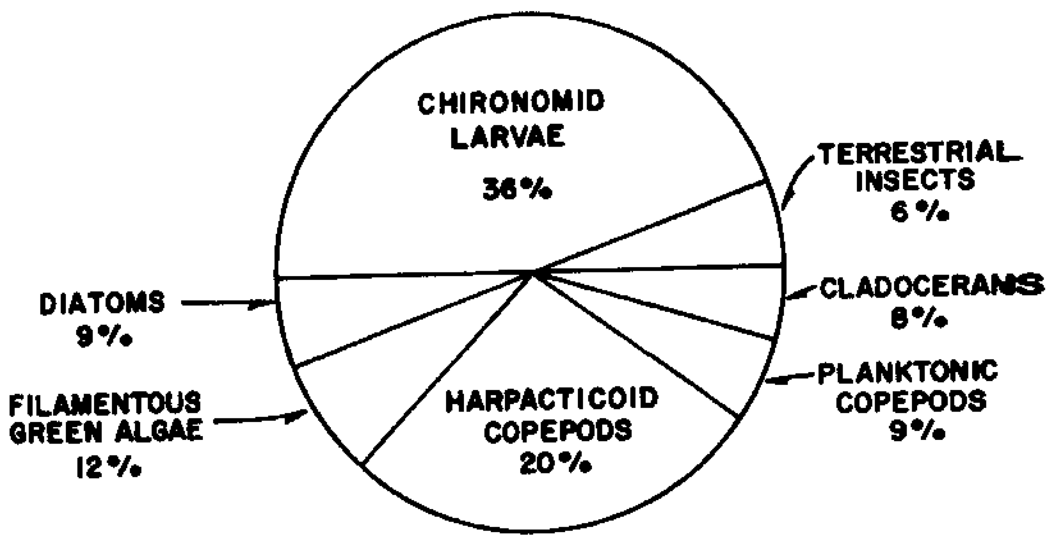


Figure 12. The volumetric per cent composition of the stomach contents of 22 least killifish, *Heterandria formosa*, 11-18 mm, collected throughout the year at station C.

Macrobrachium sp. may be of importance in fresh water feeding along with fishes such as *Menidia beryllina*, *P. latipinna* and *M. cephalus*. Cervigon (1966) states that *C. undecimalis* in Venezuelan lagoons feeds on small shrimp, anchovies and small catfish (*Bagre* sp.). Springer and Woodburn (1960) found snook in Tampa Bay, Florida, feeding principally upon fish. Those of less than 56 mm had eaten small crustaceans.

Snook of less than 100 mm are found in marginal habitats such as marsh edges, ponds and ditches (Marshall, 1958). Harrington and Harrington (1961) found specimens of this size in a Florida east coast marsh feeding on fishes and to a lesser extent on caridean shrimp. Linton and Rickards (1965) reported juveniles in Georgia marshes consuming caridean shrimp and a few *Gambusia*.

Young snook are presumed to feed on caridean shrimp, small cyprinodontiform fishes, and gobies in the *Juncus* marsh pools and small streams of the North River headwaters. Large snook probably continue to feed on fishes and also incorporate crabs, penaeid shrimp, crayfish and *Alpheus heterochaelis* into their diet.

SERRANIDAE

Epinephelus itajara (Lichtenstein)

Jewfish

Young jewfish occur seasonally along the north shore of Whitewater Bay and in the mouth of the North River, although not in the numbers found in the deep holes of the Shark River estuary. Their presence in the North River is dependent upon salinity values above 25 ppt (Tabb and Manning, 1961). For this reason they should not be considered a significant component of the North River system.

Little information exists concerning the food of juvenile jewfish. Smith (1961) states that E. itajara feeds chiefly on crustaceans. Randall (1967) found adults on West Indian reefs feeding on lobsters (68.9 per cent of volume), crabs (12.2 per cent), fishes (13.3 per cent) and sea turtles (5.6 per cent). Two E. itajara, 191 and 232 mm, were examined from the mouth of the North River. Both contained ramains of Penaeus duorarum and Rhithropanopeus harrisii.

Jewfish are not considered a significant component of the North River fish community. Insufficient data were gathered to assess their feeding habits in this environment.

LUTJANIDAE

Lutjanus griseus (Linnaeus)

Gray Snapper, Mangrove Snapper

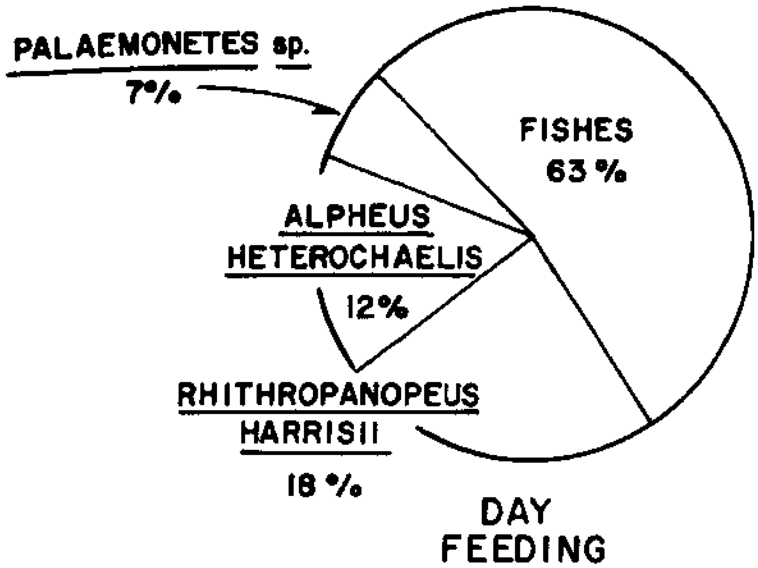
As shown by Springer and Woodburn (1960) juveniles of Lutjanus griseus spend their first few months in grass communities such as those found in Florida and Whitewater Bays. These young fish feed during daylight hours (Randall, 1967) primarily upon small crustaceans and insect larvae. At a length of about 50 mm the snappers begin to leave the grass beds and move into areas of rocky bottoms or mangrove shores as found in the North River system. This change of habitat is accompanied by a change of diet to fishes and larger crustaceans.

Of 112 mangrove snappers taken from the North River none was less than 85 mm or longer than 254 mm. This means that almost all North River snappers are in the I and II year classes (Croker, 1962). There appears to be a movement of late II and III year class snappers out of brackish areas such as the North River into Florida Bay, since the modal size of the North River fish was considerably smaller (192 mm, fork length) than for snappers collected by Croker in the vicinity of Flamingo (250 mm, fork length). Mature mangrove snappers are found on offshore reefs.

Croker (1962) concluded that the juvenile L. griseus in the Everglades estuary feed on grapsid crabs and penaeid shrimp and to a lesser degree on fish as Anchoa spp. He could not detect a significant difference in the diet from month to month or between snappers ranging from 130 mm to 475 mm. Tabb and Manning (1962) recorded shrimp, crabs and various small fish from snappers in the Whitewater Bay region. Longely and Hildebrand (1941) found L. griseus in the vicinity of Tortugas feeding on crabs, shrimp, squid and annelids. Springer and Woodburn (1960) discovered only fishes in the stomachs of gray snappers from Tampa Bay, Florida. Randall (1967) states that adults on the offshore reefs eat more fish than crustaceans.

The contents of the 112 L. griseus from the North River are summarized in Figure 13. There was no detectable difference in diet between times of the year or between snappers of different sizes in the range 95 - 254 mm. Snappers taken at night or in the early morning had been feeding almost exclusively on crustaceans, while fishes predominated in daylight feeding. By far the most commonly ingested fish was Lophogobius cyprinoides; others included Microgobius gulosus, Anchoa hepsetus, A. mitchilli, Gambusia affinis, Poeciliia latipinna, Fundulus grandis, and Anguilla rostrata. One snapper of 141 mm had managed to swallow an A. rostrata of 210 mm.

L. griseus if less than 50 mm subsist on small crustaceans obtained



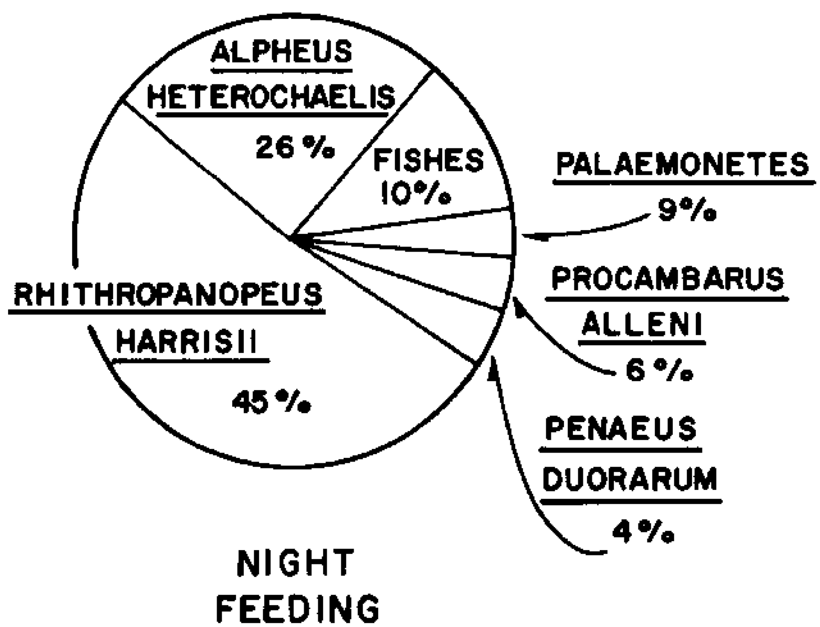


Figure 13. The volumetric per cent composition of the stomach contents of gray snappers, Lutjanus griseus, 95–254 mm, from all sampling stations throughout the year. Of 74 fish captured during the day, 60 contained food; thirty six of 38 from the night samples contained food.

in seagrass communities. The food of the larvae was not investigated. Larger juveniles move into the North River where they are found primarily in the main river channel. In the river their diet is based on the crab *Rhitropanopeus harrisii* and the snapping shrimp *Alpheus heterochaelis* supplemented by fishes.

CENTRARCHIDAE

Tabb and Manning (1961) listed five centrarchids which are normally found in the freshwater regions of the Everglades but move into the mangrove zone during the rainy season. The list was composed of the warmouth, *Lepomis gulosus*; the bluegill, *Lepomis macrochirus*; the redear sunfish, *L. microlophus*; the spotted sunfish, *Lepomis punctatus*; and the largemouth bass, *Micropterus salmoides*. All of these probably stray into the North River at times of low salinities, but only *L. punctatus* was collected commonly in this survey; *L. macrochirus* and *M. salmoides* were occasionally observed in the headwater creeks, but in very limited numbers.

Lepomis punctatus (Valenciennes)
Spotted Sunfish

Hunt (1953) reported on the stomach contents of 20 spotted sunfish from the Tamiami Canal. Principal components of the diet were copepods, ostracods, chironomids and cladocerans. The sunfish also ate rotifers, mayflies, damselflies, nymphs, Hydracarina and snails in less quantities.

Sixty seven *L. punctatus* were taken from the North River between May and February, a period when salinities did not exceed 15 to 20 ppt. They occurred first at the headwater station in May and had penetrated to the river mouth by June. The occurrence of individuals as small as 14 mm in the Juncus marsh pools in November indicates that spawning probably takes place in the mangrove belt.

Eight L. punctatus, 14 - 18 mm, taken in November had eaten cladocerans exclusively. Four others between 18 and 29 mm had eaten insects, cladocerans, chironomid larvae, isopods and amphipods. The diet of two size classes of the larger fish is depicted in Fig. 14.

L. punctatus are common in the North River at times when the salinity falls below about 15 ppt. The results of stomach examination agree with Hunt's (1953) conclusion that the fish is a carnivore which feeds upon cladocerans, small crabs, mysids, chironomid larvae amphipods and insects.

CARANGIDAE

Caranx hippos (Linnaeus)

Crevalle Jack

According to Tabb and Manning (1961), Caranx hippos is abundant throughout the Everglades estuary. In the North River I collected it in every type of habitat with the exception of the shallow Juncus marsh pools.

Darnell (1958) classified the crevalle jack as a predator which feeds on fishes, crabs, squids, shrimp and smaller invertebrates. Hildebrand and Schroeder (1928) and Reid (1954) found only fish in jack stomachs. De Sylva et al (1962) took forty C. hippos ranging from 30 to 160 mm from Delaware Bay; they found mysids most important to fish of less than 70 mm and Palaemonetes sp. eaten by those between 100 and 150 mm.

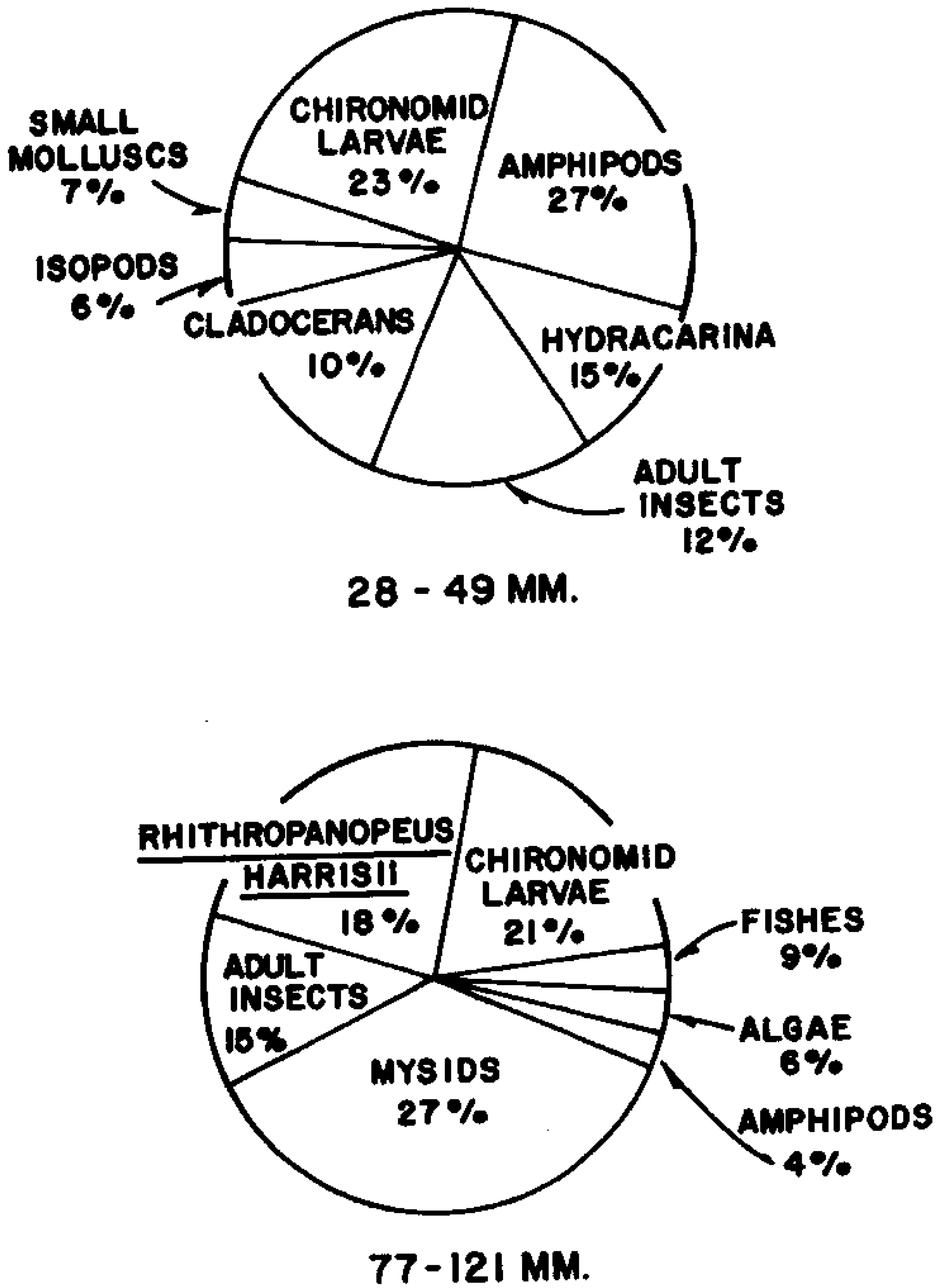


Figure 14. The volumetric per cent composition of the stomach contents of spotted sunfish, Lepomis punctatus, taken between May, 1968, and February, 1969, at stations B and C. Of 32 fish ranging from 28-49 mm which were examined, 27 contained food; nineteen of 23 in the range 77-121 mm contained food.

The few fishes which had been consumed by these young jacks included gobies, anchovies and atherinids.

Twenty two C. hippos ranging in size from 147 to 241 mm were collected from the North River, but much larger fish of at least 600 mm were observed as far inland as the small streams of the headwaters. Only six of these jacks contained food (penaeid shrimp) in their stomachs. Since all six fish were captured in traps, I regard the data as useless.

Although C. hippos is common throughout the North River system, useful information concerning its food was not obtained. From previous literature, fish of the size which occur in the river are presumed to be carnivores which feed upon fishes and crustaceans.

Oligoplites saurus (Bloch and Schneider)

Leatherjacket

This fish was listed by Tabb and Manning (1961) as common in Whitewater Bay, but only near tidal inlets. It does, however, penetrate the North River system during April and May when salinities exceed 25 ppt. In the same publication Tabb and Manning mention that leatherjackets measuring 30 to 120 mm from the Everglades estuary feed on Alpheus heterochaelis, small Penaeus duorarum and larval fishes.

I captured 24 Oligoplites saurus, 162 to 247 mm, from the North River and its mangrove lined ponds; none contained food. One juvenile fish (29 mm) was taken in June. Its stomach was full and contained a larval fish of 5 mm and three young Palaemonetes sp.

Oligoplites saurus enters the lower North River and associated ponds during periods when salinities exceed 25 ppt. Nothing meaningful can be said about its diet from my data.

GERREIDAE

Eucinostomus gula (Quoy and Gaimard)

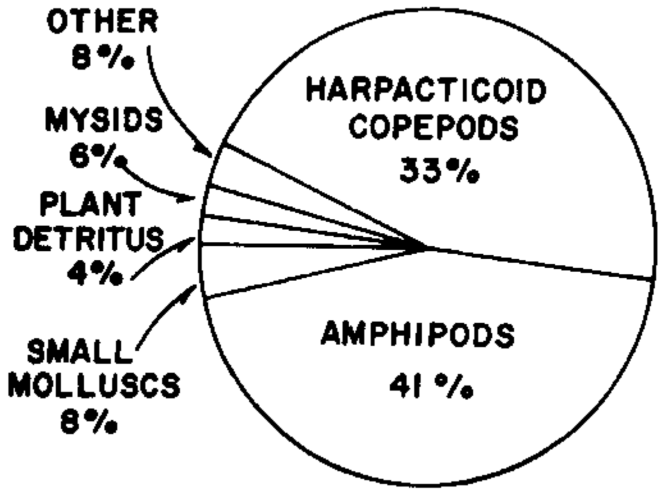
Silver Jenny

The abundance of this species in the Everglades estuary is reflected by its dominance in the biomass of Roessler's (1967) catches from Buttonwood Canal. Tabb (1966) found it the fourth most abundant fish in the North River; in my catches it occurred in equal numbers with *E. argenteus* and was outnumbered only by *Menidia beryllina*, *Gobiosoma robustum*, and *Lophogobius cyprinoides*. Waldinger (1968) discusses aspects of the biology of this and other species of gerrids from the Everglades mangrove region.

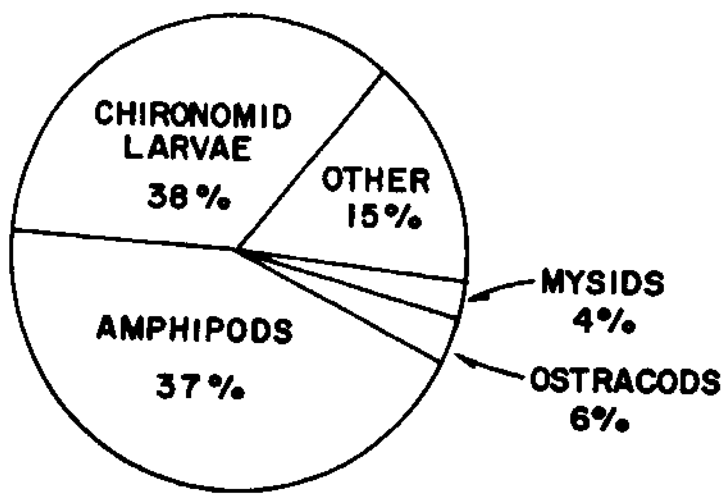
Springer and Woodburn (1960) found copepods, polychaetes, ostracods, amphipods, and small pelecypods in *E. gula* from Tampa Bay, Florida. They found no copepods in fish larger than 45 mm.

The stomach contents of 38 *E. gula*, 35 - 70 mm, taken during the saline period from January to May and 74 fish, 19 - 54 mm, from the fresh-water period during the remainder of the year are shown in Fig. 15. Harpacticoid copepods, small molluscs and *Nereis* disappear from the diet with the arrival of freshwater conditions and are replaced by chironomid larvae which are of little importance during the saline period. Amphipods are eaten in equal numbers throughout the year.

Eucinostomus gula is one of the most abundant forage fishes in the North River system. It feeds upon a combination of amphipods, chironomid larvae, harpacticoid copepods and other foods.



DRY SEASON (JAN-MAY)
SALINE CONDITIONS



WET SEASON (JUNE-DEC)
FRESHWATER

Figure 15. The volumetric per cent composition of the stomach contents of the silver jenny, Eucinostomus gula, 19-70 mm, taken from station A. Thirty eight of 46 fish from the dry season samples contained food as did 74 of 87 from the wet season.

Eucinostomus argenteus Baird and Girard

Spotfin Mojarra

This species was collected in equal numbers as E. gula and usually in the same habitats. This combination of the two species in the same samples is in contrast to the findings of Kilby (1955), Reid (1954) and Springer and Woodburn (1960) all of whom found E. argenteus primarily in brackish estuarine areas and E. gula in higher salinity sandy regions. Springer and Woodburn found E. argenteus in Tampa Bay, Florida, feeding upon polychaetes, copepods, unidentified crustaceans and their larvae and small molluscs.

The stomach contents of North River E. argenteus, 19 - 63 mm, taken in the two seasons are shown in Fig. 16. The diet is nearly identical to that of E. gula; when fish of the same size range were examined from the same sample no difference could be detected between the food of the two species.

I examined 18 very young Eucinostomus sp. (probably E. argenteus). Eight measuring nine to 13 mm had eaten planktonic organisms such as copepods, nauplii and zoea. The remaining ten, 15 - 19 mm, had decreasing amounts of these organisms and quantities of small amphipods and chironomid midge larvae.

Eucinostomus argenteus is found with E. gula in the same North River habitats, in equal numbers, feeding upon the same diet. Plant detritus is not important as food.

Diapterus plumieri (Cuvier)

Striped Mojarra

Diapterus plumieri is abundant throughout the North River. During

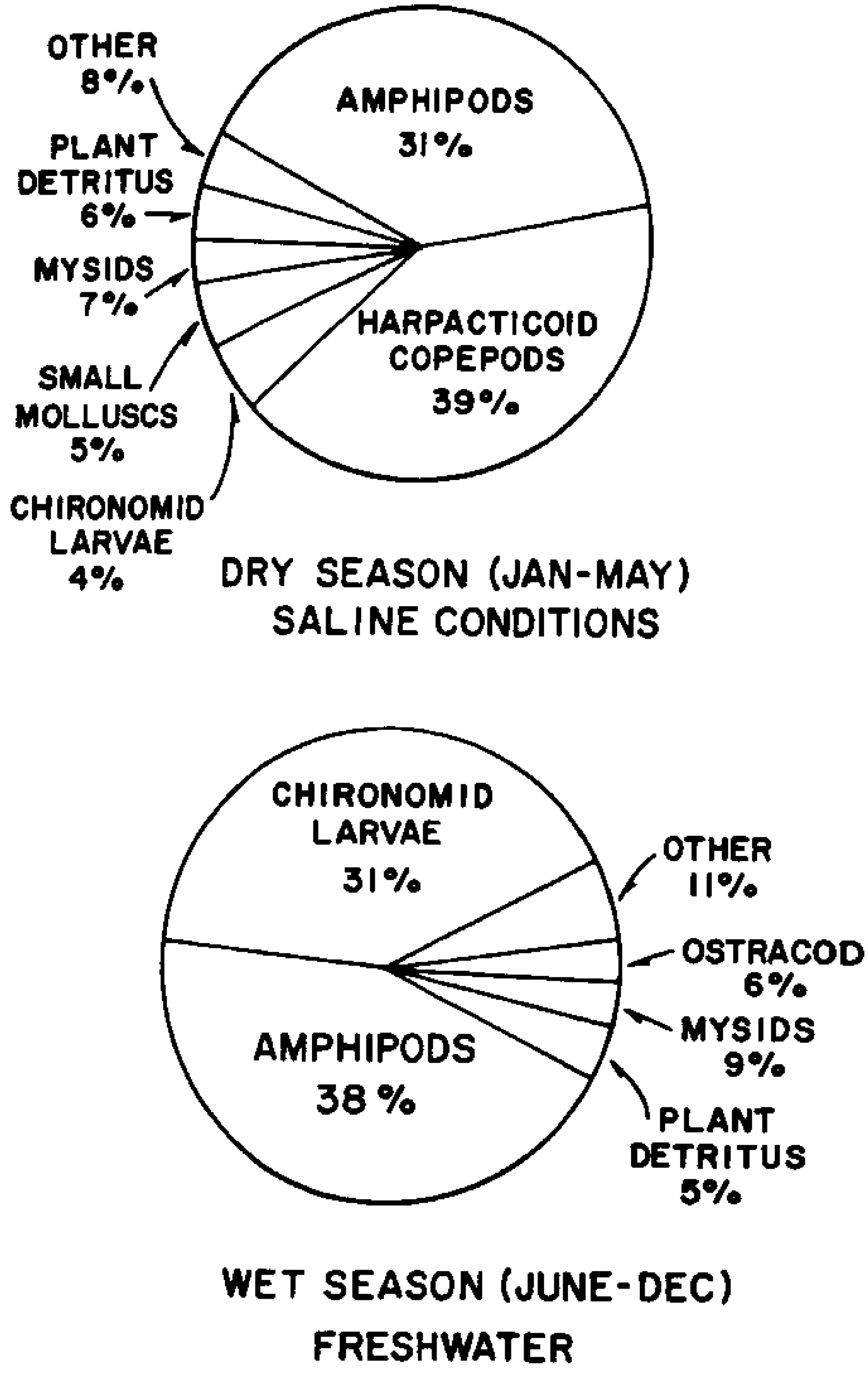


Figure 16. The volumetric per cent composition of the stomach contents of spotfin mojarra, *Eucinostomus argentius*, 19-63 mm, taken at station A. Fifty one (42 contained food) were examined during the dry season and 66 (53 contained food) during the wet season.

the summer months when the water is clear it was possible to move slowly upstream in a boat and see several hundred striped mojarras in a one hundred meter stretch of the river.

There is little information on either the biology or diet of D. plumieri. Springer and Woodburn (1960) record it from Tampa Bay in salinities ranging from 3.7 to 24.8 ppt, but report specimens from the St. Lucie River in water of less than one ppt. One fish (175 mm) from Tampa Bay had eaten polychaetes while two from the St. Lucie River (71 and 77.7 mm) contained copepods. The food of very young D. plumieri (five to 35 mm) which were found in a shallow marsh has been reported by Harrington and Harrington (1961) to consist of copepods (86 per cent of volume) and mosquito instars (nine per cent). The closely related Diapterus rhombeus was reported in Venezuela to feed on algae, Thalassia, sponges, polychaetes, bivalves and crustaceans such as ostracods and copepods (Cervigon, 1966).

Fourteen D. plumieri, 35 - 172 mm, were collected from the North River; fish as large as 359 mm occur in the region (Tabb and Manning, 1961). The food removed from 12 stomachs is summarized in Fig. 17. Surprisingly, there was no detectable difference in diet between the smallest and largest fish in this size range; one individual of 35 mm had consumed eighteen Taphromysis bowmani of three to five millimeters length while another fish of 170 mm had consumed about 50 of the same sized mysids.

The striped mojarra is a permanent resident of the North River where it is found in large schools browsing on the bottom for amphipods and mysids.

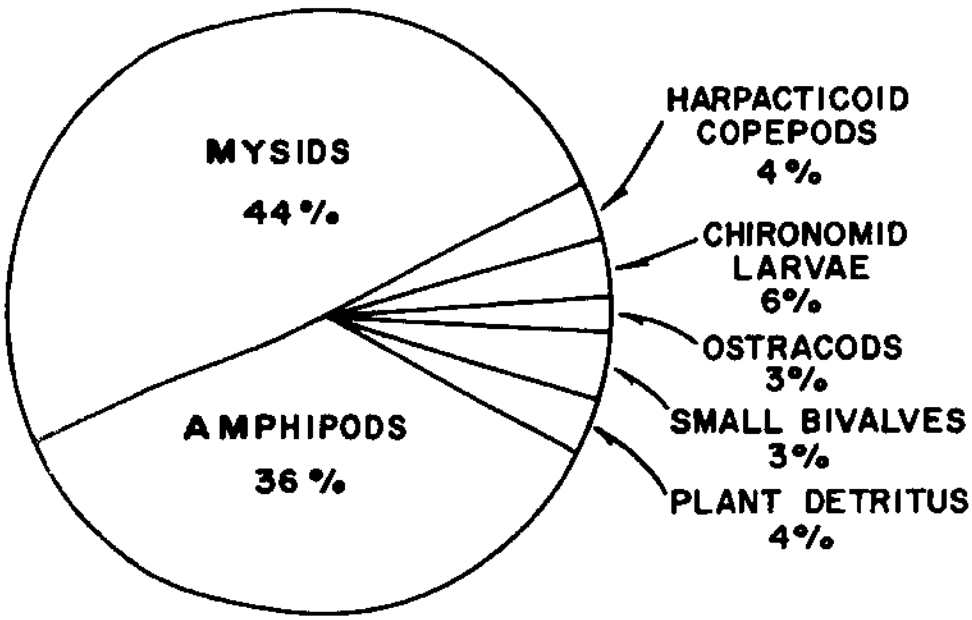


Figure 17. The volumetric per cent composition of the stomach contents of 12 striped mojarra, Diapterus plumieri, 35-172 mm, taken at stations A and C in January, May, July, August and November, 1968.

SCIAENIDAE

Sciaenops ocellata (Linnaeus)

Red Drum, Channel Bass

Yokel (1966) has studied the life history of *Sciaenops ocellata* in the Everglades estuary. This work includes extensive data on stomach contents and a review of the papers of Pearson (1929), Gunter (1945), Miles (1949, 1950), Knapp (1948), Kemp (1949), Reid (1955), Inglis (1959), Breuer (1957), Simmons (1957), Darnell (1958) and Springer and Woodburn (1960). From the results of these investigations the red drum in the range 100 - 800 mm S.L. emerges as a carnivore which consumes crabs, penaeid shrimp and fishes such as *Mugil cephalus* and *Cyprinodon variegatus*; in most instances either crabs or shrimp were the most important food item. Data on very small juveniles are scarce. Springer and Woodburn (1960) examined three specimens (31.0 to 46.3 mm S.L.) which had eaten mysids and polychaete worms. Hildebrand and Schroeder (1928) found redfish of this size range feeding principally upon *Gammarus* and *Mysis*.

Yokel's (1966) study was based on 585 fish obtained from the higher salinity waters of Florida Bay, Whitewater Bay and the Ten Thousand Islands and not from brackish areas such as the North River system. His data show red drum in the 100 - 500 mm range to be heavily dependent (about 70 per cent by volume) upon penaeid shrimp, xanthid and portunid crabs. Penaeids predominated in the diet during the summer months when smaller sized shrimp are available and crabs were most numerous during the remainder of the year. Fishes which were the only other significant food source, were important only to the smaller redifsh and were replaced by xanthid crabs in the diet of larger individuals.

I took seven redfish ranging from 308 - 403 mm from the North River and its associated ponds. Six contained remains of Rhithropanopeus harrisii exclusively; the seventh contained an additional small fraction of chironomids (10 per cent) and bits of mangrove bark (5 per cent). Forty seven larval redfish were captured. Those of 6 - 8 mm S.L. contained copepods (mostly Acartia sp. of 500 - 700 microns length). One larvae of 8 mm contained 30 copepods. At about 10 mm length the redfish begin incorporating crab zoea (1.0 - 1.5 mm) and other larval fish (2 - 4 mm) into their diet. Two individuals of 34 and 42 mm had eaten mysids, amphipods and Palaemonetes intermedius.

S. ocelata above about 50 mm feed on xanthid and portunid crabs, penaeid shrimp and small fishes. Although relatively few redfish were obtained from the North River, Rhithropanopeus harrisii seems to be the principal food. Larvae of less than 20 mm ingested planktonic copepods, crustacean zoea stages and larval fishes. Between 20 and 50 mm they probably concentrate on mysids, amphipods, caridean shrimp and possibly post larval penaeid shrimp.

Cynoscion nebulosus (Cuvier)

Spotted Seatrout

Spotted seatrout are exceedingly common in Whitewater and Florida Bays (Tabb and Manning, 1961) and rank as one of the three most sought after gamefish by anglers (Himan and Stewart, 1961). In the North River C. nebulosus are found primarily in the open waters of the mangrove lined ponds and rarely in the river itself. Eleven trout ranging from 92 to 382 mm were taken at the mangrove pond station between the months of October and March.

Moody (1950) has conducted a detailed study of the food of C. nebulosus; from examinations of 954 fish (511 contained food) at Cedar Key, Florida, he concluded that the seatrout passes through four recognizable feeding stages. The first stage, made up of fish less than 50 mm, feeds predominantly upon copepods and other planktonic crustacea. Caridean shrimp were most important to the second stage of fish measuring from 50 to about 150 mm. Penaeid shrimp dominated the food of the third group, 150 to 275 mm and were replaced to a great extent by fishes in the fourth and largest group. Although fish were most important as food to these large trout, they were ingested by fish of all sizes over 25 mm. Tabb (1966) mentions a number of fishes consumed by trout, including Mugil cephalus, Lagodon rhomboides, Eucinostomus gula, E. argentius, Cyprinodon variegatus and Gobiosoma robustum.

Environmental variations in the diet of spotted seatrout were suggested by Darnell (1958) who reviewed the extensive literature and compared it with his own data from Lake Pontchartrain, Louisiana. Due to peculiarities of the lake's environment there is a relative scarcity of penaeid and caridean shrimp so that young trout must feed upon mysids and benthic amphipods. In addition they begin to exploit the lake's enormous populations of anchovies and larval fish at an early age.

Springer and Woodburn (1960) looked at the stomach contents of 322 young seatrout, 11 to 96 mm, from Tampa Bay, Florida, and found mysids, copepods and carideans. Stewart (1961) studied the diet of trout over 150 mm from Florida and Whitewater Bays in the Everglades estuary and found that the pink shrimp, Penaeus duorarum, the most important food (60.2 per cent by volume). Fishes were next in importance (32.9 per cent) followed by porcellanid crabs (3.6 per cent) and caridean shrimp (0.3 per cent).

In the present study 11 trout measuring 92 to 382 mm were examined, all from the mangrove pond station. Eight contained food in their stomachs which included Anchoa mitchilli, Eucinostomus gula and caridean shrimp. Twenty four juveniles, 68 to 112 mm from Whitewater Bay had fed upon mysids, amphipods, chironomid larvae, carideans, and small fishes in that order of importance.

Spotted seatrout are found commonly in the North River system only in the mangrove ponds near the mouth of the river. Too few were captured to draw any conclusions about their diet or seasonal occurrence.

Bairdiella chrysura (Lacépède)

Silver Perch

A few Bairdiella chrysura were collected in the lower portion of the North River and mangrove ponds during periods when saline conditions existed. In addition, large numbers of larvae, 9 to 17 mm, were captured in the lower river between April and September, irregardless of salinity.

Darnell (1958) has summarized the literature which mentions the food of the silver perch. The smallest fish feed primarily upon copepods; this is supplemented by ostracods, cladocerans, mysids and amphipods. As the fish grow larger they consume proportionally more mysids, amphipods, isopods, small shrimp and crabs. The largest fish include other fishes in their diet. Darnell found mysids, Palaemonetes and fishes to constitute approximately one quarter each of the volume of stomach contents of *B. chrysura*, 70 to 143 mm, from Lake Pontchartrain, Louisiana.

Of 34 larval silver perch from the North River which contained food, copepods and larval fish made up approximately equal halves of the stomach contents. The larvae of *Menidia berylina* appeared most frequently in their stomachs. The proportionally large mouth of this species allows it, even when only 9 mm long, to feed upon other larval fishes. A series of 14 larger fish, 127 to 181 mm, were taken from the mangrove pond station where they had been feeding upon *Anchoa mitchilli* and mysids.

Larvae of *B. chrysura* were very abundant in the North River from April to September and fed upon a mixture of copepods and larval fishes. Larger fish seem to frequent open water areas such as Whitewater Bay, but occasionally stray into the river and mangrove ponds during high salinity periods; 14 fish sampled during one of these periods had fed upon *Anchoa mitchilli* and mysids.

SPARIDAE

Lagodon rhomboides (Linnaeus)

Pinfish

Pinfish are abundant in the seagrass and *Udotea* covered areas of Whitewater Bay, but only occasionally stray into the lower section of the North River. This may be due to the sparseness of aquatic plants in the North River.

Caldwell concluded from his own observations and from the literature that *L. rhomboides* is "completely catholic" in its choice of diet, but that the bulk is composed of small crustaceans. He explained the occurrence of plant material in pinfish stomachs as probably incidental to the capture of crustaceans. This opinion has not been shared by Darnell (1958) or Springer and Woodburn (1960) who point out that adult pinfish often contain only vegetation such as Diplanthera in their stomachs. Hansen (1967) presents feeding data for pinfish of up to 150 mm from the Pensacola estuary, Florida, which shows a seasonal progression from predominantly a plant diet in the summer to a carnivorous diet in the late fall. Large pinfish tended to consume vascular plants and filamentous algae while small pinfish contained more diatoms.

Twelve pinfish, 39 - 61 mm, were collected in June and September from the island station. They contained animal food exclusively; this included Brachidontes exustus, mysids, amphipods and Congeria leucophaeta. Pinfish from nearby Whitewater Bay, however, often contained pieces of algae and vascular plants along with crustaceans and molluscs. Every Lagodon taken in night samples had an empty stomach, confirming Caldwell's (1957) observation that the species is strictly a diurnal feeder.

Lagodon rhomboides occur only as strays in the lower North River. Their diet is highly variable and adaptable to local conditions. While in the North River they are primarily carnivorous, but feeding in Whitewater Bay includes large amounts of plant material.

Archosargus probatocephalus (Walbaum)
Sheepshead

The sheepshead is one of the five important gamefish produced in quantity in the North River system. Judging from my catches and underwater observations, it is second to the grey snapper in abundance among the five species.

There has been some disagreement in past publications concerning the trophic position of Archosargus probatocephalus. Smith (1907) and Hildebrand and Schroeder (1928) originally suggested that the fish was a carnivore which fed primarily upon mollusks and crustaceans. Gunter (1945) examined 18 specimens, 190 to 365 mm, from the Texas coast and concluded that sheepshead were herbivorous. This opinion was based on the fish's very long intestine and the discovery of "grass" and algae in most stomachs examined. Darnell (1958) quotes Viosca (1954) as concluding from many years experience that sheepshead feed on both aquatic vegetation and upon invertebrates found around oyster reefs such as mussels, hydroids, crabs, and small oysters. Darnell's data for 11 sheepshead, 218 to 410 mm, from Lake Pontchartrain, Louisiana, indicated approximately equal amounts of vegetation (Ruppia, Cladophora, Vallisneria) and invertebrates (mussels, sponge, clams, crabs) in sheepshead stomachs. Springer and Woodburn (1960) found young A. probatocephalus, smaller than 50 mm, living in seagrass beds and feeding upon amphipods, copepods and polychaetes. Larger fish ate molluscs, barnacles and algae.

In the Everglades estuary the first few months of the sheepshead life is spent in the grassbeds of Florida and Whitewater Bays where their diet is restricted first to copepods and then to amphipods, chironomids and mysids along with a few strands of algae. At a length of about 35 to 40 mm very small molluscs become incorporated into the diet and some of the fish begin to move into regions of hard substrate such as the North River. This influx of small sheepshead begins at the mouth of the river in June and continues until the late fall. As the fish work their way upstream into the scoured rocky bottom headwaters region the diet switches from amphipods and mysids to a more diversified array of items, most of which are encrusting forms which are nibbled off of the rocky stream bed (Fig. 18). Seasonally there is a slight difference in diet, primarily due to the presence of hydroids and Anomalocarda cunimeris during the winter-spring period of higher salinity. Brachidontes exustus is of primary importance during this same period, but is outnumbered by Congeria leucophaeta during the freshwater months.

Sheepshead are the second most abundant gamefish produced by the North River system. Fish of less than 40 to 50 mm feed on amphipods, mysids, copepods and chironomids in the grassbeds of Whitewater Bay. Larger fish move into the rocky bottom areas of the North River and consume Congeria leucophaeta, Brachidontes exustus, hydroids, Rhithropanopeus harrisii and other crustaceans. It is the relatively great areas of exposed rocky bottom with attached organisms which enables the North River to support a large population of sheepshead.

GOBIIDAE

Lophogobius cyprinoides (Pallas)

Crested Goby

In terms of numbers this was the second most common goby taken in the North River by rotenone sampling; in terms of biomass it was the most important goby present. While poisoning small streams it was not uncommon to take 150 Lophogobius in a 100 meter stretch of stream (and 200 Gobiosoma robustum) indicating a population density in excess of one crested goby per square meter. Such a dense population is facilitated by the diverse feeding habits of this fish, apparently

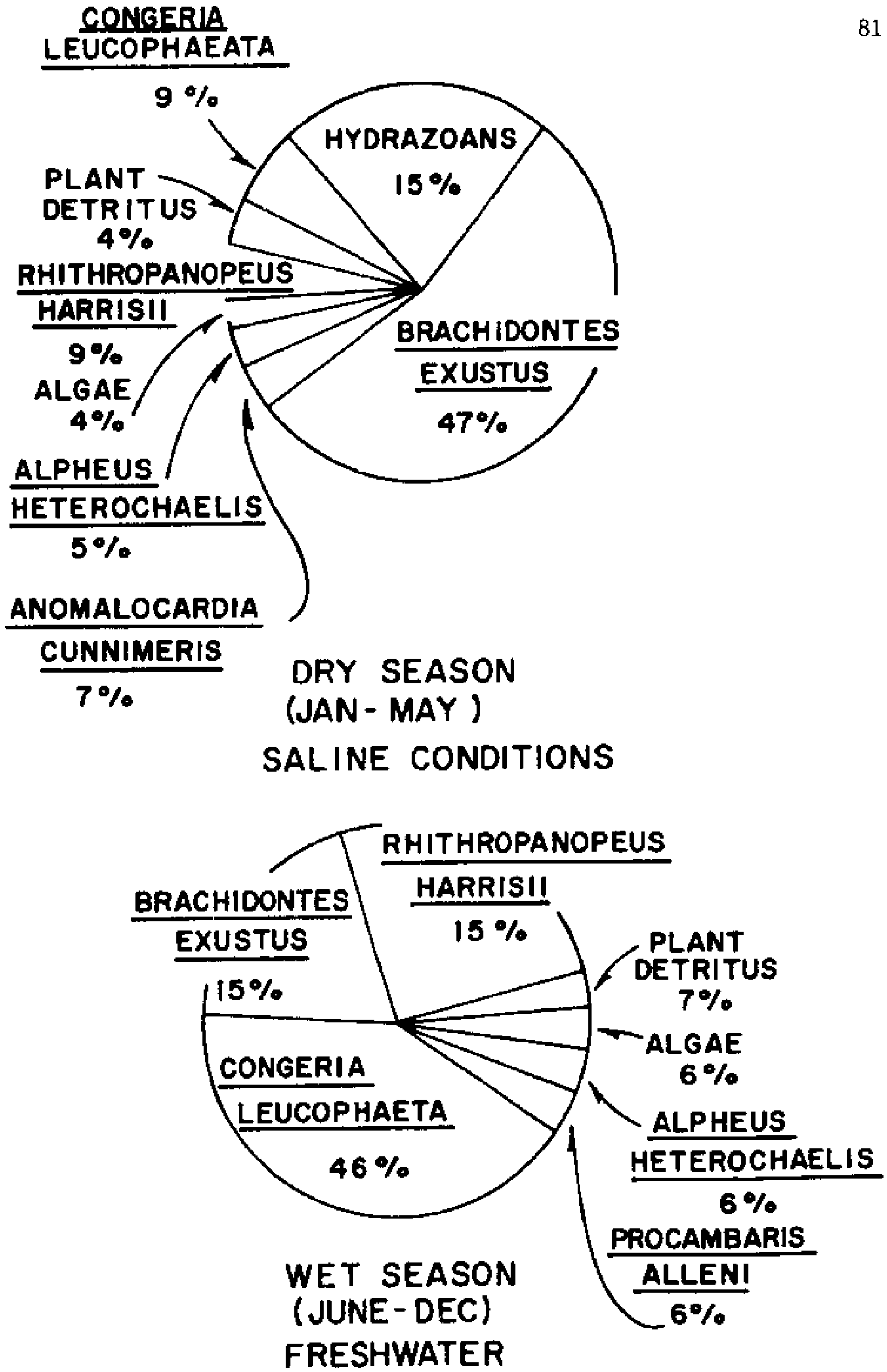


Figure 18. The volumetric per cent composition of the stomach contents of sheepshead, Archosargus probatocephalus, 48-267 mm, collected at stations A and C throughout the year. Sixty four of 69 fish examined from the dry season period contained food; fifty of 52 from the wet season contained food.

the most omnivorous species in the entire estuarine system.

Examination of 174 L. cyprinoides, 24 - 73 mm, revealed 154 which contained 14 categories of food in their stomachs. Although amphipods, mangrove detritus and filamentous algae dominated the stomach contents (Fig. 19), a great range of other items were ingested including mysids, caridean and penaeid shrimp, Neanthes, ostracods, small bivalves, chironomid larvae, harpacticoid copepods, isopods, Rhithropanopeus harrisii and snails. There was little seasonal difference in diet, but a great contrast often existed between two individuals of the same size from the same sample. Crested gobies over 60 mm ate more small crabs and caridean shrimp than those less than 60 mm. At times, vascular plant detritus and filamentous algae were eaten almost exclusively. These components occurred in 78 per cent of the filled stomachs which were examined; amphipods and other small crustaceans occurred in 67 per cent of the stomachs.

The occurrence of plant detritus particles in the stomachs of Lophogobius appears to be more than incidental. In many cases fish which had been confined in glass jar traps were observed to be filled with detritus particles which had settled into the trap.

Three Lophogobius, 45 - 55 mm, were maintained in the laboratory for over a year on a diet consisting solely of aged and ground mangrove leaves with no animal material other than microorganisms present. Although none of the fish grew in length or gained weight, they were in excellent condition at the termination of the project. Detritus and algae must be a secondary food source which is used to supplement the primary food of small crustaceans and insect larvae or to carry the animal through periods when the primary food source is difficult

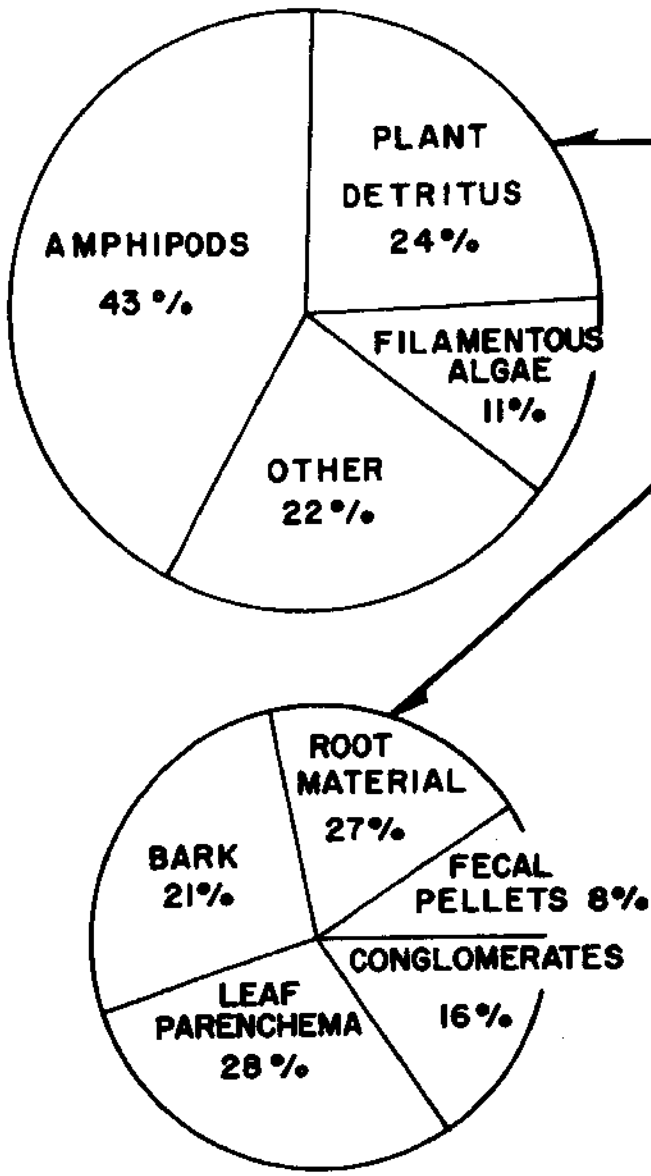


Figure 19. The volumetric per cent composition of the stomach contents of 154 crested gobies, Lophogobius cyprinoides, 24-73 mm, collected at all stations throughout the year.

to obtain.

Lophogobius cyprinoides is an important component of the North River ecosystem. Depending upon food availability, the fish feeds as a carnivore or secondarily as a detritus-algal consumer.

Gobiosoma robustum Ginsburg

Code Goby

The code goby was listed by Tabb and Manning (1961) as the most abundant goby of the Everglades estuary; this proved to be the case in the North River. It was collected in great numbers in all seasons and in all habitats, but seemed to prefer shallower water along the river banks and in the smallest creeks.

Reid (1954) looked at the stomach contents of 18 G. robustum from Cedar Key, Florida, and found "shrimp", amphipods, molluscs and copepods. In Tampa Bay the diet is composed of copepods, isopods, amphipods, tiny pelycypods and decapod shrimp (Springer and Woodburn, 1960).

The stomach contents of 66 G. robustum, 15 - 35 mm, from the North River are shown in Fig. 20. There was little seasonal change in the diet except for the presence of cladocerans and large numbers of chironomid larvae between August and December and a lack of cladocerans and fewer chironomids during the remainder of the year. Cumaceans exhibited just the opposite pattern of occurrence. Six smaller code gobies, seven to 15 mm, had eaten harpacticoid copepods, juvenile mysids, cumaceans and many penate diatoms.

G. robustum is an abundant small predator which feeds principally upon amphipods, mysids and chironomid larvae, all of a benthic origin.

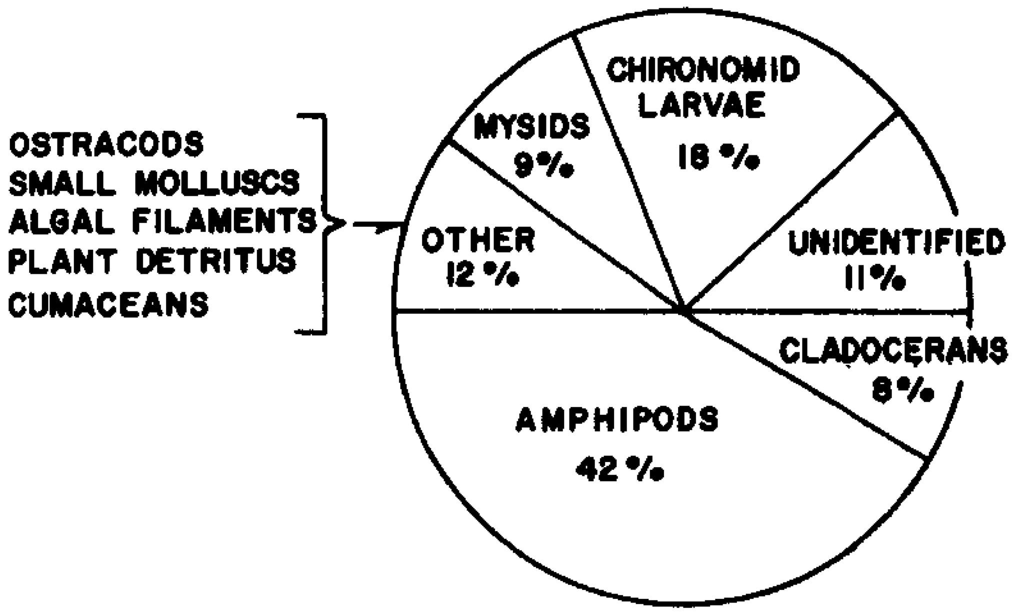


Figure 20. The volumetric per cent composition of the stomach contents of 66 code gobies, Gobiosoma robustum, 15-35 mm; collected at all stations throughout the year

Detritus is of little importance in the diet.

Microgobius gulosus

Clown Goby

Microgobius gulosus exhibited similarities in choice of both habitat and food to Gobiosoma robustum, but was outnumbered 15 to 1 by the latter in my North River samples. Reid found clown gobies, 45 - 57 mm, feeding upon copepods, mysids and amphipods. Springer and Woodburn (1960) list the same food items plus polychaetes, small bivalves and algae. The diet of 18 M. gulosus, 18 - 32 mm, from the North River is summarized in Fig. 21. No clown goby smaller than 18 mm was collected.

Microgobius gulosus is a small predator whose diet of amphipods, copepods and chironomid larvae is almost identical to that of the more numerous Gobiosoma robustum.

Bathygobius soporator (Valenciennes)

Frillfin Goby

Although the frillfin goby was captured in the North River only during periods when salinities exceeded ten ppt, their occurrence was too sporadic to conclude that they are not present during freshwater conditions. They were taken from the same type of habitat as Lophogobius cyprinoides, but were outnumbered by that species in my samples 30 to one.

Springer and Woodburn (1960) examined one B. soporator, 53 mm, from Tampa Bay, Florida, and found insect larvae and caridean shrimp in its stomach. Eleven specimens taken from the North River ranged from 38 to 86 mm. Of six which contained food, five had eaten

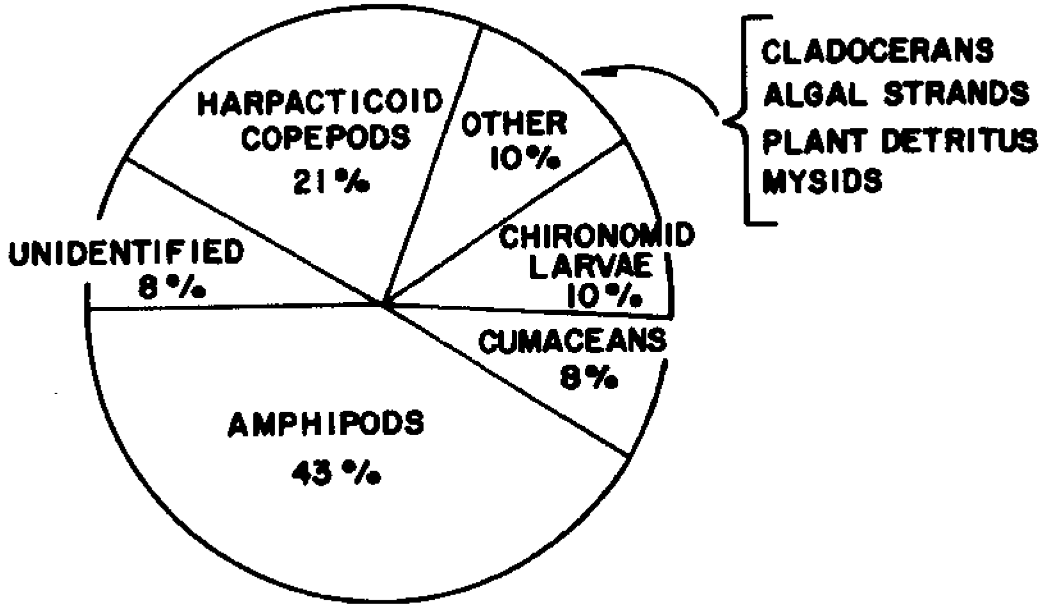


Figure 21. The volumetric per cent composition of the stomach contents of 20 clown gobies, Microgobius gulosus, 18-32 mm, collected throughout the year at stations A and C.

Palaemonetes intermedius along with a few chironomids and amphipods. The sixth had eaten chironomids exclusively.

SPHYRAENIDAE

Sphyraena barracuda (Walbaum)

Great Barracuda

Young barracuda appear occasionally near the mouth of the North River and in the mangrove ponds, but only during periods when the salinity is above ten ppt. I do not consider this species as a factor of much significance in the energy scheme of the North River.

De Sylva (1963) analyzed the stomach contents of 901 barracuda from Florida and the Bahamas and found fishes almost exclusively. Randall (1967) has similar findings from the West Indies.

Six barracuda ranging from 135 to 369 mm were taken from the North River. All contained remains of fish; identifiable species were five *E. gula*, two *Menidia beryllina* and one *Archosargus probatocephalus*.

Young barracuda occur sporadically near the mouth of the river during the high salinity period. My data are insufficient to draw definite conclusions regarding their diet, but it is probably based on small forage fishes.

MUGILIDAE

Mugil cephalus Linnaeus

Striped Mullet

Schools of striped mullet move up and down the North River, penetrating into the mangrove lined ponds and far up the smallest headwater streams. They were observed primarily in areas where soft floculent sediments are covered by shallow water.

Since I have already conducted an extensive study of this fish's feeding in a number of different habitats including a mangrove system (W. E. Odum, 1966, 1970), little effort was expended in catching mullet. In their feeding, which is conducted primarily on the sediment surface, they select fine particles including benthic diatoms, filamentous algae, vascular plant detritus, and inorganic sediment particles. In the previous study from another south Florida mangrove system (W. E. Odum, 1970), their cardiac stomach contents included 46 per cent inorganic sediments, 40 per cent fine detritus (primarily of a mangrove origin), and 14 per cent living micro-algae. There is no reason to believe that the situation is much different for mullet feeding in the North River mangrove system.

Mugil cephalus, which is abundant in the North River, has the distinction of being the only large fish in the system which is able to ingest, and apparently utilize, micro-algae, mangrove detritus particles, and fine clay-sized inorganic particles directly as food.

ATHERINIDAE

Menidia beryllina (Cope)

Tidewater Silversides

Menidia beryllina is the most ubiquitous and probably the most abundant fish in the North River system. Although Tabb's (1966) catch data for 1965-66 shows this species as only the third most numerous fish taken, the gear used in that survey did not sample the fish in numbers representative of its abundance. I made six rotenone collections, two each: (1) in the marsh pools, (2) in the small streams in the headwaters region, and (3) along the shore of the North River. In all samples the most common species by a factor of at least two to one was M. beryllina.

The food of the tidewater silversides has been analyzed from a number of different environments. In Chesapeake Bay the principal foods were listed as small crustaceans and molluscs, insects, and worms along with a few strands of algae (Hildebrand and Schroeder, 1928). Springer and Woodburn (1960) found M. beryllina from Tampa Bay, Florida, feeding on small insects, crustaceans and tiny molluscs. Reid (1954) regarded planktonic organisms such as copepods as the primary food at Cedar Key, Florida. He mentioned that M. beryllina fed actively upon insects which had been attracted by night lights. From his experience with M. beryllina from Lake Pontchartrain, Louisiana, Darnell (1958) suggested that two feeding stages exist, the young fish feeding upon zooplankton while larger individuals prey upon insects (ants, beetles, spiders) which fall into the water along with isopods, amphipods and other small invertebrates. His theory concerning the food of the small fish was speculation since no specimens of this size were examined. Harrington and Harrington (1961) present data from a Florida salt marsh which indicates that M. beryllina of the size five to 15 mm feed on both cyclopoid and benthic harpacticoid copepods. In the same paper Darnell presents data to support his contention that feeding activity in the larger fish is greatest during the morning hours. My interpretation of his data (his Fig. 6) indicates intensive night and early morning feeding with a slackening later in the morning. The fish's proportionally large eye would be an aid in nocturnal feeding.

In the North River nocturnal feeding predominates. I found 74 per cent of 315 M. beryllina, 35 to 65 mm, taken during the daylight hours to have empty stomachs while all but one of 37 fish taken at night had full stomachs. Not only is there a difference in intensity of feeding between day and night, but the items eaten during the two periods were different. The food of M. beryllina, 35 to 65 mm, from the North River system is shown in Figs. 22 and 23. During the day insects which fall into the water predominate along with copepods and chironomid midge larvae; at night mysids are of primary importance. This switch in diet can be correlated with the fish's position in the water column. During the day M. beryllina are most often found either near the surface or in midwater; they do not appear to feed actively except when a spider or an insect such as an ant or a beetle falls into the water. Examination of the water at night with an underwater flashlight reveals the fish close to the bottom, evidently in search of mysids and small amphipods.

The food of very small M. beryllina as shown in Fig. 24 is similar to that theorized by Darnell (1958). All fish of this size had full stomachs during the day and empty stomachs at night.

Menidia beryllina is apparently the most common fish in the North River system. The diet of very small fish (less than 16 mm) is primarily composed of larval stages of copepods and other crustaceans. Larger M. beryllina feed nocturnally upon mysids and amphipods. Diurnal feeding is less intensive and includes insects which fall onto the surface of the water.

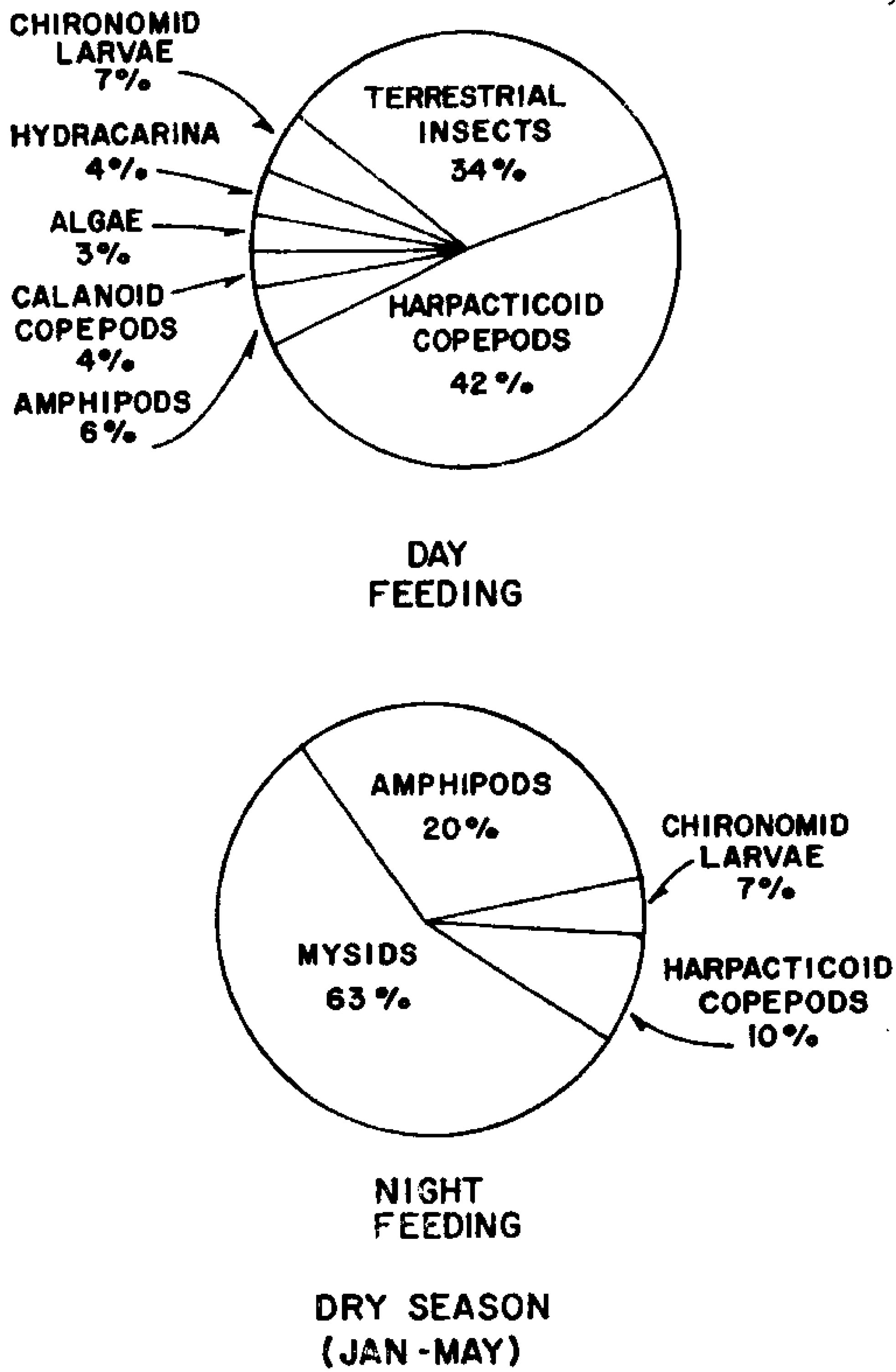


Figure 22. The volumetric per cent composition of the stomach contents of tidewater silversides, Menidia beryllina, 35-65 mm, collected at all stations during the dry season. Of 122 fish examined from daytime samples, 34 contained food. All 28 fish examined from night samples contained food.

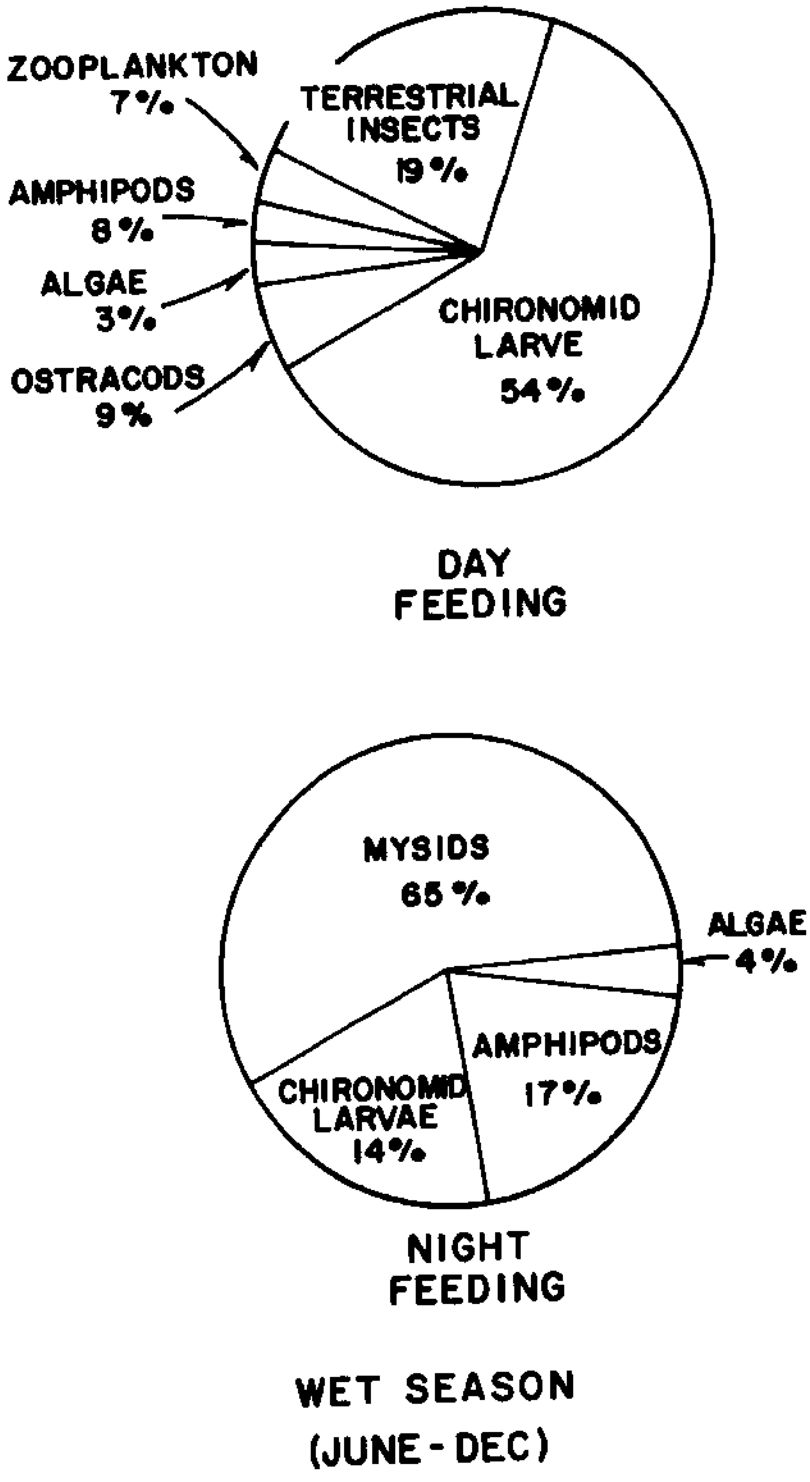


Figure 23. The volumetric per cent composition of the stomach contents of tidewater silversides, <u>Menidia beryllina</u>, 31-58 mm, collected at all stations during the wet season. Of 156 fish examined from day samples, 38 contained food; eight of nene from night samples contained food.

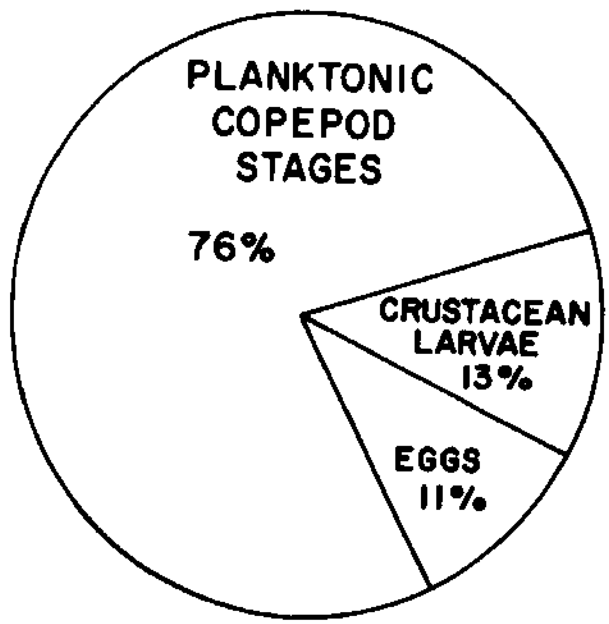


Figure 24. The volumetric per cent composition of the stomach contents of 36 tidewater silversides, Menidia beryllina, 12-16 mm, collected at station A during May and June, 1968.

SOLEIDAE

Trinectes maculatus (Bloch and Schneider)

Hogchoker

Achirus lineatus (Linnaeus)

Lined Sole

Both *Trinectes maculatus* and *Achirus lineatus* are common in the muddier areas of the river and mangrove ponds. Tabb (1966) lists each species as forming 0.1 per cent of the catch from the North River.

Few data exist concerning their feeding habits. *T. maculatus* is reported to feed upon annelids, small crustaceans and strands of algae (Hildebrand and Schroeder, 1928). Darnell (1958) examined three *T. maculatus* from Lake Pontchartrain, Louisiana, and found 50 per cent amphipods, and an equal amount of unrecognizable material and detritus in their stomachs; intestinal contents included chironomid larvae, microcrustaceans, forams and plant seeds. Springer and Woodburn (1960) found polychaetes and amphipods in *A. lineatus* from Tampa Bay, Florida, while Reid (1954) considers this species' food to be copepods, amphipods and polychaetes.

Eight *T. maculatus*, 14 - 110 mm, and six *A. lineatus*, 32 - 74 mm, were examined from the North River; only two of each species contained food and no difference in diet between the two could be ascertained. Food items included amphipods, mysids, chironomid larvae, *Neanthes pelagica* and forams.

Juveniles of *Trinectes maculatus* and *Achirus lineatus* are common residents of the North River system. Not enough data were obtained to state which is the most numerous species or whether a difference in diet exists between the two. Both species feed on amphipods, mysids, chironomid larvae and *Neanthes*.

GOBIESOCIDAE

Gobiesox strumosus Cope

Skilletfish

Gobiesox strumosus was collected under mangrove logs and dead oyster shells in December and May. Since salinities at these times were three and 21 ppt, the fish is probably present in the river at all times of the year. Hildebrand and Schroeder (1928) examined *G. strumosus* from Chesapeake Bay and found isopods, amphipods and annelids in their stomachs. Runyan (1961) found only amphipods in 20 specimens from the same area, but observed fish in captivity feeding upon young sticklebacks and attempting unsuccessfully to devour *Palaemonetes*.

All 18 fish, 10 to 32 mm, which I analyzed from the North River contained food. Stomach contents in order of greatest occurrence were amphipods, isopods and chirnonomid larvae.

G. strumosus is found commonly near or attached to debris such as logs and dead oyster shells. Its diet includes amphipods, isopods and chironomid larvae.

BATRACHOIDIDAE

Opsanus beta (Goode and Bean)

Gulf Toadfish

Small gulf toadfish ranging from 18 to 135 mm were taken at all stations in the river system except for the Juncus marsh pools. They appeared in the catches between February and June, a period when salinities were above ten ppt. Whether they are present during times of lower salinity is not known.

Examination of 26 stomachs of Opsanus beta at Cedar Key, Florida, (Reid, 1954) revealed crabs to be the most important food, followed by penaeid and crangonid shrimp, hermit crabs, mollusks, amphipods, and fish. Springer and Woodburn (1960) found decapod crustaceans and gastropods to comprise the major portion of the diet of 191 gulf toad-fish from Tampa Bay, Florida. The closely related O. tau is considered omnivorous with small crabs and other crustaceans as the principal food (Hildebrand and Schroeder, 1928); smaller individuals were reported to feed upon amphipods and isopods.

The food in the stomachs of 12 North River O. beta varied according to the fish's size. Those in the range 18 to 60 mm had eaten amphipods, chironomid larvae, mysids, isopods and a few fishes. Larger toadfish contained Palaemonetes sp., Rhithropanopeus harrisii, Alpheus heterochaelis, mussels, fish remains and bits of mangrove bark as large as five by nine mm.

The young of O. beta are common throughout the North River system with the exception of the Juncus marsh pools. Whether they are present in the river during periods of low salinity is not known. Fish of less than 60 mm concentrate on smaller crustaceans while larger fish consume crabs, caridean and snapping shrimp, mussels and fishes.

CILIATA

Moderately large numbers of ciliates were found in association with benthic deposits of vascular plant detritus and sediments. Presumably, these ciliates and other Protozoa are ingested by organisms which feed upon detritus and sediment particles. Ciliates identified during May (salinity 12 ppt) and the items which they ingest are shown in Table 2.

NEMATODA

Unidentified nematodes were observed in all sediment samples from the North River, but rarely occurred in fish stomach contents. This could be due to rapid digestion of the nematodes. Many of the sediment nematodes had small unarmed buccal cavities suggesting that they were of the type which Tietjen (1967) has suggested may be important in the breakdown of detritus.

HYDROZOA

Unidentified hydrozoans became established on the rocky bottom sections of the North River when salinities were above ten ppt. They were grazed by sheepshead, *Archosargus probatocephalus*.

POLYCHAETA

Two nereid worms occurred commonly in the North River. *Nereis pelagica* was present during periods when the salinity was above ten ppt; *Neanthes succinea* was much more abundant and was collected at all times of the year, even when salinities were below one ppt. Both worms appeared regularly in the stomach contents of fishes. Both are omnivorous feeders consuming fine detritus, algae, and even small crustaceans such as harpacticoids and amphipods.

Table 2

Ciliates isolated from mangrove detritus and their normal food as determined by T. Fenchel (personal communication)

Ciliate	Normal Diet
HOLOTRICHA	
Tracheloraphis sp.	ciliates, flagellates
Frontonia marina	diatoms
Mesodinium pupula	unknown
Lacrynaria sp.	ciliates
Pleuronema sp.	bacteria
Helicostoma sp.	dead metazoa
Prorodon sp.	ciliates, flagellates
Uronema	bacteria
Cyclidium sp.	bacteria
SPIROTRICHA	
Parablepharisma pellitum	sulfur bacteria
Holosticha sp.	bacteria
Peritronus sp.	bacteria
Condylostoma sp.	ciliates
Strombidium sp.	diatoms
Uronychia transfuga	ciliates
Aspidisca sp.	bacteria

OSTRACODA

Ostracods were often encountered in fish stomachs, but were not identified to genus or species. Ostracods eat bacteria, molds, algae and fine plant detritus (Pennak, 1953).

CUMACEA

The only two cumaceans which were present were *Cyclaspis varians*, which was the most abundant, and *Oxyurostylis* sp. I collected both of these with the ockelman dredge in the river between January and May when salinities were above 20 ppt. They were eaten by a number of fishes, but in small amounts. Examination of the digestive tracts of 15 *C. varians* revealed inorganic sediment particles, vascular plant detritus particles and a few benthic diatoms.

ISOPODA

Isopods are of little importance in the North River food web. A species of *Limnoria* was often found burrowing into dead mangrove logs. Its digestive tract contained micro-algae and detritus particles which had been scraped off of the surface of the log. Individuals captured during the day were empty, indicating nocturnal feeding.

COPEPODA

Harpacticoid copepods were collected throughout the year, but reached their greatest abundance between January and May when salinities were above 10 ppt. They are an important food source for many small fishes and other invertebrates. Harpacticoids are primarily bottom browsers which eat small algal cells and bits of detritus (Green, 1968).

Cyclopoid and calanoid copepods were present in sufficient numbers in the plankton to support the larval fish which were present. These copepods are presumed to be filter feeders which ingest phytoplankton and small bits of detritus. Examination of *Acartia* sp., *Labidocera* sp. and *Cyclops* sp., the three most common copepods in the river, revealed masses of vascular plant detritus particles along with a few phytoplankters and epiphytic diatoms.

PHYLUM MOLLUSCA

CLASS PELECYPODA

The common bivalve mollusks in the North River are the false mussel, *Congeria leucophaeata* Conrad, the scorched mussel, *Brachidontes exustus* Linnaeus, the pointed venus, *Anomalocardia cunimeris* Conrad, and the eastern oyster, *Crassostrea virginica* Gmelin. All, except *C. leucophaeata*, are most numerous from January to May when salinities are above ten ppt. *C. virginica* and *A. cunimeris* dissappear completely during the remainder of the year, but *B. exustus* maintains low level populations during most of the freshwater period. Conversely, *C. leucophaeata* is present during most of the year except for February through April when salinities are too high.

C. leucophaeata and *B. exustus* are the most important bivalves in the food web, serving primarily as food for the sheepshead, *Archosargus probatocephalus*. The materials filtered from the water and ingested into the stomachs of these two molluscs are shown in Fig. 25. Both ingest very fine particles, usually of less than 50 microns. *C. virginica* and *A. cunimeris* are less abundant and therefore, of limited importance in the food web.

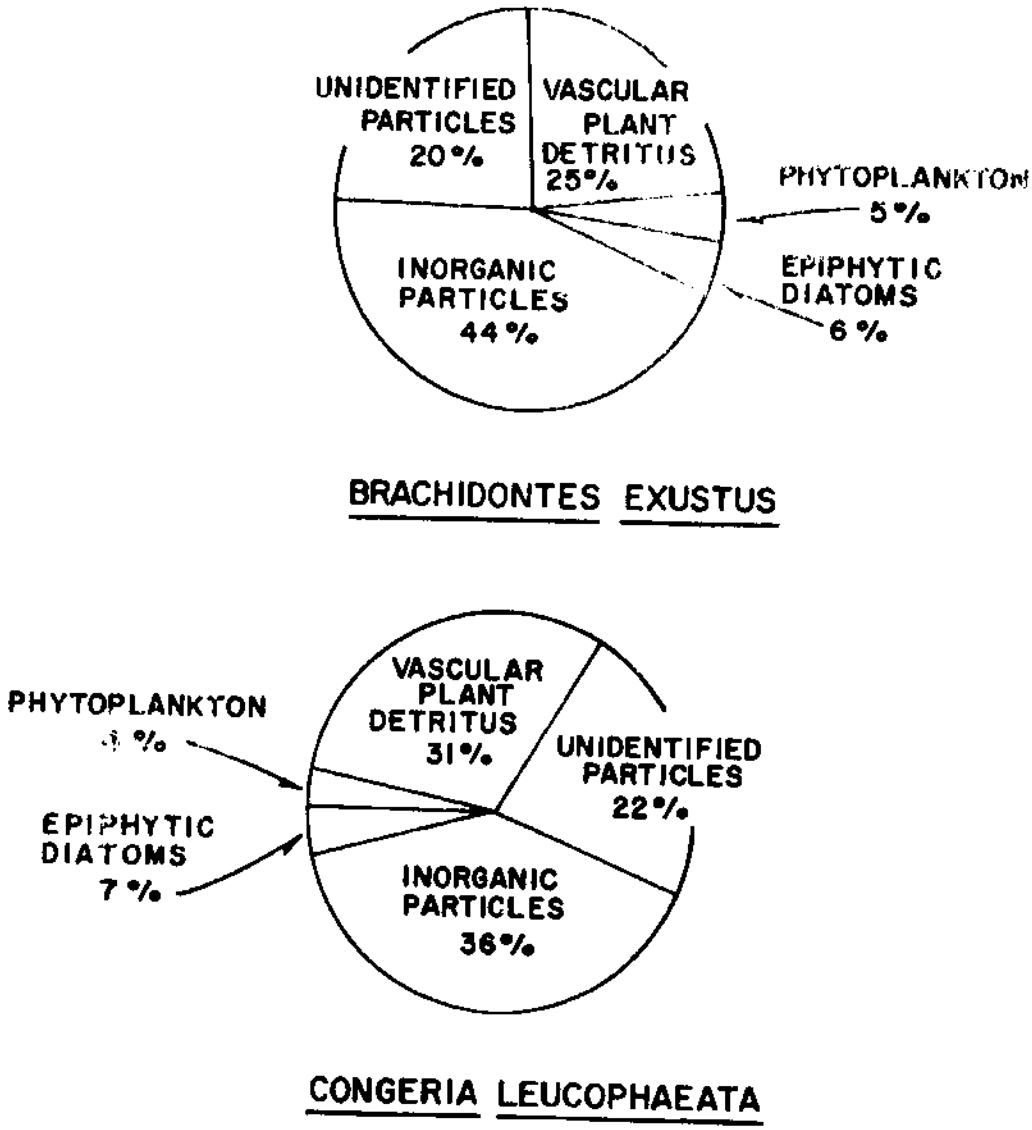


Figure 25. The volumetric per cent composition of the stomach contents of 84 false mussels, *Congeria leucophaeata*, 6-18 mm, and 63 scorched mussels, *Brachidontes* exustus, 4-24 mm, from stations A and B. The *C. leucophaeata* were collected between July and December, 1968, and the *B. exustus* between January and July, 1968.

Brachidontes exustus and *Congeria leucophaeata* are important seasonally in the North River food chain which culminates in the sheepshead, *A. probatocephalus*. Both bivalves ingest inorganic and detrital particles along with benthic diatoms and phytoplankton.

CLASS CRUSTACEA

ORDER DECAPODA

PALAEMONIDAE

Caridean shrimp of the genus *Palaemonetes* were abundant throughout the year in all environments of the North River system. During the saline period from January to June, *P. intermedius* Holthuis occurred almost exclusively except in the headwaters region where *P. paludosus* Gibbes was occasionally taken. With the onset of the rainy season and freshwater conditions in the river, *P. paludosus* moved downstream as far as the mouth, but never was taken in as great numbers as *P. intermedius*. Two other carideans, *P. pugio* Holthuis and *Periclimenes americanus* (Kingsley) appeared occasionally in samples, the former during freshwater conditions and the latter during April when salinities exceeded 20 ppt.

The food of the family Palaemonidae has received little attention from ecologists, both because of the small size of the shrimp and the very fine nature and difficulty of identification of its digestive tract contents. Hunt (1953) examined 49 *P. paludosus* from the Tamiami Canal and concluded that plants provided the primary source of food in the form of algae and vascular plant fragments. Animal remains (rotifers, copepods, ostracods, chironomid larvae and snails) occurred in only 16 per cent of the digestive tracts examined. Kawanabe et al (unpublished manuscript) regarded algae and vascular plant fragments as the food of P. pugio in small pools in the Georgia Spartina marshes.

The material from the buccal cavities of 229 P. intermedius from the North River is summarized in Fig. 26. Fifty two P. paludosus contained almost identical substances--so similar that I consider the diets of the two species to be the same. In both cases there was little variation in ingested substances between sampling stations, although there was often great variation between individuals of the same species in the same sample.

Almost all buccal cavities contained a high percentage of fine particles. Some of these were completely unrecognizable and could have been of an organic or inorganic origin. A large percentage of the particles which I recognized were inorganic (clay, quartz, broken bits of calcium carbonate) and probably served a two-fold purpose in the digestive tract. First, their presence in the gastric mill greatly facilitates the grinding and reduction of resistant tissues to a digestible form. Second, the high percentage of clay-sized particles supplies the shrimp with a source of dissolved organic substances which is sorbed onto and into the particle (see discussion of utilization of sorbed dissolved organic substances).

Other than inorganic particles the next most commonly ingested materials were bits of vascular plant detritus which were identified by their characteristic color and cell structure. Most of this material appears to be passed through the digestive tract in an unaltered form. Examination with both phase and fluorescence microscopy with acridine orange stain indicated that bacteria, Protozoa and fungi were removed from the particles.

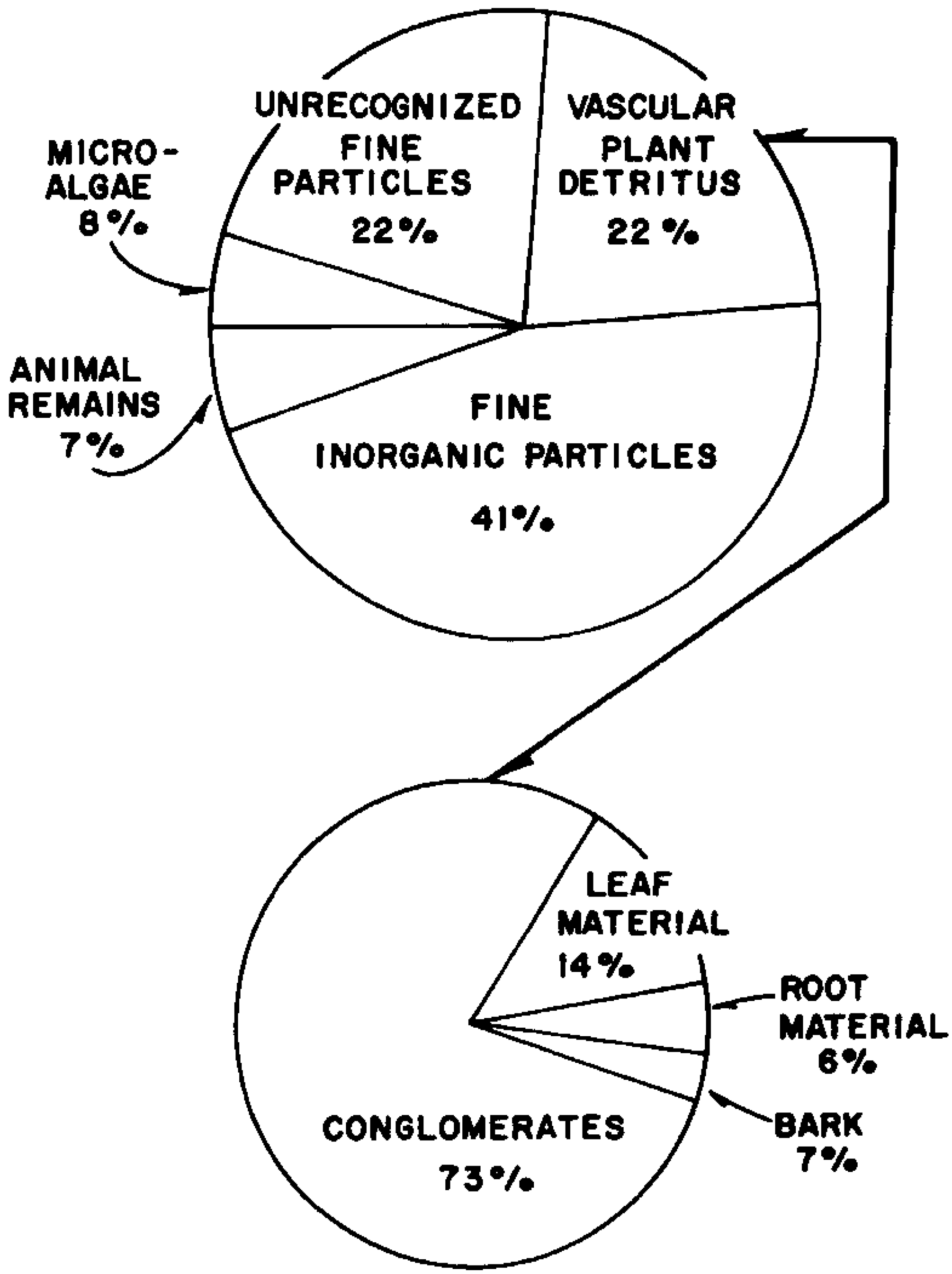


Figure 26. The volumetric per cent composition of the buccal cavity contents of 229 Palaemonetes intermedius collected throughout the year at all stations.

There was usually a small percentage of algal material present in the digestive tract which probably reflects the general scarcity of benthic algae in the North River system. Palaemonetes which I have examined from other regions of south Florida where periphyton and benthic algae are more abundant contained proportionally more algae and less vascular plant detritus than in the North River.

Occasionally the caridean shrimp ingested large amounts of animal materials. This included benthic and planktonic copepods, amphipods, chironomid larvae, ostracods and snails.

Palaemonetes, which are an important link in certain North River food chains, ingest five types of materials: (1) in organic particles (largely calcium carbonate) which are used as a grinding paste in the gastric mill, (2) clay sized particles (both inorganic and organic) which probably contain sorbed dissolved organic substances which can be utilized by the shrimp, (3) benthic diatoms, desmids, dinoflagellates, filamentous green and blue-green algae, (4) vascular plant detritus particles originating from mangroves and Juncus, (5) pieces of animals such as ostracods, amphipods and copepods. Except for animal fragments which occasionally exceeded 1.5 mm, most particles were less than 50 microns and averaged 13 microns. Fungi, bacteria and Protozoa ingested along with the fine inorganic and organic particles must be included as an important food source. In brief, Palaemonetes is an opportunistic omnivore.

PENAEIDAE

Penaeus duorarum Burkenroad

Pink Shrimp

Pink shrimp are common, but not abundant in the North River. This is in marked contrast to the large population present in nearby Whitewater Bay. Bernard Yokel (personal communication) has suggested that the limited numbers of pink shrimp in the North River may be the result of the weak or non-existent counter flow of water up the river during the incoming tide. Such a water movement is necessary for the distribution of post larval penaeid shrimp.

The food of penaeid shrimp has been summarized by Dall (1968). He concluded that penaeids are opportunistic omnivores which feed upon easily captured animals along with algal cells and filaments and sediment particles all obtained by browsing the surface of estuarine muds. He believes that most of the energy from this diet is derived from bacteria, small algae, Protozoa, harpacticoid copepods, and nematodes. Idyll and Yokel (1967) also mention the importance of films of bacteria, yeast, and slime molds which exist on mud particles.

Eighteen P. duorarum contained food (Fig. 27) which was similar to that described by Dall(1968). There was a large percentage of inorganic particles which must contribute food value in the form of sorbed microorganisms and organic compounds.

Penaeus duorarum is common, but not abundant in the North River. It is an opportunistic omnivore which ingests sediment particles, algal cells, detritus and small animals.

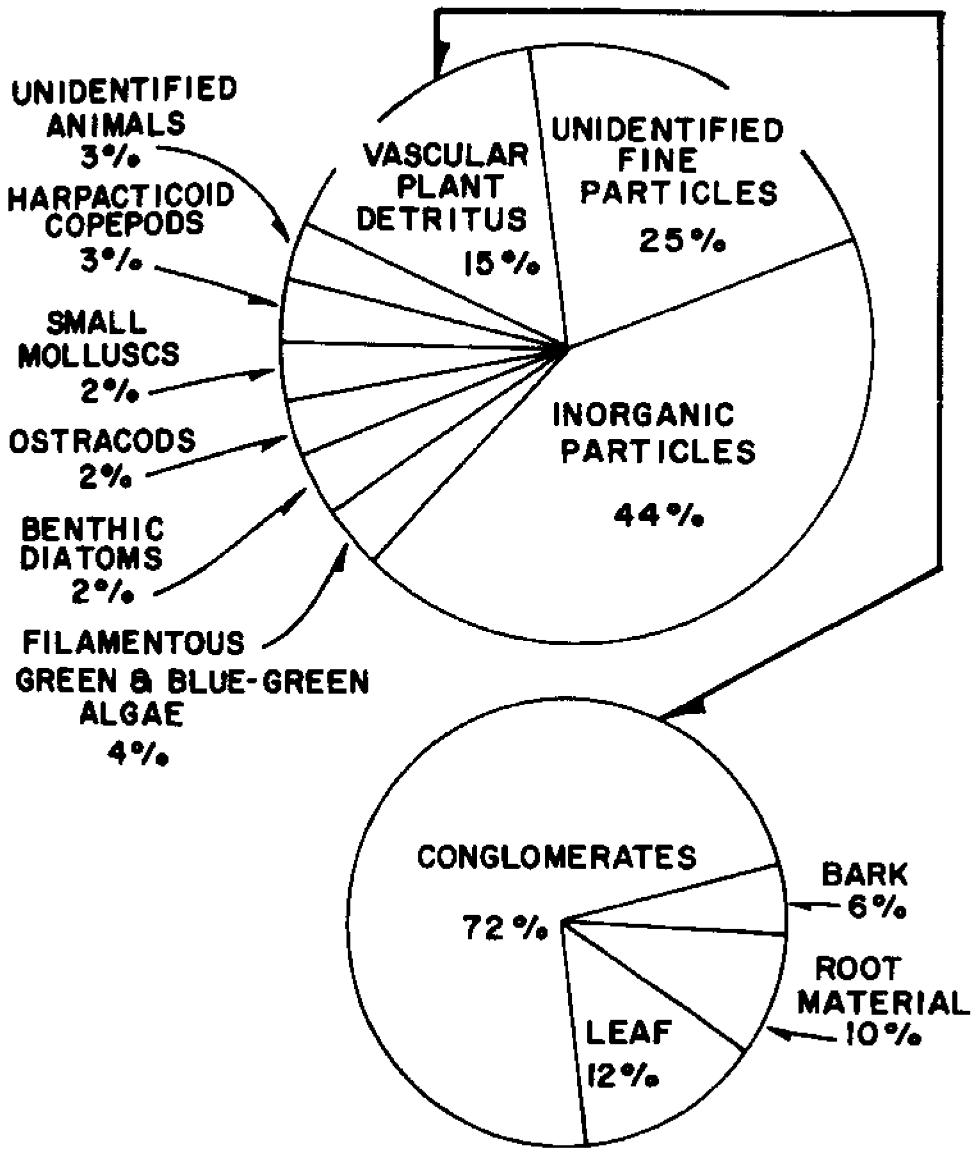


Figure 27. The volumetric per cent composition of the buccal cavity contents of 18 pink shrimp, *Penaeus duorarum*, 6-19 mm carapace length, collected from station A in September, November and December, 1968.

ALPHEIDAE

Alpheus heterochaelis Say

Big-clawed Snapping Shrimp

This snapping shrimp was collected in large numbers along the banks of the North River and in the small drainage creeks which flow out of the mangrove ponds and Juncus marshes. Individuals were collected in water of salinities ranging from less than one to 27.5 ppt. A. heterochaelis are heavily preyed upon by several species of fish.

Gary Hendrix (personal communication) notes that A. heterochaelis is an omnivore which feeds upon a variety of animal and plant material including decaying leaves. The contents of the digestive tract of 24 A. heterochaelis are shown in Fig. 28. Particles ingested ranged up to 400 microns and averaged 42. Feeding appeared to be predominantly nocturnal.

Alpheus heterochaelis is an abundant and important link in the North River food web. Much of the ingested material is mangrove detritus.

PORTUNIDAE

Callinectes sapidus Rathbun

Blue Crab

Large populations of Callinectes sapidus exist in areas of the Everglades estuary such as Hell's Bay and Coot Bay Pond which lie adjacent to shallow water marshes. Other regions including the North River basin have relatively sparse populations of blue crabs.

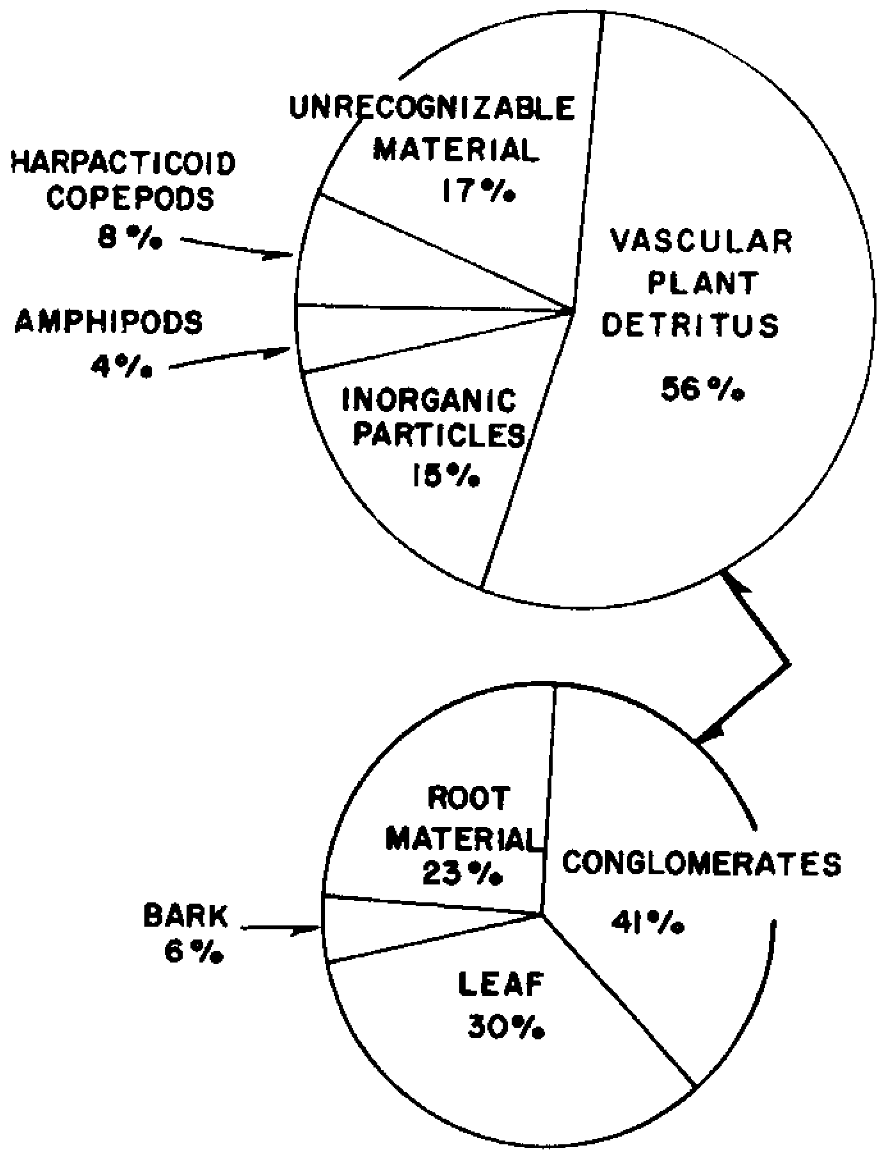


Figure 28. The volumetric per cent composition of the buccal cavity contents of 24 snapping shrimp, *Alpheus heterochaelis*, 22-46 mm total length, from stations A and B throughout the year.

Durbin Tabb (personal communication) had suggested that it is the combination of a scarcity of suitable shallow marshes coupled with the seasonal reduction of water level during the dry season further reducing marsh areas which limits blue crab production in the North River. Tagatz (1968) found juvenile blue crabs of less than 40 mm carapace width inhabiting the type of shallow water habitat which virtually disappears from the North River system during half of the year.

Whatever the reason for the shortage of blue crabs in the North River system, it is not caused by a lack of suitable food material. In Lake Pontchartrain, Louisiana, they were found by Darnell (1958) to feed primarily upon molluscs, crabs and detrital material. The extensive work of Tagatz (1968), which was done in the St. John's River, Florida, showed a similar diet. An examination of 668 crabs which contained food material revealed 39.0 per cent of the total stomach contents to be made up of mollusks, 19.4 per cent of fish, and 15.9 per cent crustaceans. The mollusks included clams and mussels of less than 15 mm length; the preferred size was 1.5 - 5.0 mm. Amphipods and crabs (Rithropanopeus harrisii) were the preferred crustaceans. Other foods included plants, annelids, insects and bryozoans. Generally, blue crabs of all sizes ate the same things, although ostracods were important to very small crabs. Tagatz (1968) did not indicate that organic detritus was of much importance, although it occurred in many crabs.

Only eight Callinectes sapidus were collected from the North River. They ranged in carapace width from 122 to 180 mm and contained the following items in order of frequency: the mussels Congeria leucophaeata and Brachidontes exustus, the crab Rhithropanopeus harrisii, amphipods, unidentified fish remains, grains of sand and a small volume of plant detritus (bark and root hairs). All mussels were less than 15 mm in length.

Callinectes sapidus is much less numerous in this estuarine system than might have been supposed prior to intensive collecting, apparently because of a lack of suitable habitat for the juveniles. The moderately small population which is present is concentrated in the mangrove lined ponds where they feed principally on mussels, R. harrisii and amphipods.

XANTHIDAE

Rhithropanopeus harrisii (Gould)

This little euryhaline crab was abundant at all stations in the North River system and is an important component of the food web. It was collected at salinities which ranged from less than one to 27.5 ppt. Quantitative samples from the bed of a small stream draining the Juncus marshes revealed more than 40 R. harrisii per square meter, hiding in holes, under logs, leaves, shells, and other debris.

Examination of the buccal cavity contents of 141 R. harrisii, three to 14 mm carapace width, revealed an omnivorous diet dominated by mangrove leaf detritus (Fig. 29). Crustaceans such as small amphipods and harpacticoid copepods were eaten more often by small crabs (2.5 - 5 mm). Detritus particles averaged 72 microns and ranged up to 800 microns in width; often they appeared to be the result of mechanical reduction by the crab of larger pieces or even pieces

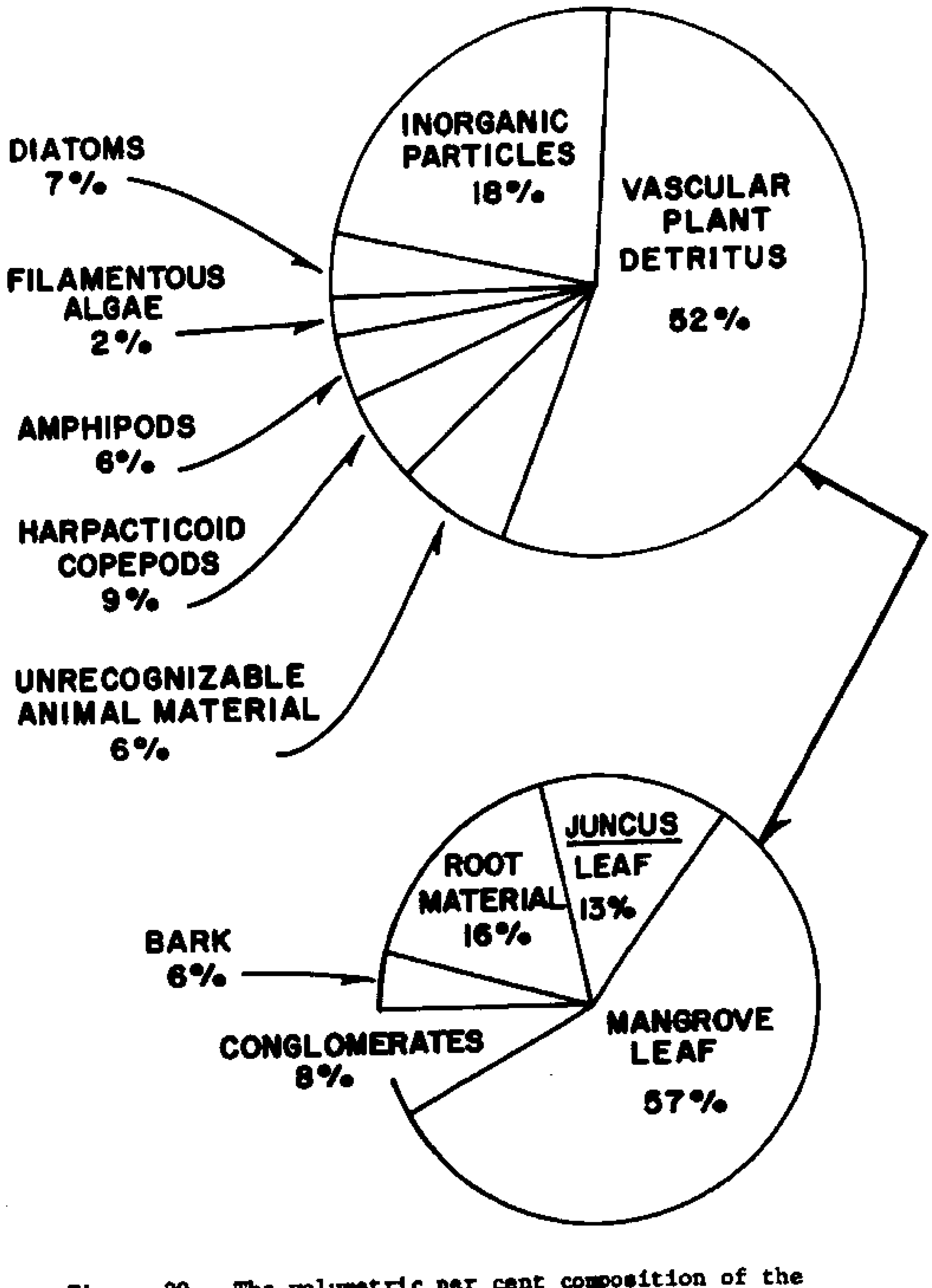


Figure 29. The volumetric per cent composition of the buccal cavity contents of 141 *Rhithropanopeus harrisii*, 3-14 mm carapace width, from all stations throughout the year.

nibbled from entire dead leaves. This leaf detritus is fragmented into very fine material (mean = 16 microns) by additional grinding in the buccal cavity, so that fecal material contains few large particles.

Rhithropanopeus harrisii is abundant throughout the North River system. Its diet is dominated by pieces of mangrove leaf detritus which are mechanically fragmented by the crab and extruded in the fecal material as fine particles.

ORDER AMPHIPODA

Amphipods are exceedingly numerous throughout the North River system and are a primary factor in the conversion of vascular plant detritus into animal protein. Although seven species were collected regularly, only three were numerous enough to be considered essential in the detritus based food web.

Amphipods are generally regarded as omnivores which feed on all types of plant and animal matter while refraining from capturing and devouring live animals (Pennak, 1953). A tendency for many species to feed upon plant detritus particles has been noted by Pennak (op. cit.) and Green (1968).

Melita nitida

This was the most common amphipod in my samples, but the least common of the three major species in fish stomachs. This apparent contradiction is caused by the preference of *M. nitida* for very shallow water where it is easily collected by the ecologist, but difficult for fish to reach. It was found in water of less than a meter and usually only a few centimeters along the shoreline where leaves and other mangrove debris accumulates. Glass plates placed in this environment required only a few days to acquire a microbial scum before they became covered with Melita. During the daytime this amphipod was under decaying mangrove leaves in shallow water where they graze the bacteria laden organic scum off of the underside of the leaf. Digestive tract contents during the day include fine inorganic and vascular plant detritus particles along with bacteria and Protozoa. Little micro-algae is present. Nocturnal grazing includes the exposed upper surfaces of decaying leaves and other smooth surfaces so that in addition to detritus particles a small percentage (five to ten per cent) of micro-algae is consumed. Particles in the digestive tract averaged 18 microns, but ranged up to 200 microns. In addition to feeding upon small particles, Melita tears apart large pieces of decaying leaves. Presumably, this leaf material is an adequate source of nutrition as Sexton (1928) has reared Gammarus on dead elm leaves.

Judging from observations in the laboratory and upon nylon litter bags placed in the environment by E. J. Heald, Melita is responsible to a great extent for the fragmentation of mangrove leaves once they have been in the water for two or three months. During the first month or two after a leaf enters the water, Melita avoid it, but after this period they appear and it is at this time that the disintegration rate increases. Litter bags placed in water of intermediate and high salinity had greater numbers of Melita than those in low salinities; these greater amphipod numbers were accompanied by an accelerated leaf fragmentation rate (Heald, 1969).

Grandidierella bonnieri

Grandidierella was by far the most commonly encountered amphipod in fish stomachs and was eaten in large numbers by every fish species which ranged from less than one to 30 ppt; it was found either in the beds of shallow streams or on the bottom a few meters from the shoreline of the river.

The food of *G. bonnieri* was composed of very fine detritus particles, largely of a mangrove leaf origin. In contrast to *Melita nitida* this amphipod was never observed fragmenting pieces of leaf material; particles in the digestive tract were generally less than 30 microns in diameter.

Corophium lacustre

The digestive tract contents of this amphipod resembled those of *Grandidierella* suggesting that it also is a small particle grazer with questionable ability to fragment entire leaves.

Other Amphipods

Cymadusa compta and *Gammarus mucronatus* were routinely collected in plankton net and ockleman dredge tows, but seldom occurred in the stomachs of North River fishes. *C. compta*, however, was commonly eaten by juvenile fishes in Whitewater Bay. Two other amphipods *Elasmopus* sp. and *Gitanopsis* sp. appeared in samples at times, but were not numerous.

Amphipods are numerous and play an important role in the food web of the North River system. *Melita nitida* is found primarily along the shore in very shallow water where it not only grazed the organic scum off of leaf and sediment surfaces, but is also responsible for mechanically fragmenting decaying leaves. It is of limited importance to fish which feed upon amphipods because its shallow water habitat makes it difficult to reach. It may be consumed by other shallow water invertebrates. Grandidierella bonnieri and Corophium lacustre which feed upon fine detrital particles were the most important amphipods as a source of fish food.

ORDER MYSIDACEA

Mysids are abundant in the North River and are an important source of food for many fishes. Four species were collected routinely. Mysidopsis almyra Bowman was the most common mysid, occurring in all habitats and at all times of the year in water which ranged from less than one to 26.2 ppt. Taphromysis bowmani Bacescu occurred under the same conditions as M. almyra, but was outnumbered three to one in ockleman dredge tows. Mysidopsis bahia Molenock was less common than the other two and was never taken in water of less than nine ppt; this is not conclusive evidence that it does not occur at lower salinities. Gastrosaccus dissimilis Coifmann was common when salinities were above 15 ppt, but was definitely not present at salinities below ten ppt.

Most mysids are filter feeders (Barnes, 1963) which ingest small particles such as diatoms and finely divided detritus (Pennak, 1953; Cannon, 1927). Mauchline (1969) identified particles of silt, fragments of leaves, spores and other terrigenous materials in Leptomysis. In addition, Green (1968) has pointed out that mysids often function as omnivores feeding on copepods and dead amphipods.

I examined the digestive tract contents of 120 Taphromysis bowmani and 153 *Mysidopsis almyra* (Fig. 30) and found essentially the same types of particles as described in the quoted literature.

Mysids are an important component of the North River food web. They ingest large quantities of vascular plant detritus and inorganic particles along with lesser quantities of living algae and animal material.

CLASS INSECTA

ORDER DIPTERA

FAMILY CHIRONOMIDAE

Chironomid midge larvae are present in all habitats of the North River system throughout the year. Although populations of larvae are somewhat reduced during the period from February to May when salinities are usually above 20 ppt, at least two species are present (*Chironomis* sp. and *Cricotopus* sp.). During freshwater conditions of the remainder of the year, additional species become established (notably *Chironomis decorus*) creating a significant source of food for predatory fishes and crustaceans.

Chironomid larvae are generally regarded as herbivores which consume algae, higher plants, and organic detritus (Pennak, 1953). Feeding may consist of: (1) ingestion of bottom deposits of organic detritus and algae (Thienemann, 1954), (2) grazing of green algae and diatoms (Jansson, 1967), (3) indiscriminate filtering of suspended particles with a mucous net (Walshe, 1947), and (4) tunneling through leaf material or leaf-mining (Walshe, 1951). Hunt (1953) found chironomid larvae from the Tamiami Canal, Florida, filled with diatoms and masses of fine debris, apparently of plant origin.

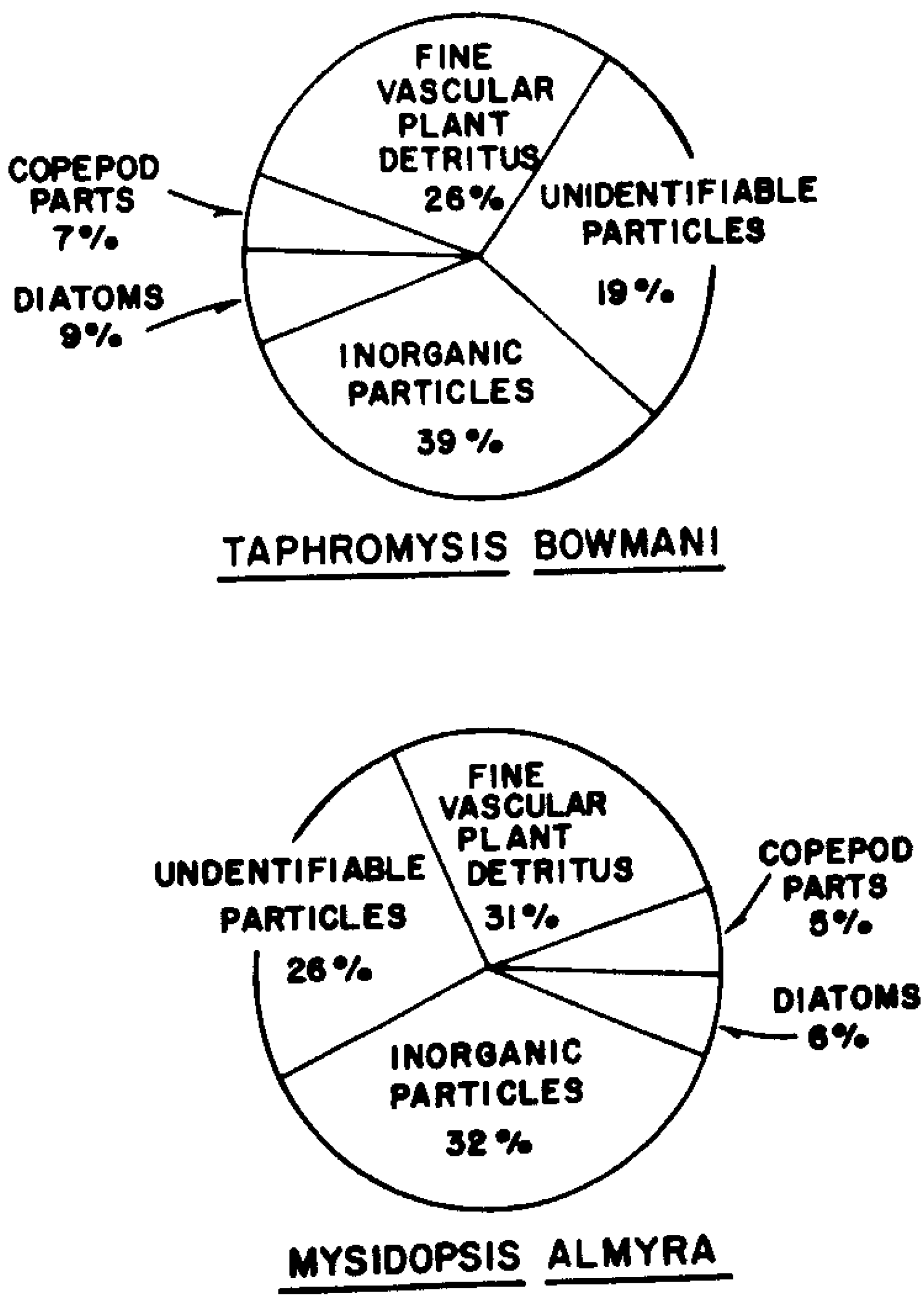


Figure 30. The volumetric per cent composition of the digestive tract contents of 120 *Taphromysis bowmani* and 153 *Mysidiopsis almyra* collected at stations A and B throughout the year.

Since the chironomid larvae from the North River were not identified to species, it is not possible to know how they feed. I examined the digestive tract contents from 120 larvae of at least four species including *Chironomus* sp. and *Cricotopus* sp. and always found very fine material (less than 50 microns, average particle = 8 microns). Included in this fine material was usually a small percentage (less than five per cent) of diatoms with the remainder of the volume composed of varying amounts of inorganic particles and organic detritus. About one third of the detritus could be recognized as originating from mangrove leaves, the remainder was completely unidentifiable. Although in some cases the leaf material appeared to have been torn from dead leaves, a large percentage was composed of decaying detritus particles which had not been macerated by the larvae. Detrital material taken from the digestive tracts of larvae which had been preserved for a few hours in a chilled brine solution was examined both with phase and fluoresence microscopy revealing numerous bacteria and ciliates and a few flagellates. Fungi are also present in the gut contents.

Chironomid larvae are present in the North River system throughout the year, but reach their greatest abundance during the freshwater period from June to December. Their food consists of a small percentage of diatoms and a large bulk of inorganic and organic detritus particles with its associated microorganisms.

TROPHIC GROUPINGS OF THE NORTH RIVER ORGANISMS

By examination of the individual trophic analyses from the preceeding section it is possible to gather the macro-heterotrophes which are larger than nematodes into a series of trophic groupings based upon the items they ingest. This investigation shows the kinds of materials ingested by most of the animals in this system, but does not establish to what extent they may be assimilated; nonetheless it can be assumed that much of the organic tissue which is ingested is assimilated. For this reason I believe that these data offer a good indication of the direction of energy flow through this diverse community.

Herbivores

Included among the herbivores are organisms which are primarily plant eaters but may on occasion derive some nourishment from animal tissues. The stomach contents are normally composed of plant detritus and smaller amounts of algal filaments and cells. Additional nourishment probably comes from microorganisms adsorbed upon ingested particles, and from dissolved organic substances sorbed upon fine inorganic particles.

The herbivores are subdivided into three groups, as shown below, based upon the extent to which macro-animal material such as copepods and insect larvae is ingested.

Group 1 false mussel, Congeria leucophaeata
scorched mussel, Brachidontes exustus
eastern oyster, Crassostrea virginica
most copepods, larval crustaceans, and larval mollusks
chironomid midge larvae
ostracods
cumaceans

Group 2 striped mullet, Mugil cephalus
sailfin molly, Poecilia latipinna

Group 3 sheepshead minnow, Cyprinodon variegatus
diamond killifish, Adinia xenica
the crab, Rhithropanopeus harrisii
mysids
amphipods

All of the species in group one are strict herbivores according both to my results and those of other investigators, provided that bacteria and fungi are considered to be plants. In examining the food of the two fishes which comprise group two, I did not find any animal in their stomachs other than Protozoa, but there are reports in the literature which indicate that both species may sometimes feed upon small crustaceans, insect larvae, and nematodes. Animals in group three occasionally change to a diet partially composed of animal materials. Over the entire year, however, macro-animal material contributed less than 20 per cent of the volume of the digestive tract contents.

Omnivores

gold spotted killifish, Floridichthyes carpio
the polychaete, Neanthes succinea
the polychaeta, Nereis pelagica
the caridean shrimp, Palaemonetes intermedius
the caridean shrimp, Palaemonetes paludosus
the snapping shrimp, Alpheus heterochaelis
the penaeid shrimp, Penaeus duorarum

These species exhibit a catholic choice in the particles which they ingest, and are best described as omnivores. In the North River they consume many types of particles, depending upon the availability of food in the particular habitat involved. In their natural environment they usually ingest more plant than animal matter, but are often grown in captivity on a diet of animal tissue.

Primary Carnivores

mosquito fish, Gambusia affinis
least killifish, Heterandria formosa
pinfish, Lagodon rhomboides
sheepshead, Archosargus probatocephalus
crested goby, Lophogobius cyprinoides

The five fishes which comprise this group are able to exist either on a predominantly plant or animal diet, but show a preference for animal material when it is available. In most habitats they feed upon a mixture of the two components, with small animal forms such as insects and crustaceans predominating.

Middle Carnivores

most larval and post-larval fishes, and juveniles of higher carnivores
blue crab, Callinectes sapidus
scaled sardine, Harengula pensacolae
bay anchovy, Anchoa mitchilli
sea catfish, Arius felis
common eel, Anguilla rostrata
marsh killifish, Fundulus confluentus
gulf killifish, F. grandis
rainwater killifish, Lucania parva
bluefin killifish, L. goodei
spotted sunfish, Lepomis punctatus
silver jenny, Eucinostomus gula
spotfin mojarra, E. argentius
striped mojarra, Diapterus plumieri
silver perch, Bairdiella chrysura
code goby, Gobiosoma robustum
clown goby, Microgobius gulosus
frillfin goby, Bathygobius soporator
tidewater silversides, Menidia beryllina
hogchoker, Trinectes maculatus
lined sole, Achirus lineatus
skilletfish, Gobiesox strumosus
gulf toadfish, Opsanus beta

These species, predominantly fishes, derive their nourishment from the small fishes and invertebrates which I classified in the preceeding omnivorous groups. Algal strands and mangrove detritus are occasionally ingested in small quantities (less than five per cent of the total stomach content volume), but their presence in the stomach contents is probably the result of accidental ingestion during capture of benthic animals.

Higher Carnivores

American alligator, Alligator mississipiensis
wood stork, Mycteria americana
white ibis, Eudocimus albus
great blue heron, Ardea herodias
little blue heron, Florida caerulea
louisiana heron, Hydranassa tricolor
green heron, Butorides virescens
great white heron, Ardea occidentalis
common egret, Casmerodius albus
snowy egret, Leucophoyx thula
turkey vulture, Cathartes aura
black vulture, Coragyps atratus
bald eagle, Haliaeetus leucocephalus
osprey, Pandion haliaetus

bull shark, Carcharhinus leucas
florida gar, Lepisosteus platyrhincus
tarpon, Megalops atlantica
ladyfish, Elops saurus
inshore lizardfish, Synodus foetus
gafftopsail catfish, Bagre marinus
needlefishes, Strongylura spp.
snook, Centropomus undecimalis and C. pectinatus
jewfish, Epinephelus itajara
grey snapper, Lutjanus griseus
crevalle jack, Caranx hippos
spotted seatrout, Cynoscion nebulosus
red drum, Sciaenops ocellata
leatherjacket, Oligoplites saurus
barracuda, Sphyraena barracuda

These species form the top level of the North River food web. Their food is derived from all of the animals of the lower trophic groupings, but the most commonly ingested organisms are those of the middle carnivore group. It should be reemphasized that the larval and early juvenile forms of most of these higher carnivorous fishes function as middle carnivores and are preyed upon by the higher carnivores. Once they reach a moderate size, the danger of being eaten by other top carnivores is reduced.

Although I conducted no investigations of the diets of the carnivorous birds, they are an important component of this top trophic level and must be considered in any summary of the North River food web. The ibis, wood stork, herons, egrets, and comorants feed heavily during the winter breeding season upon the omnivorous fishes found in the shallow Juncus marsh pools and along the shoreline of the river. As an indication of the tremendous energy requirements of the wading birds, Kahl (1962, 1964) has estimated that a breeding colony of the wood stork, Mycteria americana, consisting of 6,000 pairs and their young require 1.2 $X10^6$ Kilograms (more than 2 1/2 million pounds) of small fishes during a single nesting season of 60-65 days. After adding the energy requirements of other roosts and rookeries of birds in the south Florida mangrove belt, the total energy removed from the mangrove region becomes significantly large. Although approximately 20 per cent of this energy is returned to the environment in the vicinity of the rookeries as excrement (Kahl, 1964), the major portion is removed permanently from the system.

IMPORTANCE OF DETRITUS AS FOOD

More than 20 per cent of the material contained in the digestive tracts of all of the organisms classified here as herbivores and omnivores was "detritus" of a vascular plant origin, usually mangrove leaf. It was present in much greater quantities than were algal tissues. Furthermore, field observations revealed sparse growths of benthic algae and low phytoplankton populations (fewer than 10^5 cells per liter) in this region, indicating that vascular plant detritus is the most important element of the energy base for the North River food web. To comprehend fully the mechanism by which the energy from this detritus is transferred to higher trophic levels, it is necessary to examine the nature of detritus and how the material is produced.

The word "detritus" originates from the Latin verb deterere (inf.) which means "to rub away" or "to wear off". Although the term was used originally by geologists to denote material resulting from the disintegration of rock, it has been in use in biology at least since the time of Petersen's classic paper of 1918. As defined by E. P. Odum and De La Cruz (1963) "organic detritus" refers to particulate material that was formerly part of a living organism. Particles ranging from the freshly dead bodies of plants and animals through finely disintegrated particles of these organisms to fecal pellets and even aggregates of colloidal sized particles are included in the definition. Detritus also includes materials which are sorbed upon the basic particle: bacteria, fungi, and Protozoa, along with adsorbed dissolved organic and inorganic compounds. The entire particle and its sorbed load should be considered as a single unit---a small ecosystem within a larger system.

Organic detritus forms a significant fraction of the available food particles in many ecosystems. Its importance has been recognized in shallow estuarine embayments (Petersen, 1911, 1918; Jensen, 1915; Darnell, 1958, 1961; E. P. Odum and De La Cruz, 1967; W. E. Odum, 1969), over coral reefs (Nelson, 1965), in salt marshes (Schelske and E. P. Odum, 1961; Teal, 1958, 1962; Marples, 1966; W. E. Odum et al., 1969), in soil communities (MacFadyen, 1961; Overgaard-Nielsin, 1962; Wiegert, Coleman and E. P. Odum, 1969), in old field communities (E. P. Odum and De La Cruz, 1963), in forests (Bray and Gorham, 1964; Reiners, 1968), in temperate lakes (McConnell, 1968), in tropical lakes (Fish, 1955; Hickling, 1961) and in rivers and streams where it often is of a terrestrial origin (Ivlev and Ivassik, 1961; Hynes, 1963; Minshall, 1967; Mann, 1967; Nelson and Scott, 1962; Eggleshaw, 1964, Kawanabe, 1957; Chapman, 1966; Keast, 1966; Mathews and Kowalczewski, 1969). Organic detritus is present in the open sea and deep embayments, but recent investigations (Riley, 1961; Baylor et al., 1962; Sutcliffe et al., 1963; and other papers all summarized by Nishizawa, 1966) indicate that most of the detritus particles present are not derived directly from the breakdown of living cells, but are "organic aggregates" which have been synthesized from dissolved organic matter by physico-chemical adsorption. Such aggregates are present in shallow estuaries, but they are insignificant in comparison to the great bulk of decaying plant particles. It is the annual production of tons per acre of this plant detritus that provides the energy to drive the biological machinery of the shallow estuarine system.

Production of Vascular Plant Detritus in the North River System

The production of plant detritus in the North River system was investigated by Eric Heald (1969) as the first section of our joint project. To understand the trophic relationships of the North River animal and plant communities and before attempting to draw any conclusions, it is necessary to summarize Heald's results and to analyze additional information which we gathered jointly.

Heald estimated that over 85 per cent of the total production of vascular plant detritus in the North River basin was derived from approximately 2,600 acres of the red mangrove, Rhizophora mangle; the remaining percentage of detritus came from 400 acres of Juncus and sawgrass marshes. The contribution of aquatic algae to the detrital pool is unknown, but based on the observed small standing crop of algae within the system, it is probably an unimportant source of detritus. Utilizing leaf catchment devices, surveys of mangrove density and size, and aerial photographs, Heald estimated that the North River mangroves produce 12,400 metric tons dry weight per year of leaves, twigs, leaf scales and flowers or 8.8 dry tons per hectare per year (2.41 dry grams/M^2/day). Of this total 83 per cent was composed of leaves.

The next step was to monitor the fate of this mangrove debris once it entered the water. Using litter bags with two millimeter mesh openings, Heald found that the degradation rate of leaf material was highly variable, depending upon where the leaf fell. Those falling on dry ground decomposed slowly; those landing in freshwater broke down somewhat more rapidly; the greatest degradation rate was in full strength seawater, presumably because of the larger populations of grazing organisms present there. After four months from the time of leaf fall, only nine per cent of the original leaf remained in the litter bags placed in seawater, while 39 per cent was still present in those in brackish water and 54 per cent in fresh water.

The disintegrating leaf material was monitored closely to determine its value as a potential food source; our joint data are shown in Table 3. During the first month or two after the leaf enters the water, the relative per cent of protein present in the leaf rises significantly. This does not mean that there is an actual increase in protein, but that there is relatively more protein present. As the leaf particles disintegrate, fats, carbohydrates, and plant protein are lost through a combination of autolysis and microbial activity, and may be replaced to some extent by microbial protein. The end result is a smaller particle which, even though it has been reduced in all of its components, contains relatively more protein than the original leaf. Accompanying this increase in the relative amount of protein is an increase in the caloric value of the leaf material (Table 4).

Heald analyzed the water flowing out of the North River and computed the amounts of suspended detritus which are lost from the North River. He concluded that of the detrital material produced in the North River basin roughly one half is exported from the

Table 3.

Chemical composition of plant debris from North River brackish water samples. Each value represents the mean of four determinations. All values except the per cent ash are on an ash free basis.

	% NITROGEN	% PROTEIN (nitrogen x 6.25)	% FAT	% FIBER	% NITROGEN-FREE EXTRACT	% ASH
MANGROVE LEAVES						
fresh green leaves	1.5	9.4	1.2	17.3	74.8	3.7
dead leaves prior to falling from tree	0.9	5.6	6.9	24.1	65.6	4.5
submerged 1 month	2.1	13.1	6.2	25.9	53.6	3.4
2 months	2.3	14.4	5.3	26.9	52.8	4.1
3 months	2.8	17.5	5.3	31.9	44.8	7.7
4 months	3.1	19.4	---	----	----	7.6
6 months	3.3	20.6	---	----	----	10.1
12 months	---	----	1.7	29.2	43.4	----
SAWGRASS						
standing dead	1.0	6.2	0.8	33.3	60.4	1.8
submerged 3 months	0.9	5.6	---	----	----	2.7
6 months	0.8	5.0	---	----	----	2.1
JUNCUS						
fresh green leaves	1.3	8.1	---	----	----	1.4
standing dead	---	---	1.6	42.4	52.2	1.8
submerged 5 months	1.2	7.5	---	----	----	5.6
10 months	---	---	1.1	35.2	56.2	---

Table 4.

Caloric values of North River vascular plant material

	Kcal/gram	Kcal/ash free gram
RED MANGROVE LEAVES		
fresh green leaves	4.564	4.742
dead leaves prior to falling from tree	4.818	5.043
submerged (brackish water) 1 month	5.020	5.197
2 months	5.085	5.302
3 months	4.568	4.945
4 months	4.602	4.981
5 months	4.647	4.992
6 months	4.433	4.921
fats extracted from fresh and decaying leaves	9.690	9.750
SAWGRASS LEAVES		
standing dead leaves	4.615	4.698
submerged 3 months	4.521	4.602
6 months	4.514	4.602
JUNCUS LEAVES		
fresh green material	4.723	4.791
submerged 5 months	4.039	4.279

system into the surrounding bays and inshore waters; less than two per cent of the leaf material remains permanently in the system to form peat. The exported detritus is primarily in the form of particles between 50 and 350 microns in size. These particles were composed of 21 per cent protein on an ash free basis, and contained numbers of bacteria, fungi and yeasts.

Utilization of Detritus as Food

The tons of mangrove leaf material produced in each hectare of the North River mangrove community present a potential food source of great magnitude. There are at least four ways by which this freshly fallen leaf organic material may be utilized by the heterotrophic community: (1) dissolved organis substances → microorganisms → higher consumers, (2) dissolved organic substances → sorption on sediment particles → higher consumers, (3) leaf material → higher consumers, (4) leaf material → bacteria and fungi → higher consumers.

The first two routes of energy exchange are based upon the rapid loss of water-soluble organic substances (e.g. simple sugars, organic acids, starches) which occurs during the first few weeks after the leaf enters the water. Nykvist (1959) has found that ash leaves lose 22 per cent of their original dry weight during the first few days in the water. Soluble organic substances of mangrove leaf origin either may be used by bacteria and other microorganisms directly from the water or may become sorbed upon fine organic and inorganic particles in suspension or in the surface sediments. These particles, in turn, may be ingested by fishes and invertebrates and the sorbed substances removed in the digestive tract and assimilated by the animal. The possible importance of sediment-sorbed organics as a food source is discussed in a later section.

The third route, that of leaf material serving directly as a food source for higher consumers, may be important early in the degradation process when the leaf still retains significant amounts of digestible plant proteins, fats, and carbohydrates. Only a few of the macro-organisms in the North River system appear potentially capable of utilizing leaf material directly (e.g. the crab, Rhithropanopeus harrisii and the amphipod Melita nitida), but neither has been definitely shown to do this. As the process of degradation proceeds, little digestible material remains and this third pathway probably is of little importance.

The fourth and most important means of energy transfer in a detritus system such as the North River depends upon the ability of bacteria and fungi to break down and assimilate resistant plant substances such as celluloses and lignins. As plant detritus decomposes into decreasingly smaller particles, little remains except for empty cell walls composed of these resistant materials. When such a particle is ingested by a detritus feeder the only components of the particle which are in a digestible form are the bacteria and fungi, along with a few Protozoa which may be feeding upon the bacteria.

There is little doubt that bacteria can furnish an adequate nutritional source. Shapira and Mandel (1968) in experiments with rat growth found that bacteria fed at low levels provided an adequate sole source of protein. Baier (1935) was one of the first to hypothesize that the nourishment from detritus particles comes from the bacteria involved in decomposition. Ivlev (1945) was able to grow chironomid larvae on filter paper with the help of bacteria which were decomposing the paper. Zobell and Felthan (1938) demonstrated that certain marine invertebrates could live almost indefinitely on an exclusive diet of bacteria. Zobell (1942) suggested that bacteria were useful as food in two ways: (1) they were important directly as nourishment, and (2) they assisted the organisms digestion.

The value of bacteria as food has been emphasized by Teal (1958) for fiddler crabs, Uca sp.; Fish (1955) for Tilapia; Thompson (1954), Darnell (1958) and W. E. Odum (1969) for the striped mullet, Mugil cephalus; Fredeen (1964) for blackfly larvae; and Marzof (1966) for the sediment feeding amphipod, Pontoporeia affinis. Newell (1965) has shown that the two marine deposit feeders, the prosobranch Hydrobia ulvae and the bivalve Macoma baltica, were unable to alter or utilize ingested detritus particles, but were capable of digesting decomposer micro-organisms adsorbed on the particles.

The importance of fungi as food has not been as widely recognized as it has for bacteria, primarily because [as Cooke (1961) has pointed out] it is difficult to analyze quantitatively the presence of fungi in the aquatic environment. Although Rodina (1963) could find no fungi associated with detrital particles in Russian lakes, fungi play an important role in the breakdown of many plant materials, particularly the more resistant vascular plants. Kaushik and Hynes (1968) found most of the protein increase in decaying elm leaves to be due to fungal growth rather than bacterial activity. M. Masters has analyzed our mangrove detritus samples from the North River system and found species of Fusarium, Nigrospora, Dendryphaiella, Cladosporium, Alternaria, Phomopsis, and Mucor. Stained thin sections indicated that the relative amounts of fungi present in these particles was high.

One variation of this detritus → microorganism pathway involves the possible importance of digestive tract microbes in breaking-down detritus material which has been ingested by the host animal. This is a situation which parallels the microorganism's function in the ruminant stomach. Johannes and Satomi (1966) have shown that bacteria in the hind gut of crustacea are able to reduce and assimilate the previously undigestible portion of Nitzchia closterium in only 30 minutes. W. E. Odum (1969) has noted that there are large numbers of bacteria and Protozoa present in the digestive tracts of the striped mullet, Mugil cephalus, a fish which eats large quantities of detritus. These intestinal Protozoa may be of importance judging from the finding of Johannes (1965) that bacteria reduce detritus more rapidly in the presence of Protozoa since they are kept in a prolonged state of "physiological youth" by grazing Protozoa.

The microbial conversion of detritus and the subsequent utilization of this material as food by consumers has been summarized by W. E. Odum (1969) in the following manner. Initially the detritus particle, which may range in size from a few microns to an entire leaf, is attacked by bacteria and fungi, which begin oxidation, hydrolysis and assimilation of the basic carbon structure of the detritus particles. During the process of microbial breakdown the bacteria are continuously grazed by Protozoa creating a rich Protozoa--bacteria--fungi--detritus complex with great potential food value. At intervals the entire complex may be ingested by a larger organism such as a crab or mysid and most of the bacteria, fungi, and Protozoa digested off of the particle. In addition, there may be intestinal microbes which further reduce the particle and provide the host organism with nutrition in the form of excreted organic substances or the body of the microorganism itself. Once the particle (or fragments of the original particle) is released as fecal material into the water, the entire process begins again. A single particle may be ingested and reingested in this manner by a number of different detritus feeders with the size of the particle decreasing with the completion of each cycle. Eventually it reaches a very fine size, becomes joined together with a number of other fine particles to form a conglomerant, and the process begins again.

DETRITUS CONSUMERS: THE KEY TO THE NORTH RIVER FOOD WEB

The decaying mangrove particles with their increased caloric value, high protein content and microbial loads present a rich food source for detritus consumers. Table 5 lists the organisms from the North River whose digestive tract contents averaged at least 20 per cent vascular plant detritus particles by volume. This group of detritus consumers is dominated by invertebrates, chiefly crustaceans; only six species of fish are considered to be detritivores.

My findings from the North River are in marked contrast to the situation reported by Darnell (1958, 1961, 1967) for Lake Pontchartrain, Louisiana. He considered a detritus consumer to be any organism which contained more than five per cent "detritus" in its digestive tract. Since he lumped most materials of an organic origin in the category of detritus it is possible that well digested organisms may have been included in this classification. His list of detritus consumers is dominated by 21 species of fishes and relatively few invertebrates. In my opinion only two of these fishes, *Mugil cephalus* and *Brevoortia patronus*, definitely derive nourishment from the detritus particles which they ingest. The remaining fishes are not equipped with the extremely long digestive tract characteristic of detritus consuming species. The following species which Darnell classified as obtaining nourishment from detritus rarely contained appreciable amounts in the North River samples: the spotted seatrout, *Cynoscion nebulosus*;

Table 5.

North River organisms whose digestive tract contents averaged at least 20 per cent vascular plant detritus

sheepshead killifish, Cyprinodon variegatus
gold spotted killifish, Floridichtyes carpio
diamond killifish, Adinia xenica
sailfin molly, Poecilia latipinna
crested goby, Lophogobius cyprinoides
striped mullet, Mugil cephalus

the polychaete, Nereis pelagica
the polychaete, Neanthes succinea
cumaceans
mysids
harpacticoid and planktonic copepods
amphipods
ostracods
caridean shrimp
penaeid shrimp
the snapping shrimp, Alpheus heterochaelis
the crab, Rhithropanopeus harrisii
chironomid midge larvae

the silver perch, Bairdiella chrysura; the ladyfish, Elops saurus; the red drum Sciaenops ocellata; the needlefish, Strongylura notata; the bay anchovy, Anchoa mitchilli; and the hogchoker, Trinectes maculatus.

Darnell was correct when he stated that detritus is important to consumers in the estuary, but I consider it incorrect to state that it is important as food in significant quantities for even the most carnivorous species. The important principle, both for the North River and most shallow estuaries, is that there is a group of consumers, made up of a few species but many individuals, and that this group is composed of herbivorous and omnivorous crustaceans, mollusks, insect larvae, nematodes, and a few fishes, all of which derive their nourishment from a diet of vascular plant detritus and small quantities of fresh algae. Moreover, fecal material extruded by one organism in this group may be re-ingested a short time later by another species and the entire process of microbial enrichment and subsequent digestion by the detritus consumer be repeated. This concept of detritus cycling is depicted in a simple form in Fig. 31.

Construction of a Food Web

Utilizing the information presented in this study, it is possible to structure a schematic representation of the North River food web (Fig. 32). Although several food chains are incorporated into this food web, the principal flow of energy is along the route: mangrove leaf detritus → bacteria and fungi → detritus consumers → middle carnivores → higher carnivores. The detritus cycle of Fig. 31 is represented in this diagram by the central box containing organisms

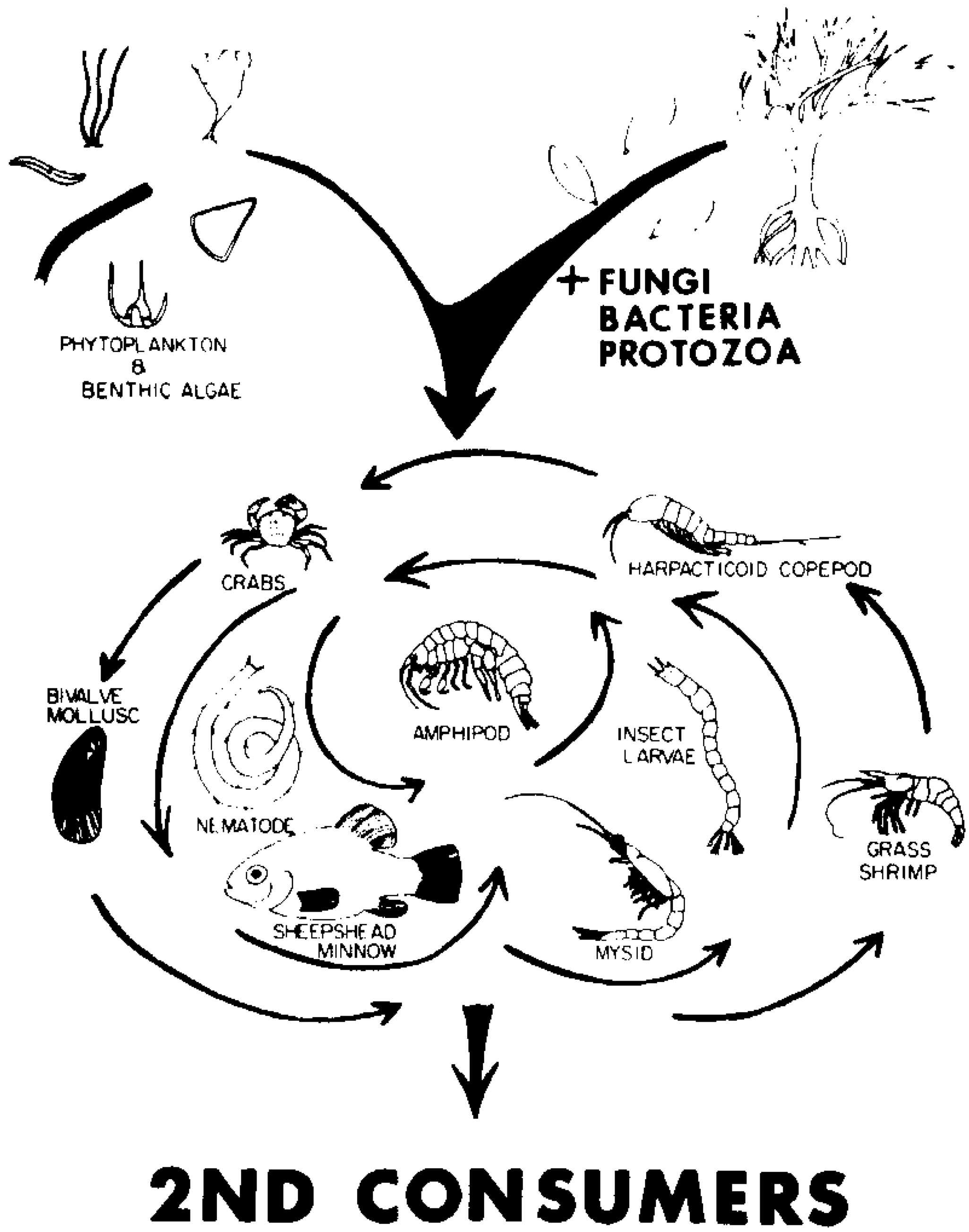


Figure 31. A schematic diagram of the detritus consuming omnivorous organisms of the North River system. These animals ingest small amounts of living algae along with large quantities of vascular plant detritus. The cyclical nature of the diagram depicts the utilization and re-utilization of detritus particles in the form of fecal material.

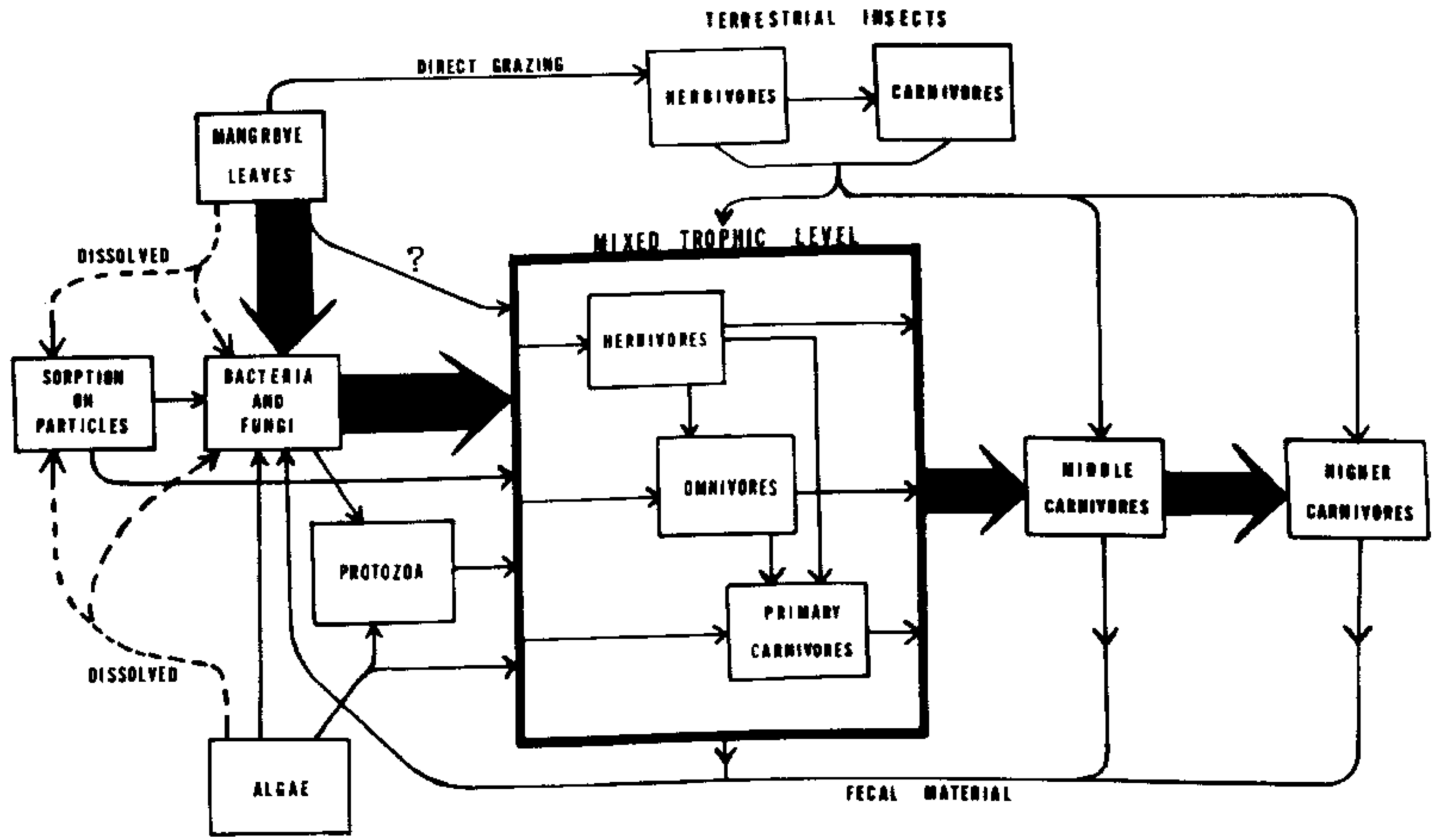


Figure 32. A model of the North River food web. The most important food chain is depicted by the broad arrow; less important food chains are represented by narrow arrows and the pathway of dissolved leaf material is shown by a dotted line.

which range from herbivores to primary carnivores; primary carnivores, it should be remembered, include small carnivores which are also able to digest algae, detritus, microorganisms, and dissolved substances sorbed upon inorganic particles. This diagram summarizes the findings of my investigation.

THE PRODUCTION OF GAMEFISHES

A number of gamefishes depend upon the Everglades mangrove estuary for varying periods of their lives. Tarpon, Megalops atlanticus, snook, Centropomus undecimalis, and ladyfish, Elops saurus, utilize the mangrove belt from the earliest time that they reach the estuary as post larvae. Grey snapper, Lutjanus griseus, sheepshead, Archosargus probactocephalus, spotted seatrout, Cynoscion nebulosus, and red drum, Sciaenops ocellata spend the first few weeks of their lives in the grass beds of Florida and Whitewater Bays and then may move into the mangrove habitat for the next several years. Of this group, the grey snapper is the most dependent upon the mangrove environment. Finally, there are other gamefishes which are found in the mangrove zone as well as in other areas; the crevalle jack, Caranx hippos, the gafftopsail catfish, Bagre marinus, and the jewfish, Epinephelus itajara.

All of these gamefishes feed on detritus feeders. The young fish depend on amphipods, mysids, and chironomid larvae. As the fish grow larger they include in their diet caridean and penaeid shrimp, snapping shrimp, crabs, and detritus consuming fish along with forage fishes such as the tidewater silver sides, Menidia berylina, the silver jenny, Eucinostomus gula, and the rainwater killifish, Lucania parva which in turn feed on detritus feeders.

From the foregoing discussion it should be apparent that the production of gamefishes from mangrove systems such as the North River is directly linked to the production of the detritus feeders (amphipods, etc.) and ultimately to the production of vascular plant detritus in the form of decaying mangrove leaves, roots, bark and wood. If mangrove estuarine systems are destroyed, not only will a valuable protective habitat for juvenile gamefishes be removed, but even more important, it will cut off an input of mangrove organic material, largely contributed in leaf fall, which supports through the detritus based food webs a large population of detritus feeders and their predators. The production of phytoplankton, benthic and epiphytic algae in such an area is so much less than the production of detritus of a mangrove origin, that the yield of gamefish must decline following mangrove destruction.

The situation is somewhat different in other areas such as Florida Bay and Biscayne Bay where there is a significant detritus production both from seagrasses (discussed by Wood et al., 1970) and from benthic macroalgae. Nevertheless, the wholesale removal of mangrove swamps, even from such diverse areas, will result in a reduced production of detritus feeders and the gamefishes which consume them.

THE CONCLUSION

In the introduction to this dissertation I indicated the general lack of knowledge concerning the productivity of mangrove ecosystems and the resulting tendency for some scientists to dismiss such environments as "ecological curiosities" which contribute little to the animal communities of surrounding waters. I believe that we are now in a position to state definitely that this is not true. From the results of the North River investigation, Eric Heald and I have concluded that the annual contribution of mangrove forests to the ecosystem solely from leaf fall exceeds three tons (dry wt.) per acre. This leaf fall when converted by bacterial and fungal action into detritus particles supports a large population of detritus consumers both in the vicinity of the mangrove forest and in surrounding coastal waters. The detritus consumers, in turn, provide food for organisms at higher trophic levels such as gamefishes and wading birds. The permanent removal of large numbers of mangroves from an estuary will reduce the annual production of organic detritus in that estuary; ultimately, this will limit the population size of detritus consumers and reduce the numbers of animals at higher trophic levels which are of interest to man from a commercial and recreational standpoint.

SUMMARY

(1) The feeding habits of more than eighty species of animals were monitored from stomach content examinations of over 7,000 individuals made over a period of 18 months.

(2) From a consideration of these feeding habits on an annual basis, the organisms were classified as herbivores, omnivores, primary carnivores, middle carnivores, and higher carnivores.

(3) The principal source of food for the aquatic animal community of the Everglades mangrove belt is vascular plant detritus originating principally from red mangrove leaves. This detrital material is formed as the leaves decompose into decreasingly finer particles and become covered with fungi, bacteria, and Protozoa. During this process of decay and microbial colonization, the detritus particles increase in relative protein content and in caloric value. After six months in brackish water the remains of the leaf contain 20.6 per cent protein (ash free dry weight) as compared to 5.6 per cent in the freshly fallen leaf; the caloric value rises from 4.742 Kcal/ash free gram in fresh green leaves to 5.302 Kcal/ash free gram for the remains of a leaf which has been submerged for two months.

(4) There are at least four pathways by which freshly fallen mangrove leaves are utilized by heterotrophes: (A) dissolved organic substances $\rightarrow$ microorganisms $\rightarrow$ higher consumers, (B) dissolved organic

substances → sorption on sediment and aged detritus particles → higher consumers, (C) leaf material → higher consumers, (D) leaf material → bacteria and fungi → higher consumers. The last pathway is believed to be the most important.

(5) There exists a key group of omnivorous estuarine organisms which ingest quantities of vascular plant detritus. It is these organisms which are reponsible for supplying the critical link between detritus production and the production of higher consumers. In the North River estuary this key group of detritus consumers includes amphipods, mysids, cumaceans, ostracods, chironomid midge larvae, harpacticoid and planktonic copepods, snapping shrimp, caridean shrimp, penaeid shrimp, crabs, filter feeding bivalves, and a few species of fishes.

(6) The omnivorous detritus consumers appear to obtain nutrition primarily from the microorganisms adsorbed upon detritus particles. These microorganisms are able to convert resistant plant tissues such as cellulose and lignin into fungal and bacterial protein which the omnivorous fishes and invertebrates are able to utilize. In addition, these omnivores always include small quantities of fresh algae in their diets.

(7) I have suggested that the destruction of mangrove forests will remove a source of food input into an estuary and directly limit the production of detritus consumers and those predators which feed upon them. This would reduce the populations of species which are of commercial and recreational value to man.

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APPENDIX

[This is an exact copy of the letter sent from Dr. Harold Humm to Mr. John McCue and subsequently used as expert testimony in a hearing before the Florida state cabinet to determine the fate of intertidal and coastal lands. It is placed in the appendix of this dissertation because it is not available in the scientific literature and I feel that the individual reader should draw his own conclusions as to its merits or mis-statements.]

February 13, 1969

Mr. John J. McCue, Director
Dade County Public Works Department
1351 N.W. 12th Street
Miami, Florida 33125

Dear Mr. McCue:

In response to a request from Mr. Ellis Hollums, I made a trip by private plane, with members of your staff, over the coastline of the western side of Biscayne Bay from Coral Gables south to the Monroe County line and then north over the northern part of Key Largo, Old Rhodes and adjacent keys, Elliott Key, Sands Key, and Ragged Keys. This trip was made for the purpose of examining the shoreline with special reference to its vegetation and natural habitats. We flew at an altitude of about 600 to 700 feet.

Having grown up in Miami and having received my education in marine biology and marine ecology (at the undergraduate level) in Miami, I have been familiar with this area, from the standpoint of a biologist for more than 35 years. I have studied the coastline of Biscayne Bay from 1930 to the present in connection with my work in marine ecology so that I am also familiar with the shoreline vegetation from the ground level. From time to time I have penetrated mangrove habitats in many localities in south Biscayne Bay.

On the basis of my knowledge of this area and of marine ecology in general, it is my opinion that it is in the best public interest to move the present bulkhead line landward to a position coinciding more or less with the outer edge of the mangrove or tree vegetation.

The shoreline from Coral Gables southward to Bay Point at the Monroe County line is characterized by a stand of mangroves. Along the northern half of this shoreline, the mangrove fringe is relatively narrow except for a few areas; along the southern half of the shoreline, the mangrove band is very wide, in some areas to a width of several miles, a reflection of the degree of slope.

The actual mean high tide line along a coastline bordered by a broad stand of mangroves is virtually impossible to determine, as the rising tide meets with such resistance through a mangrove stand that it does not reach the high tide level or distance before the tide begins to fall. Under these circumstances, a theoretical high tide line can be located on the basis of a surveyed height to which the tide reaches outside the mangrove fringe. This is also an arbitrary high tide line since the tide does not reach that level in the mangrove stand.

It is my opinion that most of this mangrove-covered land is in fact a form of waste land. It does not make a significant contribution to the productivity of Biscayne Bay or associated waters. While some areas of natural mangrove habitat should be permanently preserved along the shores of Biscayne Bay, it is my opinion that a sufficient area and an adequate number and variety of these habitats have already been placed in preservation in the Everglades National Park, in the Biscayne National Monument, and in the existing and proposed county and city parks and preserves between Rickenbacker Causeway and Barnes Sound. Those already in preservation are among the most luxurious mangrove areas of this shoreline, such as the superb stands in Matheson Hammock, at Black Point, and in Homestead Bayfront Park.

A major portion of the mangrove area not preserved, probably in excess of 75% of it, is a form of low, scrubby, sparse vegetation that is not worth preservation. Neither the bird life nor the bay would be adversely affected by its conversion into land useful to man. To maintain this vast area by locating the bulkhead line along a necessarily arbitrary mean high tide would, in my opinion, be the antithesis of conservation.

The opinions that have been expressed that "prop roots of mangroves serve as silt traps" and that the value of red mangroves is equal to that of sea grass beds in importance to marine conservation are both biologically unsound. The black organic silt that accumulates among mangrove roots is produced there by microbiological activity; it is not transported by the adjacent waters into the mangrove swamp. There are no biological research results that indicate that mangrove swamps contribute to the productivity of the adjacent waters. They certainly are far less important in this respect than an equal area of sea grass, if for no other reason than the fact that they do not provide a refuge for the young of economically valuable fish and other forms of sea food. The bottom or ground on which mangroves grow is anaerobic, toxic from hydrogen sulfide, and unsuitable for all but a few burrowing organisms in contrast to the great population of burrowers found on sea grass flats.

Removal of the mangrove stands along the western shore of Biscayne Bay and replacing them with sea walls or sandy beaches will not increase the turbidity of the adjacent water (the opposite effect is more likely) and it will not reduce the productivity of the bay waters.

Upon the basis of my recent aerial inspection of the mangrove areas in question, upon my previous knowledge of this area in connection with my work, and upon the facts and opinions stated above, I feel that the bulkhead line more or less coinciding with the outer margin of the mangrove or tree line, as proposed by the Dade County Public Works Department, is biologically sound and I hope that the Trustees of the Internal Improvement Fund will see fit to approve it.

Sincerely yours,

Harold J. Humm
Director
Marine Science Institute

HJH:kb