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# FEEDING ECOLOGY OF *LAGODON RHOMBOIDES* (PISCES: SPARIDAE): VARIATION AND FUNCTIONAL RESPONSES

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## ABSTRACT

Five major ontogenetic stages were found in the diet of pinfish, *Lagodon rhomboides*, from Apalachee Bay, Florida, but diet and dietary breadth showed high degrees of variation with space (both local and geographic), and seasonal variation within size classes was often as dramatic as ontogenetic variation. *Lagodon rhomboides* demonstrated planktivory, omnivory, strict carnivory, and strict herbivory at different times, places, and developmental stages.

Ontogenetic pattern in food habits was primarily a function of mouth size and changing dentition of the predator. Until it reaches 35 mm standard length, the pinfish is an obligate carnivore. Spatial and temporal variation in the food habits of pinfish was a complex function of absolute and relative abundances of food items in the field. Changes in plant consumption by fish larger than 35 mm standard length may be due to changing plant abundance or protection of prey species by macrophyte cover at a given station. Since seagrass biomass and the functional role of a single predator vary over both space and time, plant-animal and predator-prey relationships change continually; however, the life history of *L. rhomboides* is well adapted to seasonal patterns of productivity in food organisms. Multi-dimensional variation in diets rendered the trophic level concept inoperational. It is concluded that food webs are static neither in time nor in space and that taxonomic species may not be functional components in models of energetic pathways and predator-prey relationships.

In recent years, much research effort has been expended on experiments for testing the role of predation in seagrass meadows (Young et al. 1976; Young and Young 1977, 1978; Orth 1977; Nelson 1978; Reise 1978); yet few experimental ecologists have concerned themselves with variation in the feeding behavior or functional responses of the predators involved in their experiments. The problem is illustrated by empirical data which show the potential for wide variation in the diets of fishes with season (Keast and Welsh 1968; Bell et al. 1978a, b), time of day (Hobson 1974; Hobson and Chess 1976; Robertson and Howard 1978), age or size of the animal (Carr and Adams 1973; Hobson and Chess 1976; Ross 1978), and with locality (Feller and Kaczynski 1975; Love and Ebeling 1978). However, very few scientists have adequately characterized interactions of spatial, temporal, and ontogenetic variations (Keast 1970, 1979; Nakashima and Leggett 1975). Also, field studies that have examined relationships between prey selection by fish and structure of prey assemblages are largely limited to fishes that inhabit structurally simple mud bottom or water

column habitats (Feller and Kaczynski 1975; Nakashima and Leggett 1975; Repsys et al. 1976; Stein 1977). To date, only two field studies provide data on the functional responses of fish to prey abundance in seagrass habitats. Robertson and Howard (1978) reported that short-term (diel) dietary shifts in fishes inhabiting beds of *Zostera muelleri* and *Heterozostera tasmanica* were due to vertical movements of holoplankton and facultative zooplankton. Stoner (1979b) showed that the selectivity of prey by pinfish, *Lagodon rhomboides*, was mediated by standing crop of benthic macrophytes. I concluded that increased seagrass biomass resulted in a higher degree of selectivity for certain amphipod species by juvenile fish.

The pinfish is the numerically dominant fish on *Thalassia testudinum* meadows in the shallow subtidal areas of the Gulf of Mexico (Hoese and Jones 1963; Hansen 1969) and on *Z. marina* beds along the Atlantic coast of the United States south of Cape Hatteras, N.C. (Adams 1976). The pinfish is one of the most important predators on macrobenthic organisms of seagrass meadows and has been shown to play a role in the organization of faunal assemblages (Young et al. 1976; Young and Young 1978; Nelson 1978). Data have accumulated on the food habits of pinfish; however, most of the early work reviewed by Caldwell (1957) and

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Carr and Adams (1973) is qualitative and based on small numbers of fish with no particular attention paid to time, space, or fish size. Carr and Adams provided the best published account of food habits of pinfish, noting distinct ontogenetic patterns in the food habits of pinfish and several other fish species which dwell on seagrass beds near Crystal River, Fla. The general conclusion has been that *L. rhomboides* is a generalist feeder. Because *L. rhomboides* is an important mediator of benthic organization, and because the fish is a generalist-type feeder, an investigation was undertaken to test for functional responses of the species to food abundance in the field. Ontogenetic, spatial (local and geographic), and temporal (seasonal) variations in food habits of *L. rhomboides* were explained on the basis of predator morphology, food abundance, and habitat complexity.

## METHODS

Based on long-term macrophyte data for the area (Zimmerman and Livingston 1976a, b), four collecting stations were chosen from shallow regions offshore from the mouths of the Econfina and Fenholloway Rivers, in Apalachee Bay, Fla. (Figure 1). One station was located 2.0 km seaward from each of the river mouths and a second was located 4.0 km seaward. Each site was identified with a permanent marker in a location which was representative of a broad area. Stations Econfina 10 and 12 were macrophyte-dominated habitats (primarily *T. testudinum* and *Syringodium*

*filiforme*) with mean annual macrophyte biomasses of 214 and 320 g dry wt/m<sup>2</sup>. The inner station of the Fenholloway area (station 11) was characterized by low macrophyte densities (9.3 g dry wt/m<sup>2</sup>) and the outer station (Fenholloway 12) was characterized by macrophyte levels (141 g dry wt/m<sup>2</sup>) intermediate between those levels found at the Econfina stations and those at the inner Fenholloway station (Livingston<sup>2</sup>). All stations were polyhaline with salinities ranging from approximately 17 to 34‰. The mean water depth at all stations was between 1.6 and 2.0 m.

Pinfish were collected with a 5 m otter trawl (1.9 cm mesh wing and body, 0.6 cm mesh liner). Seven 2-min tows (2-3 kn) were taken at each station on a monthly basis. The trawling method for the study site was examined by Livingston et al.<sup>3</sup> All tows were made at midday since previous work (Kjelson et al. 1975; Peters and Kjelson, 1975; Adams, 1976) indicated that pinfish feed primarily during daylight hours. All fishes were preserved in 10% Formalin<sup>4</sup>-seawater solution, identified to species, and measured for standard length (SL).

To estimate abundance of prey items in the field, macrobenthic animals (>0.5 mm) and zooplankton were collected on each of the fish collection dates. Macrobenthic prey items were collected with 12 7.6 cm diameter cores and identified to species (Stoner in press). Zooplankton were collected with horizontal tows of a 0.5 m simple conical plankton net with 0.202 mm mesh and a T.S.K. flowmeter. A single tow was made at each station, on each sampling date, at a speed of 1.5 kn. Tow time was dependent upon the abundance of plankton but ranged from 2 to 10 min. Each plankton sample was subsampled with a Folsom plankton splitter when necessary and a 5 ml Hensen-Stemple pipette. One one-hundredth of each sample was counted. Since the importance of planktonic prey items in pinfish food habits was limited to a small part of the population, animals were identified only to major taxonomic group (e.g., calanoid copepod, crab zoea, polychaete larva, etc.)

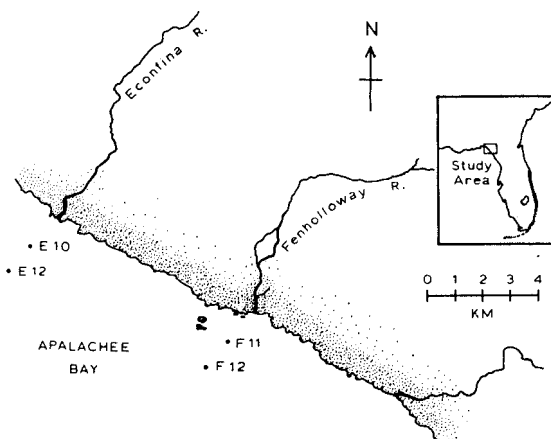


FIGURE 1.—Locations of collecting sites for *Lagodon rhomboides* and food organisms offshore from the Econfina and Fenholloway Rivers in Apalachee Bay, Fla.

<sup>2</sup>R. J. Livingston, Associate Professor, Department of Biological Science, Florida State University, Tallahassee, FL 32306, pers. commun. January 1978.

<sup>3</sup>Livingston, R. J., K. L. Heck, Jr., and T. A. Hooks. 1972. The ecological impact of pulp mill effluent on aquatic flora and fauna of north Florida: Comparison of a polluted drainage system (Fenholloway) with an unpolluted one (Econfina). Unpubl. Rep., 186 p., to the Coastal Coordinating Council, Florida.

<sup>4</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and the standing crops of each group were calculated.

Plants were quantitatively sampled (Livingston et al. 1976) at the field quadrant from where macrobenthic animals were collected, on the fish collection date. Data on the biomass and species composition of benthic macrophytes at the field stations were provided by Robert J. Livingston.

Fish, macrophytes, and prey animals were collected monthly from November 1976 to December 1977. All collections for a station were made on the same date at midday, and all of the stations were sampled within a 2-4 day period.

For analysis of stomach contents, fish were placed in 5 mm size classes up to 40 mm SL, 10 mm size classes from 40 to 100 mm, and 20 mm size classes for fish >100 mm SL. Food items taken from the stomachs of up to 25 fish in a size class were pooled for each sampling date and station and preserved with 70% isopropanol and a dilute solution of rose bengal stain. The gravimetric sieve fractionation procedure developed by Carr and Adams (1972) was used to analyze stomach contents of pinfish ranging from 11 to 160 mm SL. Stomach contents were washed through a series of six sieves of decreasing mesh size (2.0-0.075 mm mesh) and the frequency of occurrence of each food type was recorded for each sieve fraction. Because all of the items in a particular sieve fraction were of comparable size, the relative proportion of the stomach contents made up of each food type was measured directly by counting. After examination, each sieve fraction was dried overnight at 100° C and the total contribution of each food type was calculated.

With two exceptions, each food particle was placed in a mutually exclusive category. General categories such as amphipod, isopod, harpacticoid copepod, crab zoea, and mysid were employed. The categories animal remains (unidentified tissue stained with rose bengal) and plant remains were the only food categories that were not mutually exclusive from other groups. Plants specifically identified were *T. testudinum* and *S. filiforme*. The general food categories, 40 in number (Table 1), were used for statistical analyses; however, whenever an animal or plant could be identified to a more specific group (e.g., family, genus, species) this information was recorded.

Cluster analysis, employing the similarity coefficient,  $\rho$  (Matusita 1955; Van Belle and Ahmad 1974), and flexible grouping cluster strategy ( $\beta = -0.25$ ) was used to describe onto-

TABLE 1.—List of the general food categories encountered in the stomachs of pinfish and the codes employed in food habit histograms.

Code	Food category	Code	Food category
AM	Amphipod	IS	Isopod
BA	Barnacle	IT	Invertebrate tube
BI	Bivalve	MY	Mysid
BR	Branchiuran	NE	Nematode
BZ	Bryozoan	NM	Nemertean
CC	Calanoid copepod	NU	Nudibranch
CH	Chaetognath	OS	Ostracod
CR	Crab	PL	Polychaete larvae
CU	Cumacean	PM	Plant matter
CZ	Crab zoea	PO	Polychaete
DE	Detritus	SA	Sand
DI	Diatom	SC	Scallop
FE	Fish egg	SH	Shrimp
FL	Fish larvae	SL	Spicule
FO	Foraminifera	SP	Shrimp postlarvae
FR	Fish remains	SY	<i>Syringodium filiforme</i>
GA	Gastropod	TA	Tanaiid
HC	Harpacticoid copepod	TH	<i>Thalassia testudinum</i>
HY	Hydroid	VL	Veliger larvae
IE	Invertebrate egg		
MS	Miscellaneous — used in food habit histograms for all food items making up <3% of the total mass.		

genetic variation in food habits of *L. rhomboides*. The appropriateness of the cluster strategy for dealing with fish diet data was discussed by Sheridan (1978).

Stepwise multiple regression was used in certain instances to analyze the relationships between amounts of food items consumed by pinfish and abundance of food items in the field. Dependent variables included the amount of amphipod, shrimp, and plant material in stomachs (percent of contents in dry weight) and independent variables were amphipod, shrimp, plant, calanoid copepod, and polychaete abundance values. Maximization of the coefficient of determination,  $r^2$ , was the criterion for selecting the best multiple regression model. The minimum  $F$  value for inclusion of variables in the regression equations was set at 0.01.

## RESULTS

Nearly 5,000 pinfish, representing 61% of all trawlable ichthyofauna in Apalachee Bay, were collected at four field sites during a 1-yr sampling period. The number of fish collected at a station, however, was a direct function of the mean macrophyte biomass at the site ( $r = 0.998$ ,  $P > 0.01$ ). Most of the fish were collected between April and October (Figure 2).

The stomach contents of 2,174 pinfish taken from the four field sites were analyzed. Although the unvegetated site (Fenholloway 11) produced only 82 pinfish in routine trawl collections, over 600 stomachs of fish from each of the vegetated

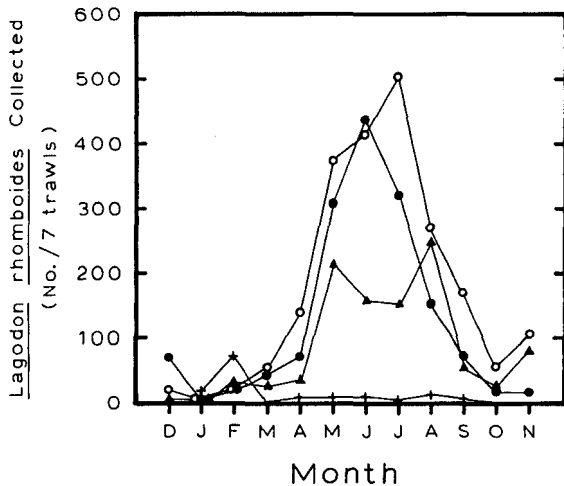


FIGURE 2.—Number of *Lagodon rhomboides* collected in Apalachee Bay, Fla., from December 1976 to November 1977. Crosses = Fenholloway 11, triangles = Fenholloway 12, dots = Econfina 10, circles = Econfina 12.

stations were examined. The relative proportions of various food items taken by pinfish of different size classes (for all dates and stations) varied widely with fish size (Figure 3) and cluster analysis showed four distinct ontogenetic trophic groups. The first group was planktivorous and includes only those fish <16 mm SL. The second group (16-35 mm) included fish which took harpacticoid copepods and amphipods in nearly equal proportions plus small amounts of shrimp post-larvae, invertebrate eggs, and other animals. This group was largely carnivorous. Fish of group three (36-80 mm) were omnivores, taking about 30% of their diet in the form of plant material (mostly microepiphytes) and the rest from the macrobenthic fauna (mainly amphipods, small shrimp, and some harpacticoid copepods). Group four (>80 mm) included mostly adult fish, >1 yr old. At least one-half of the diet was plant material; however, stomach contents of fish >100 mm SL were <10% animal matter. A large portion of the plant matter consumed was seagrass, especially *S. filiforme*.

Pinfish diet was dependent upon the place of capture as well as size of the fish (Table 2). Although a large percentage of the stomachs were empty, the primary food item of pinfish between 11 and 15 mm SL was calanoid copepods at Fenholloway 11, Fenholloway 12, and Econfina 12. Fish of the same size class took a large number of invertebrate eggs at the inner stations, Econfina 10 and Fenholloway 11. Harpacticoid copepods and

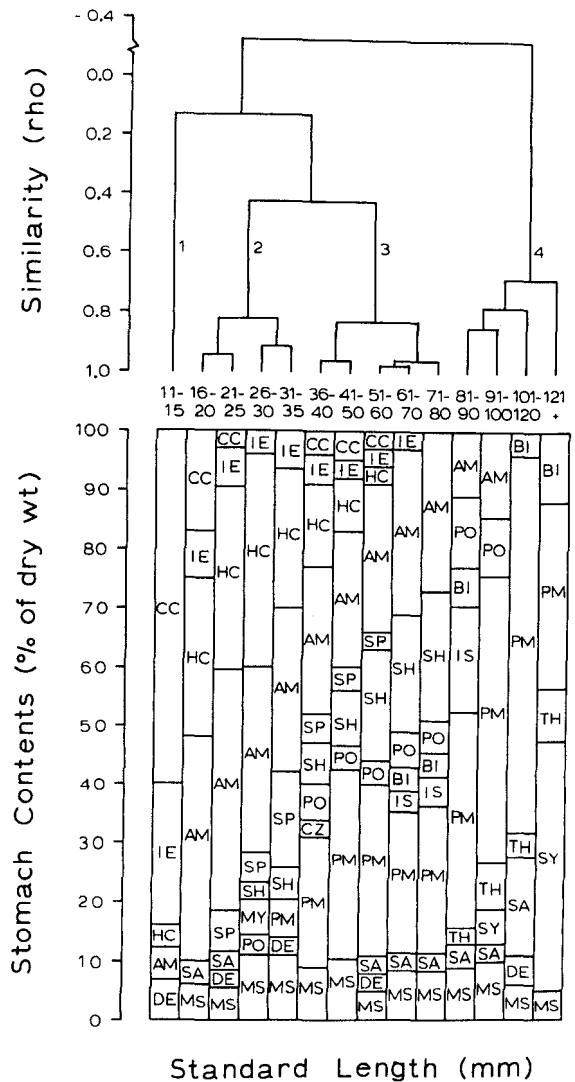


FIGURE 3.—Ontogenetic changes in diet of *Lagodon rhomboides* from Apalachee Bay, Fla. Histograms represent relative proportions of major dietary components (dry weight). Dendrogram represents cluster analysis of diet similarity among size classes. Codes for the food items are given in Table 1. (See text for explanation of the cluster strategy.)

amphipods were important food items only at Econfina 10. The percentage of diet made up by calanoid copepods was directly related to the mean calanoid copepod standing crop (number per cubic meter) at a given station and time ( $r = 0.804$ ,  $P < 0.05$ ) (Figure 4). No significant relationships were found between amphipods consumed by the small pinfish and abundance of amphipods in the field; however, amphipods were consumed by post-

TABLE 2.—Composition of stomach contents of *Lagodon rhomboides* at four stations in Apalachee Bay, Fla. Each value is the mean percentage of the total dry weight of stomach contents for the fish size class indicated.

Item	Fen 11	Fen 12	Econ 10	Econ 12
SL = 11-15 mm				
n (% empty)	23(70.0)	10(70.0)	35(42.8)	28(42.8)
Calanoid copepods	58.1	91.9	17.3	79.7
Invertebrate eggs	23.9		47.7	8.8
Detritus	18.0	8.1		4.3
Harpacticoid copepods			19.0	2.3
Amphipods			16.0	4.9
SL = 16-35 mm				
n (% empty)	14(14.3)	140(5.0)	213(1.4)	235(2.1)
Harpacticoid copepods	7.0	40.8	26.5	38.3
Amphipods	30.0	18.3	38.5	28.3
Invertebrate eggs	9.5	8.0	2.7	7.3
Shrimp postlarvae	3.0	6.0	13.5	7.5
Polychaetes		2.8	1.7	1.0
Plant matter		2.9	2.5	4.2
Shrimp	3.0	5.3	1.5	0.2
Calanoid copepods	40.0		1.0	5.2
Miscellaneous	7.5	15.9	12.1	8.0
SL = 36-80 mm				
n (% empty)	35(8.6)	380(6.6)	460(3.0)	408(4.4)
Amphipods	56.8	27.2	27.2	30.1
Plant matter	16.5	25.3	30.0	23.0
Harpacticoid copepods	0.8	5.6	6.4	6.0
Shrimp postlarvae	0.8	2.8	4.2	1.4
Shrimp	1.3	12.3	9.7	17.7
Polychaetes	3.3	5.0	2.5	5.2
Calanoid copepods	3.3	2.9	2.6	3.6
Invertebrate eggs	0.8	3.5	2.9	5.0
Bivalves		3.7	0.4	
Miscellaneous	16.4	11.7	14.1	8.0
SL > 80 mm				
n (% empty)	10(30.0)	85(15.3)	78(11.5)	20(15.0)
Plant matter	6.0	63.3	84.3	91.7
Polychaetes	0.7	4.9	0.1	
Amphipods	6.0	8.1	2.4	2.0
Bivalves	81.3	10.1	0.4	
Miscellaneous	6.0	13.6	12.8	6.3
Total number	82	615	786	691
% Empty	29.3	8.4	5.2	5.5

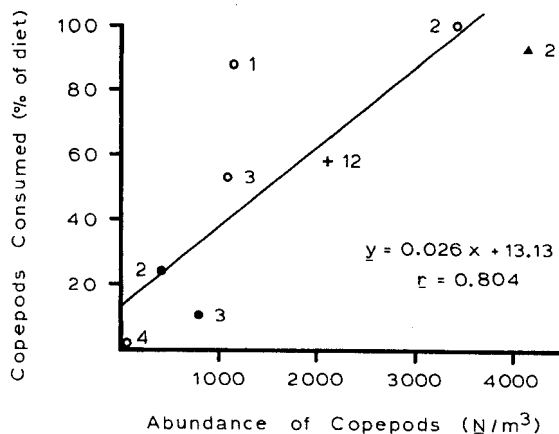


FIGURE 4.—Percentage of stomach contents (dry weight) of post-larval pinfish composed of calanoid copepods shown as a function of copepod abundance in Apalachee Bay, Fla. Cross = Fenholloway 11, triangle = Fenholloway 12, dots = Econfina 10, circles = Econfina 12. Months are indicated by numbers beside the plotted points.

parently substituted for shrimp at Fenholloway 11, although the copepods were less abundant at that site than at other stations (Econfina 10 and 12) between April and July (Table 3). Low abundance of harpacticoid copepods may explain their relatively low contribution to the food habits of young pinfish at the unvegetated site.

Diets of fish from 36 to 80 mm were similar at the three vegetated stations and included large amounts of amphipod, shrimp, and plant material. At the unvegetated site, amphipods made up approximately twice the percentage found in fish from vegetated stations. Because of low shrimp abundance at the unvegetated site, shrimp contributed little to the diets of fish inhabiting that site. Amphipods appear to have been substituted for shrimp.

Fish >80 mm demonstrated wide variability in the percentage of the stomach contents composed of plant material, ranging from 6.0% at Fenholloway 11 to 91.7% at Econfina 12. The diet of fish from the unvegetated station was dominated by the mussel *Brachidontes exustus*. For adult fish, the mean percentage of the diet composed of plant material was a direct function of the mean standing crop of benthic macrophytes at a given station ( $r = 0.952, P < 0.05$ ); however, there was wide temporal variation in the standing crop of benthic macrophytes at the vegetated sites (Table 3) which was not followed by proportional changes in plant consumption at Econfina 10 and Fenholloway 12.

larval fish at Econfina stations 10 and 12 only. The small epifaunal amphipod *Gitanopsis tortugae*, one of the few species consumed by small pinfish, was collected only at these two stations during these months (see Stoner (1979a) for a detailed analysis of prey species consumed by *L. rhomboides*). Because no data are available on abundance of harpacticoid copepods in Apalachee Bay, the importance of their abundance to food habits of pinfish remains unknown.

The main components of the diets of pinfish between 16 and 35 mm were amphipods, harpacticoid copepods, and shrimp postlarvae at the three vegetated sites; amphipods and calanoid copepods at Fenholloway 11. Shrimp and shrimp postlarvae were abundant at the vegetated stations, but few in number at the unvegetated site (Table 3). This probably explains the differences in shrimp consumption. Calanoid copepods were ap-

TABLE 3.—Abundance of prey organisms and biomass of benthic macrophytes<sup>1</sup> in Apalachee Bay, Fla., from December 1976 to November 1977. Only epifaunal species commonly consumed by *Lagodon rhomboides* were included in the abundance of amphipods.

Stn	Prey organisms	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
F 11	Amphipods, no./m <sup>2</sup>	95	0	38	189	114	0	152	0	0	95	152	151
	Shrimp, no./m <sup>2</sup>	19	0	0	0	0	19	19	38	38	0	19	0
	Polychaetes, no./m <sup>2</sup>	171	246	719	908	1,834	794	284	416	739	701	361	1,287
	Copepods, no./m <sup>3</sup>	2,144	4,423	3,469	946	659	0	327	2,232	4,651	2,583	1,576	1,775
	Macrophytes, g dry wt/m <sup>2</sup>	—	3	1	6	5	5	8	11	16	10	20	18
F 12	Amphipods, no./m <sup>2</sup>	379	246	152	245	1,209	397	479	246	454	794	730	1,493
	Shrimp, no./m <sup>2</sup>	57	38	38	0	94	38	190	19	341	133	76	57
	Polychaetes, no./m <sup>2</sup>	1,948	1,194	1,436	1,325	1,722	2,005	1,477	701	965	1,760	607	2,460
	Copepods, no./m <sup>3</sup>	1,973	5,935	4,182	2,202	81	109	411	798	2,730	3,123	1,792	686
	Macrophytes, g dry wt/m <sup>2</sup>	—	110	152	96	197	70	145	165	175	243	117	84
E 10	Amphipods, no./m <sup>2</sup>	114	76	359	870	1,133	2,910	1,514	416	1,720	567	302	1,846
	Shrimp, no./m <sup>2</sup>	19	0	19	19	19	0	95	189	114	114	208	208
	Polychaetes, no./m <sup>2</sup>	1,154	663	1,079	814	569	2,119	910	758	907	853	625	2,947
	Copepods, no./m <sup>3</sup>	1,020	543	385	803	1,981	7,130	1,069	4,042	3,404	2,898	1,315	1,227
	Macrophytes, g dry wt/m <sup>2</sup>	—	96	164	58	230	246	216	234	279	392	319	126
E 12	Amphipods, no./m <sup>2</sup>	926	1,191	2,230	1,190	813	1,512	1,000	624	339	435	549	1,343
	Shrimp, no./m <sup>2</sup>	76	19	19	38	76	0	57	57	95	38	76	0
	Polychaetes, no./m <sup>2</sup>	946	1,665	1,304	1,097	890	1,553	1,062	815	797	683	380	1,156
	Copepods, no./m <sup>3</sup>	807	1,147	3,440	1,070	0	527	258	1,387	3,447	2,745	2,136	948
	Macrophytes, g dry wt/m <sup>2</sup>	—	259	237	118	240	319	456	390	374	619	401	104

<sup>1</sup>Macrophyte data were provided by R. J. Livingston (see text footnote 2).

This point will be discussed later. Polychaetes, bivalves, amphipods, and other taxa were consumed by adult pinfish where macrophyte cover was low.

Seventy percent of the postlarval pinfish from Fenholloway stations were empty and 42.8% of the fish from Econfina stations had no stomach contents (Table 2). Empty stomachs in pinfish >15 mm SL were less common than found in postlarval fish, but fish collected at the unvegetated site consistently had the highest percentage of empty stomachs. Between 11.5 and 15.3% of adult fish taken from vegetated sites had empty stomachs, but 30% of the adults from Fenholloway 11 were empty.

Ontogenetic and spatial variations in pinfish diet were interrelated with changes in diet with season. Overall diet of the pinfish population at a given station was highly dependent upon the length-frequency composition of the population (Figure 5); therefore, to examine independently the effect of season on food habits, size was held constant. Individual size groups, based on the cluster analysis of feeding ontogeny (Figure 3) were tested for seasonality in diet. Although the mean length of fish in the 16-35 mm SL size class increased from 20 to 32 mm between March and August, an analysis of dietary changes within 5 and 10 mm size classes indicated that the bias was not serious and that the change in food habits over time within the larger size group was an accurate representation of dietary seasonality. Length-fre-

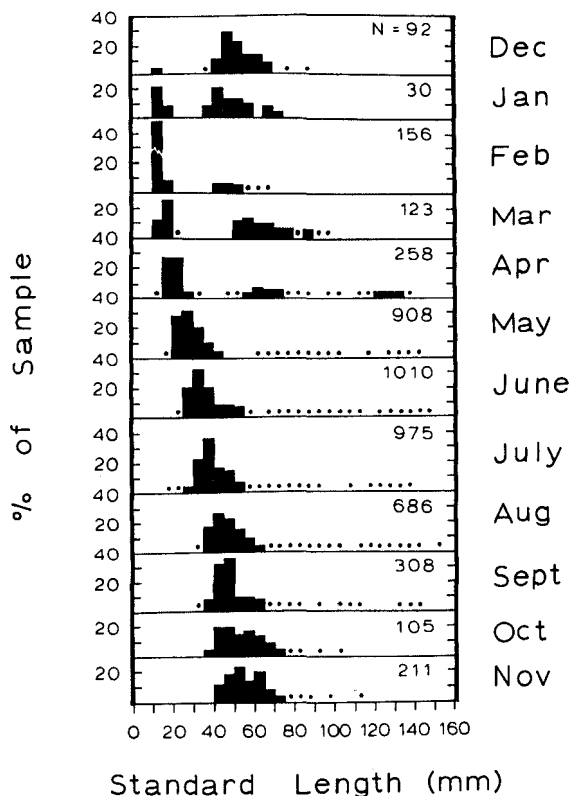


FIGURE 5.—Length-frequency distributions for *Lagodon rhomboides* collected in Apalachee Bay, Fla., from December 1976 to November 1977. Dots indicate that <3.0% of the sample occurred in the size class.

quency changes related to season within the 36-80 mm and adult size groups were minor. Because of insufficient data for the site, Fenholloway 11 was eliminated from analysis of seasonal variation in pinfish diet.

Data were sufficient for seasonal analysis of diet in postlarval pinfish only at Econfina 12. Pinfish <16 mm SL were collected at this site from January through April. In January and February, postlarval pinfish consumed primarily calanoid copepods, plus a small number of invertebrate eggs. Later, they consumed harpacticoid copepods and amphipods in large quantities, and no calanoid copepods were taken by postlarvae in April. The relative abundance of calanoid copepods and invertebrate eggs in the diet of these fish coincided directly with the absolute abundance of the planktonic food items as determined by plankton tows taken on the day of fish collections. Copepods and invertebrate eggs were most abundant in January and February, and declined to annual lows in April (Table 3). Amphipod abundance remained relatively high at Econfina 12 through the winter and spring with annual minima occurring in the fall. Because amphipods were most abundant in January and February (Table 3), when copepod consumption was highest, it would appear that calanoid copepods are the preferred prey of postlarval pinfish. Only when calanoid populations fell to near zero did amphipods become a major portion of the diet.

Pinfish of the carnivorous feeding group (16-35 mm SL) were collected from March through August. In the spring and summer, amphipods and harpacticoid copepods were the primary dietary components of these fish (Figure 6). Clearly, however, amphipods were most important at Econfina 10. Amphipod consumption decreased with time and by late summer the primary dietary components were harpacticoid copepods and small shrimp. A small amount of plant material was taken at all three vegetated stations in midwinter. Invertebrate eggs and other animal foods consistently contributed small amounts to the diets of pinfish between 16 and 35 mm SL.

Temporal variations in diet of pinfish from 16 to 35 mm were analyzed by stepwise multiple regression using calanoid copepod, shrimp, amphipod, and benthic macrophyte abundance (Table 3) as independent variables. Amphipod consumption was positively correlated with amphipod abundance (except Econfina 10) and negatively related to plant, shrimp, and calanoid copepod abundance.

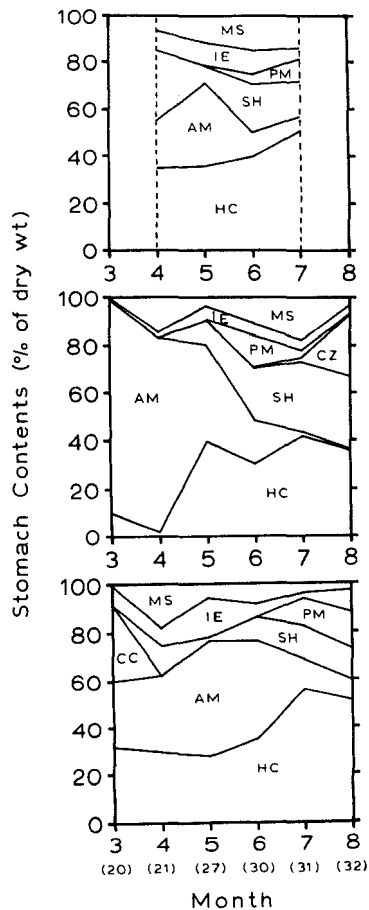


FIGURE 6.—Seasonality in diet of *Lagodon rhomboides* between 16 and 35 mm SL from three stations (F 12-top, E 10-middle, E 12-bottom) in Apalachee Bay, Fla. (March to August 1977). Diet is given as the relative proportion of the dry weight of stomach contents. Codes for the dietary components are given in Table 1. Numbers in parentheses are the mean lengths of fish.

At least 97.6% of the variation in amphipod consumption was explained by three independent variables for all three stations. Significant multiple correlation values for temporal variation in shrimp consumption were obtained for fish from Econfina 10 and 12 ( $r^2 = 0.986$  and  $0.999$ , respectively) (Table 4). Shrimp consumption was positively correlated with shrimp abundance, plant biomass, and calanoid copepod abundance. Negative relationships were found with amphipod abundance. Harpacticoid intake was positively related to plant biomass.

Pinfish between 36 and 80 mm SL were available year-round at vegetated sites and were considered to be omnivores. Examination of temporal



TABLE 4.—Pearson correlation coefficients ( $r$ ) and coefficients of determination ( $r^2$ ) for percentages of total stomach contents (dry weight) composed of: amphipods and shrimp in *Lagodon rhomboides* from 16 to 35 mm SL, tested as functions of food abundance. AM = amphipods/m<sup>2</sup>, CC = calanoid copepods/m<sup>3</sup>, PM = grams dry weight benthic macrophytes/m<sup>2</sup>, and SH = shrimp and shrimp postlarvae/m<sup>2</sup>.

Fenholloway 12			Econfinia 10			Econfinia 12		
Step	$r$	$r^2$	Step	$r$	$r^2$	Step	$r$	$r^2$
Amphipods consumed								
CC	-0.909	0.826	SH	-0.802	0.643*	AM	0.887	0.787*
SH	-0.234	0.995*	AM	-0.083	0.994**	SH	-0.716	0.866*
AM	0.482	n.s.	CC	-0.388	0.999**	PM	-0.090	0.976*
PM	-0.391		PM	-0.692	n.s.	CC	-0.792	n.s.
Shrimp consumed								
CC	0.789	n.s.	SH	0.872	0.760*	AM	-0.825	0.681*
SH	0.318		AM	-0.066	0.972**	CC	0.231	0.868*
AM	-0.741		CC	0.257	0.986*	PM	0.662	0.998**
PM	-0.056		PM	0.604	n.s.	SH	0.783	n.s.

\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; n.s. = not significant.

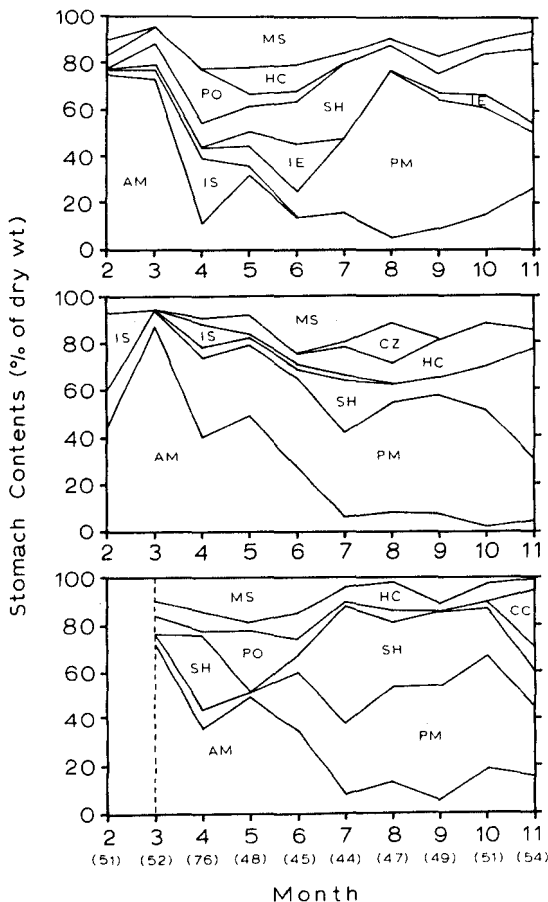


FIGURE 7.—Seasonality in diet of *Lagodon rhomboides* between 36 and 80 mm SL from three stations (F 12-top, E 10-middle, E 12-bottom) in Apalachee Bay, Fla. (February to November 1977). Diet is given as the relative proportion of the dry weight of stomach contents. Codes for the dietary components are given in Table 1. Numbers in parentheses are the mean lengths of fish.

variation in the diet of this ontogenetic group, however, showed that plant material made up only a small portion of the diet in winter and early spring (Figure 7). Amphipod consumption was highest in March and decreased through the spring and fall, during which time plant material became the most important food item. Consumption of shrimp and shrimp postlarvae was low in the spring but increased to as much as 30% of the diet in the summer and fall. Consumption of calanoid copepods by this fish size class was generally limited to winter. Harpacticoid copepods consistently contributed a small amount to the diet of these fish but consumption of isopods, crab zoea, and polychaetes was sporadic.

For fish from 36 to 80 mm, temporal variations in consumption of amphipods, plant matter, and shrimp were analyzed with stepwise multiple regression, using abundance of shrimp, amphipods, polychaetes, and benthic macrophytes as independent variables. Pearson correlation coefficients show that consumption of amphipods was negatively correlated with abundance of shrimp and macrophytes in the field and positively related to amphipod abundance (Table 5). The relationships with polychaete abundance were mixed. Multiple correlation coefficients explained between 60.8 and 79.4% of the temporal variation in amphipod consumption using from two to four independent variables. Consumption of plant matter by fish from 36 to 80 mm was positively related to plant biomass and shrimp abundance.

TABLE 5.—Pearson correlation coefficients ( $r$ ) and coefficients of determination ( $r^2$ ) for percentages of total stomach contents (dry weight) composed of: amphipods, plant matter, and shrimp in *Lagodon rhomboides* from 36 to 80 mm SL, tested as functions of food abundance. AM = amphipods/m<sup>2</sup>, PO = polychaetes/m<sup>2</sup>, PM = grams dry weight benthic macrophytes/m<sup>2</sup>, and SH = shrimp and shrimp postlarvae/m<sup>2</sup>.

Fenholloway 12			Econfinia 10			Econfinia 12		
Step	$r$	$r^2$	Step	$r$	$r^2$	Step	$r$	$r^2$
Amphipods consumed								
SH	-0.561	0.315	SH	-0.802	0.643**	AM	0.616	0.380
AM	-0.462	0.500*	PM	-0.588	0.746**	SH	-0.126	0.664*
PO	0.105	0.608*	PO	-0.090	0.758*	PM	-0.574	n.s.
PM	-0.448	0.631*	AM	0.126	0.794*	PO	0.524	
Plant matter consumed								
SH	0.639	0.408*	PM	0.912	0.831**	PO	-0.714	0.510
AM	0.105	n.s.	SH	0.594	0.912**	SH	0.214	0.652*
PO	-0.257		PO	-0.304	0.926**	AM	-0.694	0.786*
PM	0.428		AM	0.022	0.955**	PM	0.635	n.s.
Shrimp consumed								
PO	-0.034	n.s.	PO	0.654	0.428*	PM	0.496	n.s.
AM	0.316		AM	0.013	0.667**	SH	-0.116	
PM	-0.218		SH	0.389	0.698*	AM	-0.388	
SH	0.024		PM	-0.401	0.741*	PO	-0.197	

\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; n.s. = not significant.

Plant consumption was inversely related to polychaete field density at all three stations and relationships with amphipod abundance were mixed. Multiple regression did not provide a satisfactory model for variation in plant matter consumed at Fenholloway 12, but plant and food item abundances explained 78.6 and 95.5% of the variation at Econfina 12 and 10. Explanation of temporal variation in shrimp consumption by multiple regression methods was successful only for fish from Econfina 10 ( $r^2 = 0.741$ ). Shrimp intake increased with shrimp abundance in the field and decreased with plant and polychaete abundances. Other correlations were low. Harpacticoid copepod consumption was positively related to plant biomass and negatively correlated with amphipod abundance; however, multiple correlation coefficients were not computed since no data were available on harpacticoid abundance.

Diet of large pinfish (>80 mm SL) showed little seasonality at Econfina 10, where plant material made up at least 80% of the stomach contents on

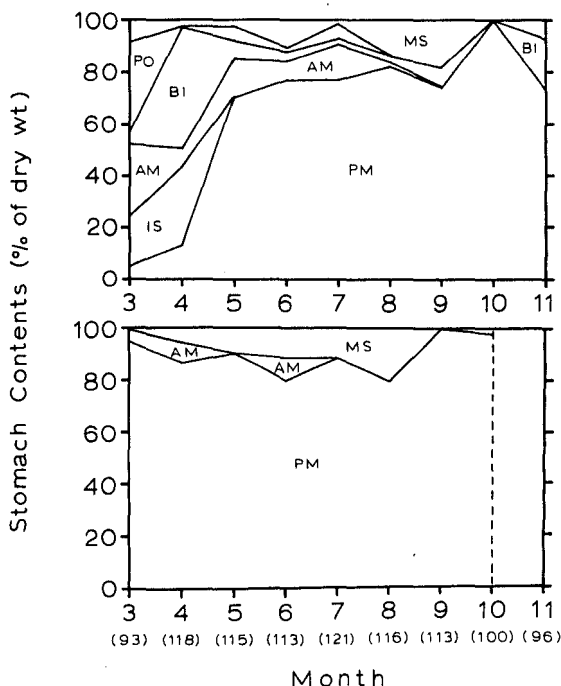


FIGURE 8.—Seasonality in diet of *Lagodon rhomboides* >80 mm SL from two stations (F 12-top, E 10-bottom) in Apalachee Bay, Fla. (March to November 1977). Diet is given as the relative proportion of the dry weight of stomach contents. Codes for the dietary components are given in Table 1. Numbers in parentheses are the mean lengths of fish.

all dates. At Fenholloway 12, however, benthic vegetation was less abundant than at Econfina 10 and major changes in diet occurred with season (Figure 8). Clearly, large pinfish were carnivorous during winter and early spring at Fenholloway 12, but became herbivorous in May. Winter diet included polychaetes, bivalves, amphipods, and isopods. Animal material was unimportant in the diets of fish taken during the rest of the year.

Temporal variation in the diets of adult fish was not adequately explained with multiple regression, as obvious trends in plant consumption did not follow seasonal patterns in macrophyte abundance. Lack of temporal variation in diet at Econfina 10 is due to the fact that plants were readily available at that station when adult pinfish were present (March through October). On the other hand, at Fenholloway 12, macrophytes were patchy in distribution and a high biomass in April (Table 3) was composed largely of *T. testudinum* which was generally not consumed by pinfish. Abundance of alternative prey organisms, such as isopods and bivalves, may also explain carnivory of adult pinfish at Fenholloway in the spring.

Breadth of diet in pinfish was examined by calculating Shannon-Weiner diversity indices,  $H'$ , and by tabulating the number of food items that individually contributed >1.0% of the total mass of stomach contents for each fish size class, sampling date, and station (Table 6, Figure 9). Dietary diversity of pinfish between 16 and 80 mm was lowest at the unvegetated site because two food items, amphipods and calanoid copepods, overwhelmed the importance of other foods. Low abundance of alternative prey such as shrimp, shrimp postlarvae, and benthic macrophytes probably explain this occurrence. For fish >80

TABLE 6.—Dietary diversity,  $H'$ , and number of food types (individually contributing >1.0% of the total mass of stomach contents) in *Lagodon rhomboides* from four stations in Apalachee Bay, Fla. (mean  $\pm$  SD). Within a fish size group, no mean values were significantly different (ANOVA and Duncan's multiple range test,  $P > 0.05$ ).

Size group (mm)	Fen 11	Fen 12	Econ 10	Econ 12
	Dietary diversity, $H'$			
11-15	—	—	0.57 $\pm$ 0.39	0.54 $\pm$ 0.64
16-35	0.99 $\pm$ 0.50	1.68 $\pm$ 0.17	1.28 $\pm$ 0.59	1.45 $\pm$ 0.13
36-80	1.27 $\pm$ 0.46	1.68 $\pm$ 0.44	1.64 $\pm$ 0.44	1.58 $\pm$ 0.25
>80	—	0.92 $\pm$ 0.44	0.50 $\pm$ 0.36	0.41 $\pm$ 0.22
	Number of food types			
11-15	—	—	2.2 $\pm$ 0.9	2.7 $\pm$ 2.0
16-35	5.0 $\pm$ 2.8	7.5 $\pm$ 2.1	5.5 $\pm$ 2.3	5.8 $\pm$ 1.2
36-80	6.2 $\pm$ 1.7	8.6 $\pm$ 2.4	8.1 $\pm$ 3.0	7.2 $\pm$ 1.2
>80	—	6.2 $\pm$ 2.3	4.4 $\pm$ 1.7	4.5 $\pm$ 0.7

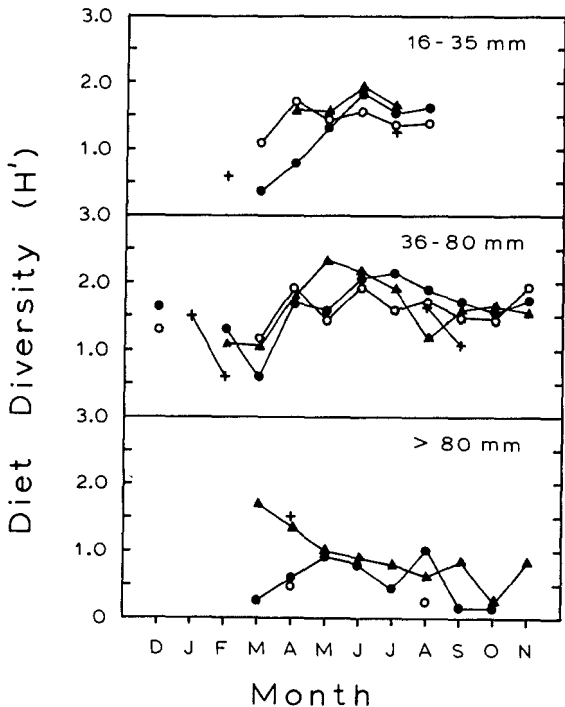


FIGURE 9.—Breadth of diet in *Lagodon rhomboides* from four sites in Apalachee Bay, Fla., shown as a function of season. Each value is the Shannon-Weiner index,  $H'$ , for the food items consumed by fish of three size classes. Crosses = Fenholloway 11, triangles = Fenholloway 12, dots = Econfina 10, circles = Econfina 12.

mm, dietary diversity was highest at the sparsely vegetated station because, in addition to plant material, mussels, polychaetes, and other animal prey made an important contribution to the diet. At the Econfina stations, the diets of adult fish were dominated by plant material causing low dietary diversity.

Pinfish between 36 and 80 mm SL showed greatest breadth in diet; however, some degree of seasonality in dietary diversity occurred in all fish >15 mm (Figure 9). In fish between 16 and 35 mm, peak dietary breadth in June and July corresponded with periods of low amphipod abundance and a change in food habits to alternative prey types including shrimp and plant material. Lowest dietary breadth in fish between 36 and 80 mm occurred in the late winter and spring when amphipods were abundant and macrophyte biomass was low. Diversity of food items available was probably lowest at this time. Dietary diversity in fish >80 mm SL reflected the degree of carnivory by the fish. At Fenholloway 12 dietary diversity

was highest in March and April when various animal foods were consumed in large quantities. At Econfina 10, highest diversity occurred in August when a large number of animal foods supplemented a normally herbivorous diet. During late spring and summer months, dietary diversity indices at Econfina 10 and Fenholloway 12 converged to similar values as fish at both stations became largely herbivorous. Very low dietary diversities occurred at Econfina 10 in September and October because over 98% of the diet was composed of plant material.

## DISCUSSION

Pinfish from Apalachee Bay passed through five major ontogenetic feeding stages, including 1) planktivory; 2) carnivory on amphipods and harpacticoid copepods; 3) omnivory on amphipods, shrimp, and microepiphytes; 4) omnivory on epiphytes, amphipods, polychaetes, and isopods; and 5) herbivory on epiphytes and vascular plant material (primarily *S. filiforme*). Darnell (1958) and Carr and Adams (1973) provide the most reliable data for comparison with the present study on food habits of *L. rhomboides* since each provided information on ontogenetic variation in the diets of the fish. Darnell, studying stomachs of pinfish from Lake Ponchartrain, La., found that the importance of amphipods and other small crustaceans decreased with pinfish length (40-150 mm SL), while vegetable material became increasingly important in diet with fish size. Except that Darnell found dipterans to be a common food item in fish from Lake Ponchartrain, his findings were similar to mine. Pinfish collected near Crystal River, Fla., showed five trophic stages (Carr and Adams 1973); the stages were different from those reported here (Table 7). Unlike pinfish from Apalachee Bay, those from Crystal River became herbivores at an early stage (36-60 mm SL), and later showed strict carnivory on fish and shrimp (>80 mm SL). Fishes were rarely found in the stomachs of pinfish from Apalachee Bay and the pattern of increasing herbivory with fish length appeared to hold except at the unvegetated site where plant material was not available. Because stomach analyses for both geographical areas covered a full year, differences between the findings of the two studies cannot be attributed to artifacts introduced by seasonal variation in diet. Rather, it is likely that different abundances of suitable prey or plant items explain geographical differences in

TABLE 7.—Trophic ontogeny of pinfish collected at Crystal River and Apalachee Bay, Fla. Crystal River data were taken from Carr and Adams (1973).

Feeding stage	Size of fish (mm SL)
Crystal River	
1. Planktivore on copepods	10- 20
2. Carnivore on shrimp, mysids, and amphipods	26- 30
3. Herbivore on epiphytes	36- 60
4. Omnivore on epiphytes, shrimp, and fish	61- 80
5. Carnivore on shrimp and fish	81-110
Apalachee Bay	
1. Planktivore on copepods and invertebrate eggs	11- 15
2. Carnivore on amphipods and harpacticoids	16- 35
3. Omnivore on amphipods, harpacticoids, shrimp, and epiphytes	36- 80
4. Omnivore on epiphytes, amphipods, polychaetes, and isopods	81-120
5. Herbivore on epiphytes and vascular plants	>120

food habits just as food abundance explained local variations in food habits among stations in Apalachee Bay. Carr and Adams described their study site as dominated by *Ruppia maritima* and *Halodule wrightii*. In Apalachee Bay, benthic vegetation was dominated by *T. testudinum*; therefore differences in food habits of pinfish between the two areas, may be due to characteristics of the habitat other than prey abundances. For example: 1) the wide blades of *T. testudinum* may provide better refuge from predation for shrimp and other crustaceans than that provided by narrow blades of *R. maritima* and *H. wrightii*, and/or 2) the plant material near Crystal River was, in some way, unsuitable as food for large pinfish. Hansen (1969) also reported that plant material was the dominant food item of pinfish from dense *Thalassia* and *Ruppia* beds in Pensacola Bay, Fla., suggesting that some characteristic of *Thalassia* beds promotes herbivory in pinfish. Similar to the present study, Hansen found that seasonal variation in plant consumption was related to seasonal availability of benthic macrophytes.

Trophic ontogeny in pinfish can be explained in terms of fish morphology. Width and height of the mouth in the open position was linearly related to standard length of pinfish and increased body and mouth size permitted pinfish to capture a broader range of prey sizes (Stoner 1979a). The same characteristics undoubtedly explain increases in numbers of prey types associated with increasing body size in juvenile fish. Increasing range of prey sizes and types with fish body and mouth size has been reported by many authors (e.g., Wong and Ward 1972; Ware 1972, 1973; Ross 1978). Transition to herbivory by pinfish, first as a microepiphyte nibbler and later to a seagrass grazer is associated with changes in dentition with

growth. Very fine conical jaw teeth only are found in fish at 15 mm SL, but conical teeth are replaced by longer caninelike teeth in fish between 23 and 35 mm. Conical and canine teeth are well adapted for capturing small animal prey, but chisel-shaped incisors, which appear in fish >35 mm, provide pinfish with the dentition required to graze plant material. Because of its dentition, the pinfish is probably an obligate carnivore until it reaches about 35 mm SL (for further discussion and illustration of ontogeny in pinfish dentition, see Caldwell 1957).

Given the morphological constraints of *L. rhomboides*, its reproductive seasonality is particularly well adapted for exploitation of food resources in seagrass meadows of Apalachee Bay. Postlarval pinfish entered the seagrass beds in midwinter at the time of peak abundance of calanoid copepods, appropriately small prey organisms. Winter spawning placed juvenile fish (16-35 mm) on the seagrass beds in the spring when the most valuable prey species, amphipods and harpacticoid copepods, were beginning to reproduce and reaching maximum abundance (Stoner<sup>5</sup>; Thistle<sup>6</sup>). Optimal prey for larger pinfish (36-80 mm) probably includes larger organisms such as shrimp which had peak abundance in the fall. Reproductive timing and growth placed large pinfish on the grass beds in the fall. The life history strategy of *L. rhomboides*, therefore, appears to be adapted to seasonal patterns of productivity and abundance in prey and macrophyte species. Although pinfish were among the fishes that were shown to influence the abundance of zooplankton in the Newport River estuary (Thayer et al. 1974), it is unlikely that pinfish postlarvae affect the abundance of calanoid copepods in Apalachee Bay because of the low number of pinfish postlarvae in the shallow bay (Brady 1980). However, pinfish probably do regulate the abundance of certain amphipod species in the bay (Stoner 1979a, b).

Variation in food habits with space, both on local and geographic scales, was a function of food availability and habitat structure. Food habits of fishes in Apalachee Bay were dramatically different at stations separated by distances as little as 2

<sup>5</sup>Stoner, A. W. 1980. Abundance, reproductive seasonality, and habitat preferences of amphipod Crustacea in seagrass meadows of Apalachee Bay, Florida. Manuscript in review.

<sup>6</sup>D. Thistle, Assistant Professor, Department of Oceanography, Florida State University, Tallahassee, FL 32306, pers. commun. December 1978.

km. At the station where vegetation and epibenthic prey organisms were sparse, pinfish took more food from the water column (e.g., copepods, chaetognaths, and polychaete larvae) than at other stations. Due to the lack of vegetable matter at this station, pinfish consumed *Brachidontes exustus* which lives on oyster bars near the unvegetated site. A high percentage of empty stomachs at the unvegetated site indicates that feeding conditions there were poor, especially for postlarval and adult pinfish. Although selection of food by fish is confounded by food preferences, the consumption of food by pinfish appears to reflect local, geographic, and seasonal abundances of the food organisms and the morphological limitations of the consumer.

Temporal variations in the food habits of *L. rhomboides* were well explained by abundance of prey types in the field, but the correlations were complex. Amphipod, shrimp, and plant consumptions were all directly related to the abundance of these primary food items in the field. Seasonal relationships between food abundance and consumption by fishes were observed by Lawler (1965), Repsys et al. (1976), and Hickey (1975). Diurnal changes in food habits have also been explained by changes in prey availabilities (Hobson and Chess 1976; Robertson and Howard 1978). Keast's (1970) observation that close correlation of prey availability with seasonality in food habits holds for only the most important prey types was also observed in this study. For example, polychaetes were relatively minor components of pinfish diets and showed no correlation with seasonal abundance patterns. On a statistical basis, however, absolute abundance of a food item in Apalachee Bay explained only part of the variation in consumption of that item. For example, although amphipod consumption by juvenile pinfish was directly related to amphipod abundance in the field, amphipod intake was also inversely related to shrimp and plant abundances. These inverse relationships were often stronger than the positive relationship with amphipod abundance. Similarly, shrimp consumption was negatively correlated with amphipod and plant abundances, suggesting that the relative abundance of preferred prey items may be as important as absolute abundance of any one type. The picture is further clouded by the fact that plant material, which serves as an important food source for pinfish >35 mm, is also an obvious component of the habitat that lends protection to many small

prey species (Nelson 1978; Stoner 1979a). Two explanations for the increased plant consumption with benthic macrophyte biomass are plausible: 1) plant material is taken as a simple response to its abundance, and/or 2) *T. testudinum* blades provide amphipods, shrimp, and other animal prey with protection from fish predation and inhibit the consumption of these animals; therefore, as blade density or plant biomass increases, macrophytes and epiphytes are taken as alternative food. Both mechanisms are probably influential in the determination of food habits in pinfish; however, the latter hypothesis is probably the most important mechanism since cellulase activity is not found in the alimentary tract of *L. rhomboides* (Stickney and Shumway 1974). Densely vegetated seagrass habitats support greater densities and biomass of potential prey species than unvegetated or sparsely vegetated substrates (O'Gower and Wacasey 1967; Orth 1977; Brook 1978; Stoner in press), although it is unknown as yet whether this relationship is due to reduced predation on the animals or some property inherent in the structure of the habitat. The problem of omnivory in pinfish would be an especially fertile area for investigation in terms of optimal foraging theory, but a large array of carefully controlled field and laboratory experiments would be required.

Dietary specialization is generally found to be correlated with increasing food abundance. This conclusion is supported by models of predator-prey relationships (see review by Pyke et al. 1977) and empirical studies with fishes (Ivlev 1961; Zaret and Rand 1971; Werner and Hall 1974). On the basis of seasonal prey abundance patterns and the diets of pinfish between 16 and 80 mm SL, dietary specialization did occur with periods of high prey abundance. For example, at the vegetated stations amphipods and other macrobenthic organisms were most abundant between February and May. Lowest dietary diversities occurred during the same time period. With adult fish, however, the characteristic relationship did not seem to hold. Fenholloway 12 and Econfinia 10 showed similar seasonal trends in abundance of food organisms yet seasonality of dietary diversity was entirely different at the two stations. Also, on a spatial basis, lowest dietary diversity occurred at the site with extremely low food abundance (Fenholloway 11) for fish between 16 and 80 mm SL. More generalized diets were found at the vegetated sites where food was more abundant. The predicted relationship of increasing dietary specialization

with increasing food abundance did not hold in certain instances because the abundance of macrobenthic organisms at the study site was closely related to standing crop of benthic macrophytes at the site (Stoner in press). Also, since seagrasses and epiphytes serve as important dietary components of larger pinfish, prediction of dietary diversity is further complicated.

Data provided in this study further verify the conclusion that *L. rhomboides* is a generalist feeder. Schoener (1969) suggested that generalist feeding strategy is favored when: 1) food density is low and there is a premium on the ability of the animal to take a range of prey, 2) the predator has a relatively long period to gain energy, and 3) prey densities fluctuate widely. Given the relatively low abundance of prey species in Apalachee Bay, the great diversity of potential prey items, and their high degree of variability with time and space, the generalist feeding strategy exhibited by *L. rhomboides* would be predicted by Schoener's model.

The detailed analysis of the food habits of *L. rhomboides* provided in this study accentuate difficulties inherent in the description of a trophic niche. Because of dramatic variation in food habits and dietary breadth in coastal fishes, serious methodological problems arise in description of food habits. In most cases, length-frequency distributions of fish are not constant with time; consequently, when animals are not placed in size classes or when placed in overly large size classes, dietary variation may be due to either seasonal changes in food habits or increasing fish size. The diet of a group of fish will be a function of the length-frequency distribution of the population if variation with size occurs. When food habits are examined by size and not by season, variation within a given size class may appear greater than is actually true at any particular time, and seasonality of diet is completely obscured. Variability in food habits as a function of space (a common occurrence) adds still one more dimension to the problem of describing an animal's food and feeding habits, but spatial variation is usually ignored. Keast (1970), in a study of the bioenergetic interrelationships of cohabiting freshwater fishes in Ontario, provided insight into the complex interactions of fish size and season in determining food habits. One other study (Nakashima and Leggett 1975), an investigation of responses of yellow perch to different levels of phytoplankton and benthic biomass in Lake Memphremagog,

Quebec-Vermont, showed interactions of time and fish size in diet determination. The dimension of space was added by comparing the diets of fish from the northern and southern basins of the lake. Few studies have described more than one dimension of an animal's food habits.

Peters (1977) stated that the "Trophodynamic Concept" (Lindeman 1942) is based upon the premise that organisms in an ecosystem are categorized according to their distance along a food chain from the sun. He pointed out, however, that the real world is constructed of complex food webs and organisms do not fall into neat categories such as "primary consumer" or "secondary carnivores." This is not a new idea. In 1961, Darnell asserted that "trophic level" is an inoperational term since: 1) animals of a given size and belonging to a single species take food from several sources, 2) alternate foods are frequently utilized as a function of their availabilities, 3) an ontogenetic progression of food habits is common in animals, and 4) many animals are dependent upon detrital material which is itself of a complex origin and an undefined distance from primary producers. Regier and Henderson (1973) and Kercher and Shugart (1975) provided similar reasoning for the inadequacies of the trophic level concept. Darnell recommended a spectral approach to the food habit problem and Kercher and Shugart defined an "effective trophic position," actually a continuous index of trophic position rather than the conventional discrete level. Neither solution to the problem addressed all of Darnell's objections and gave an accurate portrayal of the functional role of the organism in its ecological context. Data provided in this paper show that, in addition to ontogenetic pattern in food habits, animals within given size classes take foods from several sources with the possible exception of postlarval pinfish which are collected only in the winter and early spring. Fish of many size classes consumed significant quantities of calanoid copepods which are probably herbivores; harpacticoid copepods which may be detritivores, herbivores, or carnivores; amphipods which show wide variety in food habits; plus shrimp, invertebrate eggs, and many other invertebrate taxa. In most cases, the prey species themselves cannot reliably be placed in any one trophic level and, since individuals of a given species were consumed at different developmental stages, and prey species may show trophic ontogeny, the problem of assigning a trophic level to the predator is further

confounded. Pinfish >35 mm SL nearly always contained both plant and animal material in their stomachs. Omnivory, of course, automatically makes the fish both a "primary" and "secondary consumer." Darnell's (1961) suggestion that predators commonly utilize food resources according to their availabilities was clearly demonstrated in this paper as it related to other spatial and temporal patterns of food abundance in Apalachee Bay. Although pinfish do not rely directly on detrital material as a source of nutrition, many of its prey organisms do (e.g., certain harpacticoid copepods, amphipods, shrimps, and polychaetes). Because it is difficult to place detritivores in trophic levels, the predatory fish also falls within no discrete level. On these bases, the trophic level concept is rendered inoperational for relationships involving the dominant epibenthic fish in Apalachee Bay. Furthermore, because of migration of consumers and wide variation in food habits with season and consumer growth, one may never assume that food webs, predator-prey relationships, or the functional role of a predator are static. The taxonomic species is not, in many cases, a functional ecological unit. At the very least, ontogenetic feeding groups should be incorporated in ecological models. These "trophic units" would be particularly useful where the true ecological role of the animal in a model is important. Except in the most simple food webs, without precise knowledge of variation in food habits and diet breadth, models of energetic pathways and predator-prey relationships and measurement of niche breadth and overlap will be accurate neither in theory nor in practice.

Characteristics of prey species which mediate predation include absolute and relative abundances, conspicuousness, size, palatability, defensive morphology and behavior, spatial distribution including microhabitat and aggregation, and nutritional value. All of the above, however, are limited or mediated by various elements of the environment including temperature, turbidity, dissolved oxygen, light, water motion, and structural aspects of the habitat. Although a great deal of research has been conducted concerning the importance of predator and prey characteristics, most of the work has been done in structurally simple systems, including mud bottom, freshwater pond, and water column habitats where the number of food species is relatively low. Data from this and another paper (Stoner 1979b) show that seagrass blades and rhizomes provide a very

important structural component in seagrass meadows which affect both predator and prey species and their interactions. Since seagrass biomass, blade densities, and species compositions vary over both time and space, plant-animal and predator-prey relationships are in constant flux. The seagrass habitat, therefore, is an extremely complex system within which the ecological roles of predation and habitat structure are ever changing. The need for further investigation is obvious.

## ACKNOWLEDGMENTS

This research was supported by grant number R-805288010 from the U.S. Environmental Protection Agency to Robert J. Livingston. I wish to thank all of those graduate and undergraduate students who helped with field collections. E. L. Bousfield, H. Greening, H. Kritzler, F. G. Lewis, S. L. Santos, P. F. Sheridan, and J. L. Simon provided assistance with the taxonomy of various benthic organisms. Aid with computer programming and statistical procedures was generously provided by G. C. Woodsum and D. Zahn. L. G. Abele, W. F. Herrnkind, R. A. Laughlin, K. M. Leber, F. G. Lewis, R. J. Livingston, R. W. Menzel, R. W. Yerger, and an anonymous reviewer helped to point out several inconsistencies in the manuscript at various stages.

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