

Ontogenetic Food Habits of Four Common Fish Species in Seagrass Meadows

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해초생태계에 서식하는 4 우점어종의 성장에 따른
먹이의 변화에 관한 연구

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부산수산대 해양학과

Abstract: Ontogenetic food habits of the four most abundant fish species in seagrass meadows of Redfish Bay, Texas, were examined quantitatively during 1982-1983.

The darter goby (*Gobionellus boleosoma*) and pinfish (*Lagodon rhomboides*) were trophic generalists, which used a wide range of food items. The darter goby had relatively diverse, omnivorous diet which included amphipods, copepods, polychaetes, filamentous algae, diatoms, and detritus. This species did not show distinct ontogenetic changes in food preferences.

Unlike the darter goby, the pinfish showed ontogenetic progression of four feeding stages. An initial feeding stage was a planktivorous stage in which copepods were the major food items, followed by a carnivorous stage in which amphipods became the major food items, an omnivorous stage in which filamentous algae, diatoms, amphipods, and polychaetes were the major food items, and finally a herbivorous stage in which seagrass pieces with attached epiphytes and their debris were the major food items.

The code goby (*Gobiosoma robustum*) and Gulf pipefish (*Syngnathus scovelli*) appeared to be relatively specialized in food habits as carnivorous. Similar ontogenetic changes in food habits were observed for these two species; i.e. initially, copepods were the major food items, followed by a gradual transition to amphipods with growth.

요약 : 미국 Texas 남쪽 해안에 위치한 Redfish Bay 의 해초생태계에 우점종으로 나타나는 4 어종인 darter goby (*Gobionellus boleosoma*), pinfish (*Lagodon rhomboides*), code goby (*Gobiosoma robustum*), 그리고 Gulf pipefish (*Syngnathus scovelli*)에 대한 성장에 따른 먹이 선택의 변화를 정량적으로 연구하였다.

가장 우점종인 darter goby 는 비교적 다양한 먹이를 먹는 잡식성 어류로 amphipods, copepods, polychaetes, filamentous algae, diatoms 그리고 detritus 등이 주된 먹이었다. 이 종은 성장에 따른 먹이 선택의 변화가 크지 않았다.

반면에 pinfish, code goby 및 Gulf pipefish 는 성장함에 따라 먹이 종류가 크게 달라졌다. pinfish 의 경우, 4 단계의 먹이 선택의 변화를 보이는 데, 초기에는 육식성으로 주로 copepods 를 섭식하였으나, 조금 성장하면 주된 먹이가 amphipods 로 바뀌며, 조금 더 성장하면 잡식성으로 변해 filamentous algae, diatoms, amphipods 그리고 polychaetes 등의 다양한 먹이를 먹으며, 그 후 더욱 성장하면 seagrass 와 seagrass 위에 붙어있는 algae 그리고 그들의 debris 를 주로 먹는 초식성으로 먹이 습성이 바뀌었다.

code goby 와 Gulf pipefish 는 비교적 적은 종류의 동물성 먹이에만 의존하는 육식성 어류들이었다. 또한 두종은 비슷한 성장에 따른 먹이 선택의 변화를 보이는데, 초기에는 주로 copepods 를 섭취하였으나 성장함에 따라 점진적으로 보다 큰 amphipods 로 먹이 선택이 바뀌었다.

INTRODUCTION

Seagrass meadows are known to provide food and protection for a variety of animals, including many species of juvenile fish (Hellier, 1962; Hoese and Jones, 1963; Nagle, 1968; Carr and Adams, 1973; Adams, 1976a; Huh, 1984). Detailed food habit studies of fishes utilizing such areas help to illustrate the role of seagrass meadows in fish ecology and also are important in the determination of energy flow pathways in the seagrass ecosystem. From a practical standpoint, information on the quality and quantity of food consumed by fish is needed for estimating fish production (Paloheimo and Dickie, 1970; Mill and Fournier, 1979).

The present study was undertaken in connection with investigations of the functional aspects of seagrass fish communities in Redfish Bay, Texas. Redfish Bay is one of a series of inland bays formed by barrier islands which characterize the coast of Texas. It contains extensive meadows of turtlegrass (*Thalassia testudinum*) and shoalgrass (*Halodule wrightii*). Huh (1984) describes details of the study area and seasonal changes in abundances of each common fish species sampled from the study area. Objectives of this study were to determine the major components of the diets of common fish species and their ontogenetic changes in food habits with growth.

The primary species considered were the darter goby (*Gobionellus boleosoma*), code goby (*Gobiosoma robustum*), pinfish (*Lagodon rhomboides*) and Gulf pipefish (*Syngnathus scovelli*). None of these is directly valuable as fisheries species, but they are the most abundant fish species among local seagrass meadows. Huh (1984) reported that these four species repre-

sented approximately 85% of the total number of fish and 81% of the total biomass of fish in the study area.

METHODS AND MATERIALS

Fish samples used for this study were taken every month from March, 1982 through March, 1983 at seagrass meadows of Steadman Island in Redfish Bay. Collections of fishes were made throughout the day and night (at 6-h intervals) on each sampling date. The majority of fishes were collected with a throwing cage (1m²) of fine mesh netting on a steel frame, hurled \approx 2m away and reaching the bottom within 1 sec. Huh (1984) describes the details of the throwing cage sampler. Other fish samples were collected with a push net, a fine mesh in a square frame pushed along the bottom. No food appeared to be disgorged by the fishes during collection. All fishes sampled were preserved immediately in the field in 10% formalin.

In the laboratory, fishes were measured to be nearest 1.0 mm standard length ("SL") and sorted into size classes of 5- or 10- mm increments, depending on the number and size of fish available.

Stomachs of at least 50 individuals of each species were analyzed each month. If \geq 50 individuals were collected, 15-50 individuals (proportional to the abundance of each major size class) were taken at random from each size class in the samples, and these stomachs were then analyzed. For the pinfish and Gulf pipefish, which are daytime feeders, fishes from daytime collections were used for stomach analyses. After removal of the stomach of each fish, stomach contents were removed with the aid of a dissecting microscope. The stomach contents were

sorted to broad categories (i.e. amphipods, copepods, alg'e, etc.) "Diatom" was separated from the category "algae" to distinguish other forms of algae such as filamentous, coralline, and drift algae. All decomposing plant material, mainly brown seagrass pieces, were designated as "debris". All unidentifiable fine organic matter was designated as "detritus". A list of food items in the stomachs and repective codes used in the food habit figures is provided in Table 1.

Dry weight of each food item of fish was determined with a Mettler balance after 24 hr of oven drying at 80°C. The percentage contributions of each food item to a fish was calculated based on sums of dry weights (mg) of various items.

A Shannon-Weaver index (H') was used to determine the dietary breadth:

$$H' = -\sum_{i=1}^s P_i \cdot \ln P_i$$

where P_i = the proportion of the i th food item, based on dry weight and s = total number of food items (Shannon and Weaver, 1963).

Table 1. List of the general food categories encountered in the stomachs of fish and the codes employed in figures on food habits (Figs. 1-4).

AL= algae	MY= mysids
AM= amphipods	OS= ostracods
BT= <i>Bittium</i> snails	PE= pellets
CO= copepods	PO= polychaetes & oligochaetes
CR= crabs	SA= sand grains
DB= debris (large)	SE= seagrass pieces
DE= detritus (fine)	SH= shrimps
DI= diatoms	TA= tanaids
EG= eggs of fish	UN= miscellaneous
IS= isopods	(<1% of diets)

RESULTS

I. Darter Goby (*Gobionellus boleosoma*)

In the present study, analyses were made of

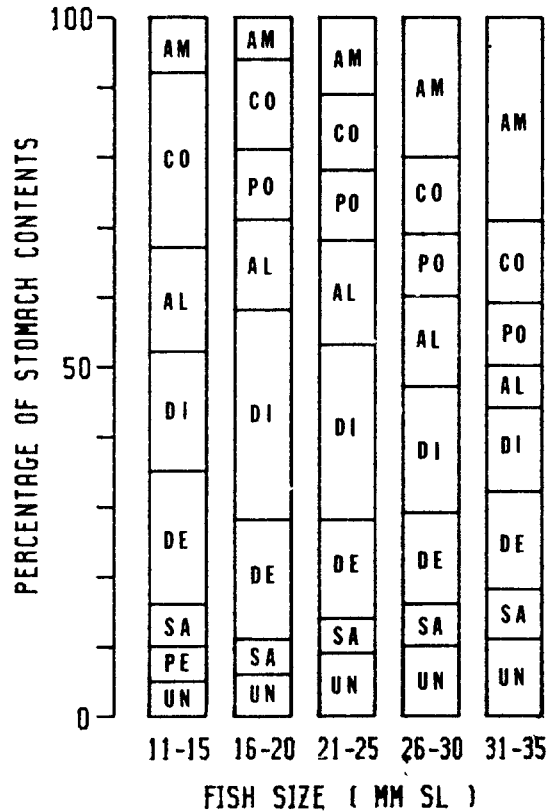


Fig. 1 Ontogenetic changes in food habits of the darter goby from seagrass meadows of Redfish Bay. The codes employed in this figure are the same as those used in Table 1.

stomach contents of more than 1,000 darter gobies in five size classes between 11 and 35 mm standard length ("SL"). Fig. 1 shows the relative proportions of various food items taken by darter gobies in each size class (for all dates). Generally, a high degree of omnivorous feeding behavior was evident from the stomach contents of each size class of the darter goby. All size classes of this species showed similar food taxa (85% dietary overlap); i.e. the darter goby had virtually no ontogenetic progression among major food taxa. Darter gobies consumed significant quantities of amphipods, copepods, polychaetes, filamentous algae, diatoms, detritus, and sand as well as minor quantities of many other items. Most copepods ingested were identified as the benthic dwelling harpacticoid group. Consump-

tion of significant amounts of fine, unidentifiable organic matter (i.e. detritus) and sand suggested bottom feeding. The relatively high dietary diversity (Table 2) of this species suggests that this species is a trophic generalist. The mean size of prey selected by this species increased progressively with increasing fish size.

II. Pinfish (*Lagodon rhomboides*)

In the present study, the stomach contents of about 1,100 juvenile pinfishes were analyzed in 10 size classes between 11 and 90 mm SL. The pinfish fed almost exclusively during daylight hours. Relative proportions of various food

items taken by pinfish of different size classes are shown in Fig. 2. The pinfish showed several ontogenetic changes in feeding habits; four distinct ontogenetic feeding groups were noted: 1) 11-15 mm SL individuals occurred only during late winter and early spring, and showed a planktivorous feeding behavior; copepods were more than 60% of the diet. 2) 16-25 mm SL individuals occurred during spring months, and showed largely carnivorous feeding behavior. They consumed copepods and amphipods in nearly equal proportions plus small amounts of polychaetes and other animals. 3) 26-60mm SL individuals occurred from spring until October, and showed

Table 2. Summary of ontogenetic dietary diversity (breadth) of the four most abundant fish species of seagrass meadows in Redfish Bay from March, 1982 through April, 1983. Shannon-Weaver index, H' (species diversity), for food items consumed, and the number of food types, N , which made up $\geq 1\%$ of total diets are shown.

A. Darter goby

	Fish size class (mm)						Total
	11-15	16-20	21-25	26-30	31-35	36-40	
H'	2.02	2.05	2.21	2.25	2.21	1.78	2.26
N	10	10	12	11	12	8	10

B. Pinfish

	Fish size class (mm)									
	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-60	51-60	Total
H'	1.40	1.61	1.47	1.85	1.95	2.10	1.89	2.10	1.85	2.17
N	7	11	7	10	9	10	10	12	9	12

C. Cude goby

	Fish size class (mm)							Total
	6-10	11-15	16-20	21-25	26-30	31-35	36-40	
H'	0.98	1.54	1.43	1.07	0.92	1.14	0.75	1.15
N	4	6	6	6	6	6	7	7

D. Gulf pipefish

	Fish size class (mm)								Total
	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-120	
H'	0.61	0.63	1.02	1.10	1.21	1.03	0.92	0.67	1.08
N	4	3	6	4	5	5	5	4	5

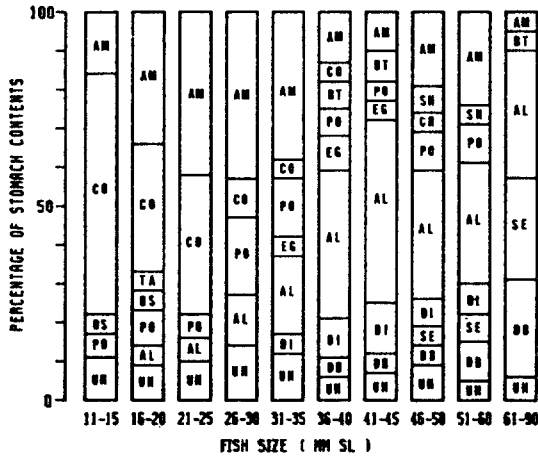


Fig. 2. Ontogenetic changes in food habits of the pinfish from seagrass meadows of Redfish Bay. The codes employed in this figure are the same as those used in Table 1.

an omnivorous feeding behavior. Their diets included significant quantities of filamentous algae, diatoms, amphipods, and polychaetes as well as minor quantities of many other food items. 4) 61-90 mm SL individuals were caught very occasionally throughout the year, and showed largely herbivorous feeding behavior. They fed mainly on seagrass pieces with attached epiphytes (especially on shoalgrass pieces) and their debris. The first two carnivorous feeding groups (11-25 mm SL) had moderate dietary diversity, whereas the omnivorous and quite herbivorous feeding groups (25-60 and 61-90 mm SL) had quite high dietary diversity values (Table 2). The mean size of prey selected by this species increased progressively with increasing fish size.

III. Code Goby (*Gobiosoma robustum*)

In the present study on this species, analyses were made of the stomach contents of approximately 600 individuals in 7 size classes between 6 and 40 mm SL. Fig. 3 shows the relative proportions of various food items that were taken by the code gobies of different size classes. Code gobies were carnivores and preyed heavily on small crustacean. Two broad ontogenetic feeding

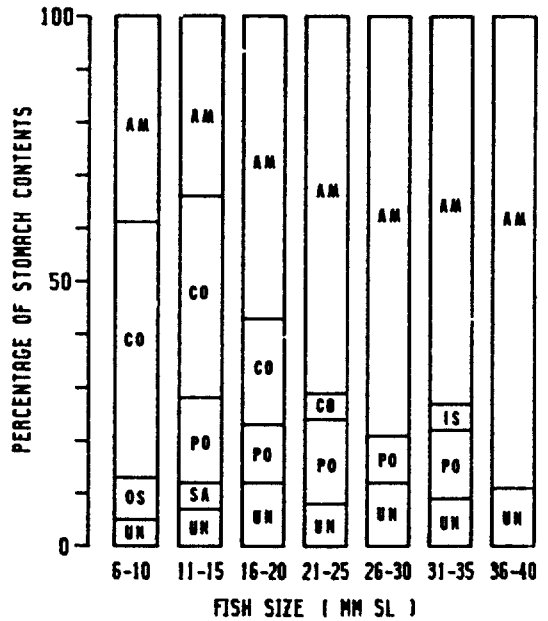


Fig. 3. Ontogenetic changes in food habits of the code goby from seagrass meadows of Redfish Bay. The codes employed in this figure are the same as those used in Table 1.

groups were noted for this species: 1) 6-20 mm SL individuals, which were common between June and February, consumed mainly small foods such as copepods and smaller amphipods plus a significant amount of polychaetes. 2) 21-40 mm SL individuals, which were common between January and July, consumed mainly larger amphipods plus a significant amount of polychaetes. Amphipods accounted for at least 70% of the diets. The mean size of prey selected by this species increased progressively with increasing fish size. Code gobies had diets of lower overall diversity, although smaller size classes (6-20 mm SL) had somewhat higher dietary diversity than did larger (21-40 mm SL) size classes (Table 2). This indicates that the larger fishes appeared more selective among the food items.

IV. Gulf Pipefish (*Syngnathus scovelli*)

In the present study, the stomach contents of about 600 Gulf pipefish, belonging to 8 size classes between 31 and 120 mm SL, were analy-

zed. Like the pinfish, the Gulf pipefish was almost exclusively diurnal in its feeding. Fig. 4 shows the relative proportions of various food items taken by the Gulf pipefish of different size classes. The Gulf pipefish was a carnivore, and all size classes of this species showed an almost strict specialization on small crustaceans. Amphipods and copepods were heavily selected. Two distinct ontogenetic feeding groups were noted: 1) 31-70 mm SL individuals, which were common during summer and fall, preyed heavily on copepods, especially harpacticoid copepods. However, the portion of the diet attributable to copepods decreased steadily with increasing size, and this decrease was paralleled by an increased consumption of amphipods. 2) 71-120 mm SL individuals, which were common during winter and spring, preyed heavily on amphipods. The mean size of prey selected by this species increased progressively with increasing fish size. The low dietary diversity (Table 2) of this species represents this pipefish as a trophic specialist, when compared with other species.

DISCUSSION

In the study area, the two most common species, the darter goby and the pinfish, were the trophic generalists, which used a wide range of food items (Table 2). The observation that pinfish have highly diverse diets is supported by earlier studies on food habits of this species at other localities (Reid, 1954; Caldwell, 1957; Darnell, 1958; Springer and Woodburn, 1960; Hansen, 1969; Odum, 1970). The fact that the pinfish undergoes ontogenetic changes in feeding habits has been reported by recent studies at other localities (Carr and Adams, 1973; Adams, 1976b; Stoner, 1979, 1980; Livingston, 1982). Numerous coexisting fish species were often more common than in the present study, but food availability was not monitored in detail. Carr and Adams (1973) who examined pinfish in turtlegrass meadows near Crystal River, Florida, found that pinfish showed ontogenetic progression of five feeding stages, and that the three major stages would be an initial planktivorous stage in which copepods were the major food items, followed by a marked herbivorous stage during which large amounts of epiphytic algae were consumed, and terminated with a carnivorous stage in which shrimp and fish were the major food items. Stoner (1979, 1980) and Livingston (1982) examined pinfish taken from turtlegrass meadows in Apalachee Bay, Florida and also reported that the pinfish undergoes five ontogenetic feeding stages. But the stages of ontogeny of pinfish in Apalachee Bay were somewhat different from those of Crystal River. Unlike pinfish from Crystal River, those from Apalachee Bay became omnivores, which mainly fed on amphipods and epiphytes after planktivorous and carnivorous stages, and terminated with a herbivorous stage in which epiphytes and vascular plants were the major food items. Some differences in diet of the pinfish, therefore, exist between localities. It is possible that these differ-

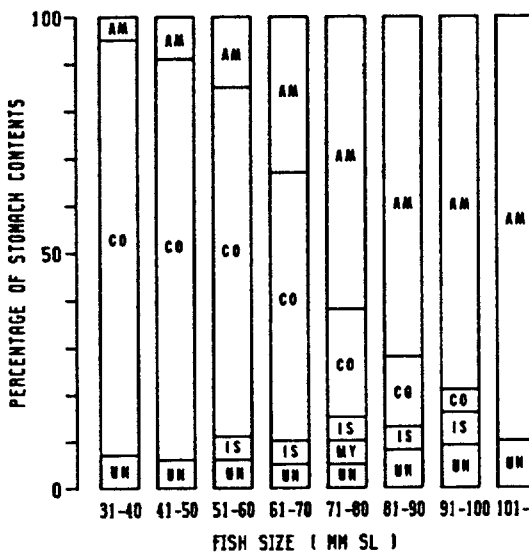


Fig. 4. Ontogenetic changes in food habits of the Gulf pipefish from seagrass meadows of Redfish Bay. The codes employed in this figure are the same as those used in Table 1.

ences are due to the differences in food availability between localities. The pinfish in Redfish Bay showed ontogenetic variations similar to those of Apalachee Bay. This suggests that food availability in Redfish Bay might be more similar to that of Apalachee Bay rather than to that of Crystal River.

The darter goby had relatively diverse, omnivorous diet in this study area. The high frequency of epiphytic algae in diets of this most common fish may be related to its especially high abundance, in that various animals may demonstrate selectivity for beneficial mixed diets (Kitting, 1980) and the most common macroinvertebrates in the habitat consume much epiphytic algae. Unlike the pinfish, the darter goby did not have distinct ontogenetic progressions of food preferences. Comparison between localities cannot be made because only one previous study on the diets of the darter goby in another locality is available (Carble and Hastings, 1983). Recently, Carble and Hastings who examined the darter goby from Indian River lagoon, Florida, reported that this species sieves meiofaunal organisms from ingested sediment bits and that copepods and ostracods were significantly selected by this species.

In contrast to the darter goby and pinfish, the code goby and Gulf pipefish appeared to be relatively specialized in food habits as carnivores, with diets of lower diversity throughout their life (Table 2). The high dependence of the Gulf pipefish on small crustaceans such as amphipods and copepods in its diet was also observed by Reid (1954) who examined fishes from Cedar Key, Florida, Joseph (1957) from Lake Pontchartrain, Louisiana, Springer and Woodburn (1960) from Tampa Bay, Florida, and by Brook (1975, 1977) from Card Sound, Florida. Joseph (1957) reported that the Gulf pipefish under 50 mm in standard length fed primarily on copepods, and that amphipods constitute the main food item of larger pipefishes. Brook (1975, 1977) also reported that amphipods were the

most important food items for the pipefish, followed by isopod and then tenaid crustaceans.

The tendency of the code goby to concentrate on small crustaceans was also observed by Reid (1954) and Springer and Woodburn (1960). Reid (1954) found that the code goby from Cedar Key fed on primarily crustaceans, especially shrimp and amphipods, and supplemented their diets with mollusks. Springer and Woodburn (1960) reported that stomach contents consisted primarily of small crustaceans, especially copepods, isopods, and gammarids, although tiny pelecypods and decapod shrimp occasionally occurred. These studies on food habits of the code goby and Gulf pipefish showed that these two species had fairly constant food habits in different localities, where food availability was probably different.

Similar ontogenetic variations in food habits were observed for the code goby and Gulf pipefish in the study area. Initially, copepods were the major food items, followed by a gradual transition to amphipods with growth. This gradual ontogenetic dietary shift from small copepods to larger amphipods might be mediated by gradual changes in functional morphology of the feeding apparatus (e.g. mouth width) and speed of locomotive movements. Small code gobies and pipefishes had a relatively small mouth width and low darting and swimming speed; they might be unable to efficiently catch and eat the amphipods since amphipods were one of the largest and most mobile benthic invertebrates consumed by these two fish species. Possibly as a result, small fishes preyed mainly on small harpacticoid copepods. However, gradual increase in mouth width and mobility of fish with increasing fish size may allow them to prey efficiently on larger and fast moving prey (e.g. amphipods). As the fish size increased, the code goby and Gulf pipefish showed a tendency to prey on fewer but more rewarding amphipods of larger size. This change in feeding strategy seems to explain the progres-

sive increase in mean prey size and the rapid decrease in the mean number of prey per individual over larger fish size classes. The mean size of prey selected also increased progressively with growth for the pinfish and darter goby.

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REFERENCES

- Adams, S.M. 1976a. The ecology of eelgrass, *Zostera marina* (L.), fish communities. I. Structural analysis. J. exp. mar. Biol. Ecol. 22:269-291.
- Adams, S.M. 1976b. Feeding ecology of eelgrass fish communities. Trans. Am. Fish. Soc. 105: 514-519.
- Brook, I.M. 1975. Some aspects of the trophic relationships among the higher consumers in a seagrass community in Card Sound, Florida. Ph. D. Dissertation, Univ. Miami, Coral Gables, Florida. 133 pp.
- Brook, I.M. 1977. Trophic relationships in a seagrass community (*Thalassia testudinum*), in Card Sound, Florida. Fish diets in relation to macrobenthic and cryptic faunal abundance. Trans. Am. Fish. Soc. 106:219-229.
- Caldwell, D.K. 1957. The biology and systematics of the pinfish, *Lagodon rhomboides* (Linnaeus). Bull. Fla. State Mus. Biol. Ser. 6: 77-173.
- Carble, K.J. and P.A. Hasting. 1983. Selection of meiofaunal prey by the darter goby, *Gobionellus boleosoma* (Gobiidae). Estuaries 5:316-318.
- Carr, W.E.S. and C.A. Adams. 1972. Food habits of juvenile marine fishes: Evidence of the cleaning habit in the leatherjacket, *Oligoplites saurus* and the spottail pinfish, *Diplodus holbrooki*. Fish. Bull. 70:1111-1120.
- Darnell, R.M. 1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publs. Inst. Mar. Sci. Univ. Texas 5:353-416.
- Hansen, D.J. 1969. Food, growth, migration, reproduction and abundance of pinfish, *Lagodon rhomboides*, and Atlantic croaker, *Micropogon undulatus*, near Pensacola, Florida, 1963-1965. U.S. Fish Wildl. Serv. Fish. Bull. 68:135-146.
- Hellier, T.R., Jr. 1962. Fish production and biomass studies in relation to photosynthesis in the Laguna Madre of Texas. Publs. Inst. Mar. Sci. Univ. Texas 8:1-22.
- Hoese, H.D. and R.S. Jones. 1963. Seasonality of larger animals in a Texas turtle grass community. Publs. Inst. Mar. Sci. Univ. Texas 9: 37-47.
- Huh, S.H. 1984. Seasonal variations in population of small fishes concentrated in shoalgrass and turtlegrass meadows. J. Oceanol. Soc. Korea 19(1):44-55.
- Joseph, E.B. 1957. A study of the systematics and life history of the Gulf pipefish, *Syngnathus scovelli* (Evermann and Kendall). Ph.D. Dissertation, Florida State Univ., Florida, 105 pp.
- Kitting, C.L. 1980. Herbivore-plant interactions of individual limpets maintaining a mixed diet of intertidal marine algae. Ecol. Monogr. 50:527-550.
- Livingston, R.J. 1982. Trophic organization of fishes in a coastal seagrass system. Mar. Ecol. Prog. Ser. 7:1-12.
- Mills, E.L. and R.O. Fournier. 1979. Fish production and the marine ecosystems of the Scotian shelf, Eastern Canada. Mar. Biol. 54:101-108.
- Nagle, J.S. 1968. Distribution of the epibiota of macrobenthic plants. Contr. Mar. Sci. Univ. Texas 13:105-144.
- Odum, W.E. 1970. Pathways of energy flow in a south Florida estuary. Ph.D. Dissertation,

- Univ. Miami, Coral Gables, Florida. 162 pp.
- Paloheimo, J.E. and L.M. Dickie. 1970. Production and food supply. In: J.H. Steele (ed.) Marine food chains. Univ. Calif. Press pp. 499-527.
- Reid, G.K., Jr. 1954. An ecological study of the Gulf of Mexico fishes in the vicinity of Cedar Key, Florida. Bull Mar. Sci. Gulf & Carib. 4:1-94.
- Shannon, C.E. and W. Weaver. 1963. The mathematical theory of communication, University of Illinois Press, Urbana.
- Springer, V.G. and K.D. Woodburn. 1960. An ecological study of the fishes of the Tampa Bay area. Fla. State Bd. Conserv. Mar. Lab. Prof. Pap. 1:1-104.
- Stoner, A.W. 1979. The macrobenthos of seagrass meadows in Apalachee Bay, Florida, and the feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae). Ph.D. Dissertation, Florida State Univ., Tallahassee, Florida. 175 pp.
- Stoner, A.W. 1980. Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): Variation and functional responses. Fish Bull. 78:337-352.

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