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## TROPHIC RELATIONSHIPS OF FISHES OCCURRING WITHIN A SURF ZONE HABITAT IN THE NORTHERN GULF OF MEXICO

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**Abstract:** We studied trophic relationships of Florida pompano (*Trachinotus carolinus*), gulf kingfish (*Menticirrhus littoralis*), scaled sardine (*Harengula jaguana*), striped anchovy (*Anchoa hepsetus*) and dusky anchovy (*A. lyolepis*) during their spring residency in the Horn Island, Mississippi, surf zone. *Harengula jaguana*, *A. lyolepis* and *A. hepsetus* were zooplanktivores, utilizing primarily calanoid copepods, mysids and various decapod larvae. *Menticirrhus littoralis* and *T. carolinus* utilized benthic prey including *Donax*, *Emerita* and polychaetes; however, small pompano also fed on zooplankton. *Menticirrhus littoralis*, *T. carolinus*, *H. jaguana* and *A. lyolepis* also showed distinct dietary changes with increasing fish size. Three species, *A. lyolepis*, *H. jaguana* and *M. littoralis* fed at least partially at night, while *T. carolinus* and *A. hepsetus* were primarily diurnal predators. Cluster analysis of size intervals of all species based on presence or absence of prey taxa formed groups consistent with taxonomic relationships, thus indicating considerable interspecific resource separation.

### INTRODUCTION

Surf zone regions of the Gulf of Mexico are important habitats for the juvenile stages of many fishes (Gunter 1958; Springer and Woodburn 1960; Naughton and Saloman 1978; McMichael and Ross 1980; Modde 1980; Modde and Ross 1981). In general, young fishes occur in surf zones during the spring and summer, although fall and winter spawned species such as *Lagodon rhomboides*, *Leiostomus xanthurus*, *Mugil cephalus*, or *Brevoortia patronus* may occupy them during winter and early spring (Modde and Ross 1981). In addition to seasonal periodicity, fishes show diel utilization patterns of surf zones, with the greatest abundance occurring in the early morning (Modde and Ross 1981). Thus, the surf zone, in addition to being a physical-

ly dynamic habitat, is characterized by a dynamic ichthyofauna in which different suites of species may be interacting daily and seasonally.

Trophic relationships of fishes in surf zone areas are largely unknown even though many species, such as pompano (*Trachinotus carolinus*), gulf kingfish (*Menticirrhus littoralis*), scaled sardine (*Harengula jaguana*), and mullet (*Mugil* spp.) are of commercial importance. Thus, the purpose of our study was to compare food habits and relationships of the numerically dominant spring-summer fishes of the Horn Island, Mississippi, surf zone. Species selected for analysis were: *Anchoa lyolepis* (dusky anchovy), *A. hepsetus* (striped anchovy), *Harengula jaguana* (scaled sardine), *Trachinotus carolinus* (Florida pompano), and (*Menticirrhus littoralis* (gulf kingfish).

### METHODS AND MATERIALS

Sampling stations were in the surf zone habitat along the windward shore of Horn Island, Jackson County, Mississippi. Horn Island is one of a chain

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of barrier islands lying parallel to the Mississippi-Alabama Gulf coast (Fig. 1). The island is approximately 14 km offshore, 19 km long and less than 1.2 km wide. The center of the island is at  $30^{\circ} 14''$  N and  $88^{\circ} 40'$  W (Franks 1970). The windward beach is partially protected from oceanic wind driven waves by a series of sand bars which extend the length of the island. The exposed beach is characterized by a sand substrate, moderate wave activity, and the absence of any rooted vegetation. The four stations (Fig. 1) were located within an environment categorized by Odum and Copeland (1974) as a high energy beach system.

Fishes were collected with a 9.1 x 1.8 m bag seine with 3.2 mm mesh. The net was hauled perpendicular to the beach face, beginning 16-18 m offshore. The sampled area was from the swash zone to the midlongshore trough and included only areas exposed directly to

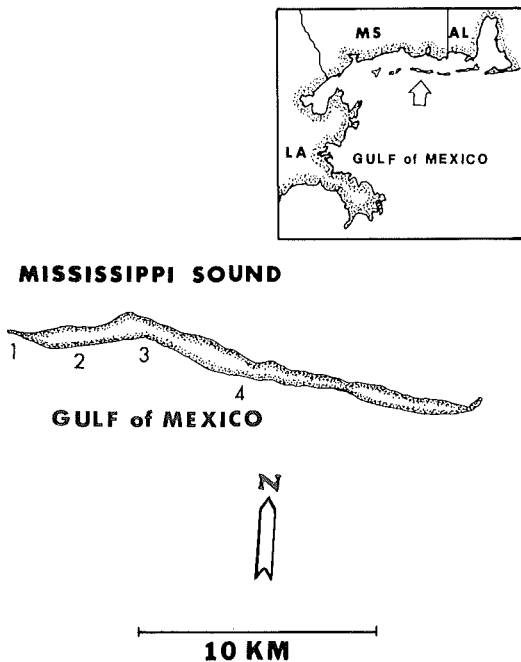
surf. Five to nine seine hauls were taken at each location between 0900 and 1500 CST (see also Modde and Ross 1981).

Stomach contents of *M. littoralis* and *H. jaguana* were examined for May (N = 45, 181), June (N = 11, 85) and July (N = 37, 59). Stomach contents of *T. carolinus* were analyzed for May (N = 150) and June (N = 28), while stomachs of *A. hepsetus* were examined only for May (N = 127). Stomach contents of *A. lyolepis* were studied in May (N = 51) and September (N = 101). The September data were included due to better representation of fish within most time periods. The duration for which stomachs were collected for the different species was dependent upon the occurrence of fishes in the surf zone for the spring and summer of 1976.

Every month between March-September 1976 (excluding August) we sampled either Station 1, 3 or 4 over a 24 h period, taking samples at approximately 4 h intervals. The choice of station was based in part on the availability of a safe anchorage for our boat.

Immediately upon capture, fishes were placed in MS 222 to prevent regurgitation and then fixed in 10% Formalin. Stomach content analysis included identification, determination of volume and percent occurrence of prey items within the stomachs. The section of the alimentary tract examined was that anterior to the pyloric sphincter. We determined the volume of food organisms smaller than .05 cc by a squash technique modified from Hellowell and Abel (1971) by Ross (1974), and the volume of larger food items by displacement.

Plots of cumulative taxa versus the number of stomachs examined indicated that sample sizes sufficient for description of prey kind were obtained for all length groups with the exception of the



**Figure 1.** Map of the study area on Horn Island, Jackson County, Mississippi.

41-80 mm interval for both *M. littoralis* and *T. carolinus*. Spearman rank correlation coefficients ( $r_s$ ) were used to test differences between the percent occurrence of prey among length intervals of fishes. Intraspecific size groups used to examine diel changes in stomach content volume were selected by volume similarity ( $\alpha = .05$ ) as determined by ANOVA and Duncan's multiple range test (Nie *et al.* 1975). Similarity of diet among length intervals for all species was analyzed by presence/absence of prey following the approach in Modde and Ross (1981). The clustering algorithm

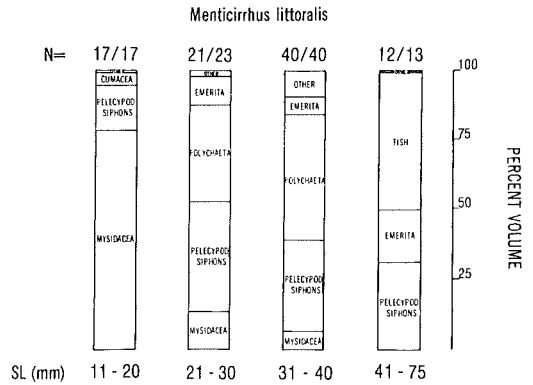


Figure 2. Percent volume of the major food items from *Menticirrhus littoralis* stomachs collected from the surf zone of Horn Island during May through July 1976. N = number of fish with food in stomachs/number of fish examined.

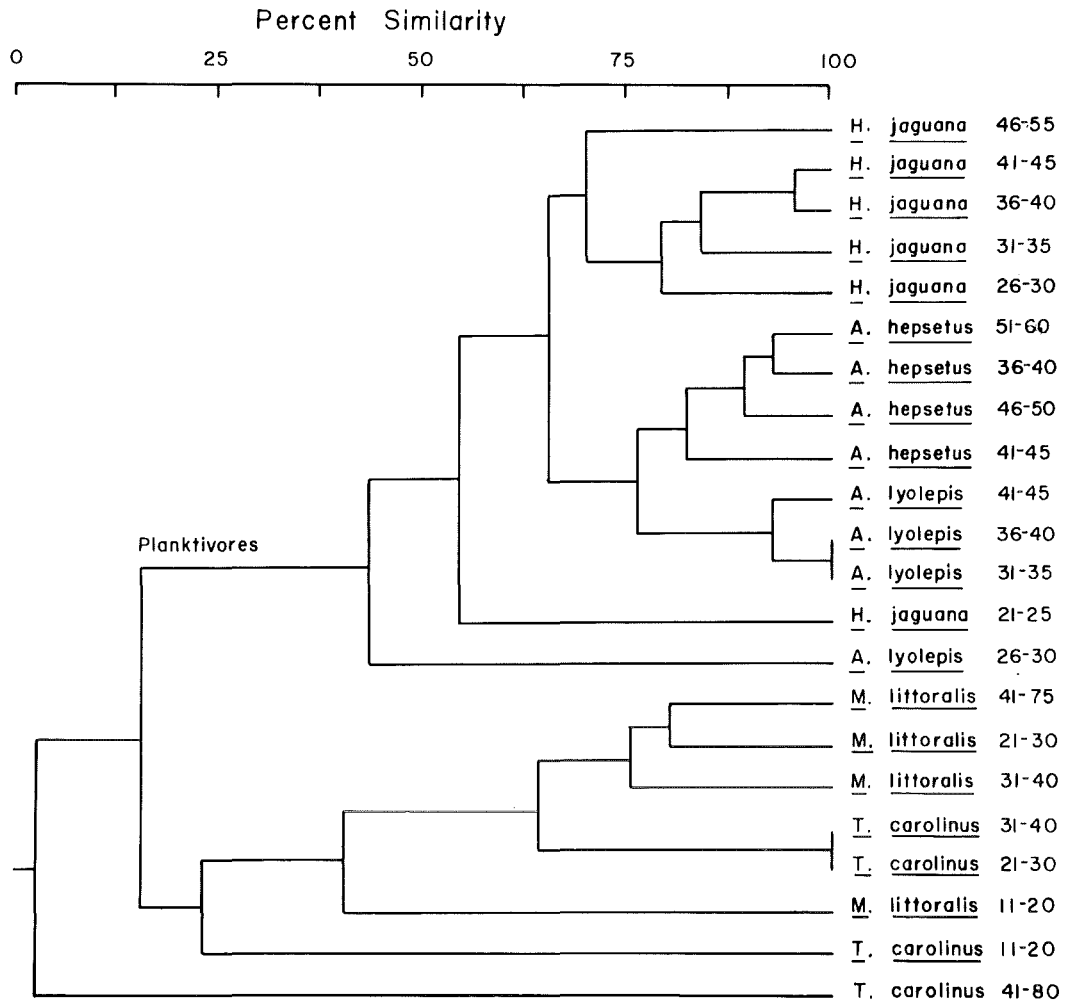


Figure 3. Cluster analysis of ration similarity, based on presence or absence for each length group within *Menticirrhus littoralis*, *Harengula jaguana*, *Trachinotus carolinus*, *Anchoa hepsetus*, and *Anchoa lyolepis*.

was the unweighted pair-group arithmetic average (UPGMA) (Sneath and Sokal 1973). Fish lengths are given as standard length (SL).

**RESULTS**

***Menticirrhus littoralis***

Although sample size was low, a change in diet (based on % volume) occurred between length groups of *M. littoralis* (Fig. 2). Smaller fish (11 to 20 mm) fed predominantly on mysids, whereas the diet of larger individuals (21 to 40 mm) was dominated by polychaetes and pelecypod (*Donax*) siphons. In the few stomachs examined from fish exceeding 41 mm, *Donax* siphons continued as an important food item, with the mole crab, *Emerita*, and small fishes increasing in importance.

The three larger size groups showed significant correlations in percent occurrence of prey. Rank correlations between 21-30 mm and 31-40 mm fish ( $r_s = .83$ ) and the 31-40 and 41-75 mm fish ( $r_s = .70$ ) were both significant ( $P < .05$ ). Cluster analysis based on prey similarity further supports the distinction between the 11-20 mm interval and the larger size intervals (Fig. 3). The three larger size groups linked at 75% similarity,

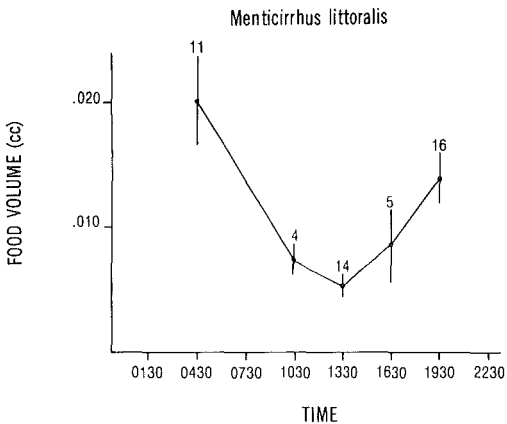


Figure 4. Mean stomach volume per time period ( $\pm 1$  SE) of *Menticirrhus littoralis* between 26 and 40 mm SL collected during May through July 1976.

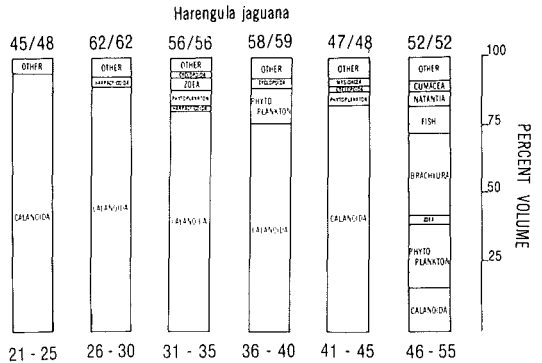


Figure 5. Percent volume of the major food items from *Harengula jaguana* stomachs collected from the surf zone of Horn Island during May through July 1976. Upper number = N; lower numbers = SL (mm).

while the smallest size group joined at the 40% level.

Diel feeding activity was determined for fish ranging between 26 and 40 mm. The volume of stomach contents increased in the late afternoon and was greatest in pre-dawn hours, suggesting that feeding occurred during the afternoon and night (Fig. 4). Feeding activity declined during late morning and early afternoon.

***Harengula jaguana***

The diet of all but the largest length group of *H. jaguana* was dominated volumetrically by calanoid copepods (Fig. 5). Other pelagic food items regularly occurring were harpacticoid and cyclopoid copepods, pelecypod veligers and decapod zoea. Although the first five length intervals were similar with respect to the volumetric dominance of calanoids in the diet, there were subtle changes in prey. The ranking of prey by percent occurrence in the smallest length interval (21 to 25 mm) was significantly different (non-correlated) from the 36 to 40 mm ( $r_s = .42, P > .05$ ), 41 to 45 mm ( $r_s = .54, P > .05$ ), and 46 to 55 mm ( $r_s = .19, P > .05$ ) intervals. The distinction of the smallest and largest size intervals from the intermediate sizes is further supported by cluster analysis

(Fig. 3). *Harengula jaguana* between 26-45 mm all linked at greater than 77% similarity. The smallest size interval was only loosely associated with the overall planktivore cluster. Major differences included the higher occurrence of nauplii and lower occurrence of zoea in the smaller fish. The largest size interval examined was significantly different from all other length groups except the 36 to 40 mm ( $r_s = .60, P < .05$ ) interval. However, many of the largest fish were collected in July, whereas the greatest number of smaller fish were collected in May and June, thus differences in both length and time may be confounded.

Feeding activity patterns of *H. jaguana* changed from both nocturnal and diurnal activity in smaller fish to strictly nocturnal or crepuscular in larger fish (Fig. 6). There were two peaks in feeding activity by fish 21 to 35 mm, the first between 0300 and 0600 h CST and the second between 1200 and 1500 h CST. Fish between 36 and 45 mm fed more during the nocturnal or crepuscular

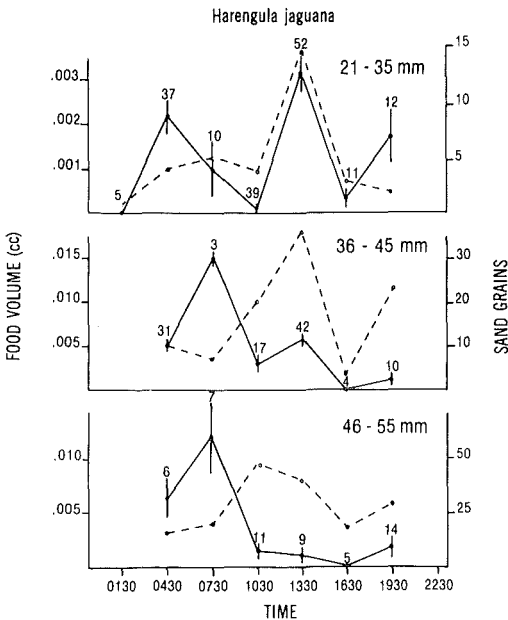


Figure 6. Mean stomach volume (solid line) and number of sand grains (broken line) per time period of *Harengula jaguana* for May through July 1976. Vertical lines are  $\pm 1$  SE.

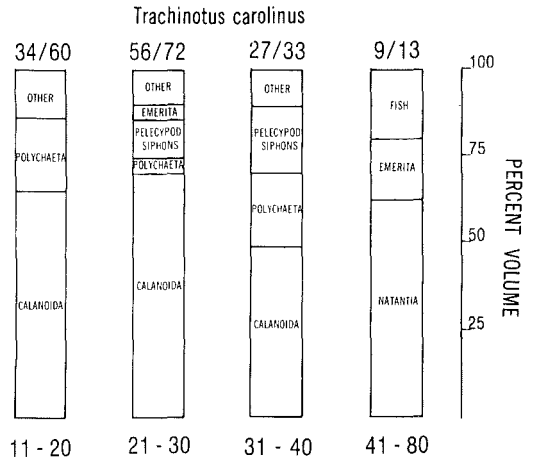


Figure 7. Percent volume of the major food items from *Trachinotus carolinus* stomachs collected from the surf zone of Horn Island during May and June 1976. Upper number = N; lower numbers = SL (mm).

hours, although there was a secondary peak during midday. Larger fish (46 to 55 mm) exhibited only nocturnal or crepuscular feeding as stomach content volume declined steadily after sunrise. The greatest number of sand grains appeared in stomachs of fish during the day coincident with the period of active diurnal feeding among smaller fish.

**Trachinotus carolinus**

Juvenile *T. carolinus* fed primarily on calanoid copepods (Fig. 7). In addition to utilizing a pelagic food source, young pompano also fed on benthic organisms such as polychaetes and the mole crab, *Emerita*. Calanoid copepods were less important to fish over 30 mm and did not occur in the few fish examined over 41 mm. In fish 31 to 40 mm polychaetes and *Donax* siphons comprised a major portion of the ration in addition to copepods. In the few stomachs examined from fish longer than 41 mm, small shrimp were most abundant. In addition, small fish and *Emerita* were also present in the diet of the larger fish. The dietary shift between the smaller (< 21 mm) and larger (> 40 mm) fish is reflected in the rank correlation analysis of percent occurrence

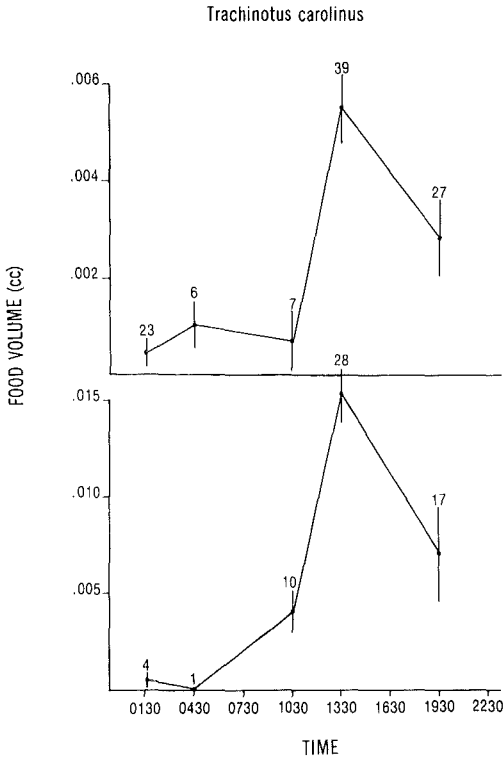


Figure 8. Mean stomach volume per time period ( $\pm 1$  SE) of *Trachinotus carolinus* 11 - 25 mm SL (upper) and 26 - 35 mm (lower) for May and June 1976.

of prey and the cluster analysis (Fig. 3). Only the intermediate size intervals (21-30 and 31-40) were significantly correlated ( $r_s = .91, P < .05$ ), and these linked at 100% similarity based on the presence/absence of prey. The smallest and largest size intervals showed low similarity to all other groups.

Foraging activity of juvenile pompano was primarily diurnal. Stomach volume rose in the late morning and peaked in the early afternoon (Fig. 8). Very few sand grains were present in the alimentary tract. Although mean stomach volume was much higher in fish between 26 and 35 mm, than 11 and 25 mm, the patterns were similar. Length intervals for comparison were selected by volume similarity as determined by Duncan's multiple range test.

Although both *H. jaguana* and smaller *T. carolinus* fed predominantly

upon calanoid copepods, the latter consumed much larger individuals (Fig. 9). There was no difference in mean prey volume between juvenile *T. carolinus* of 11 and 30 mm, although prey size increased for fish over 30 mm. Prey volume of *H. jaguana* increased slightly with fish length.

**Anchoa hepsetus**

*Anchoa hepsetus* fed primarily on

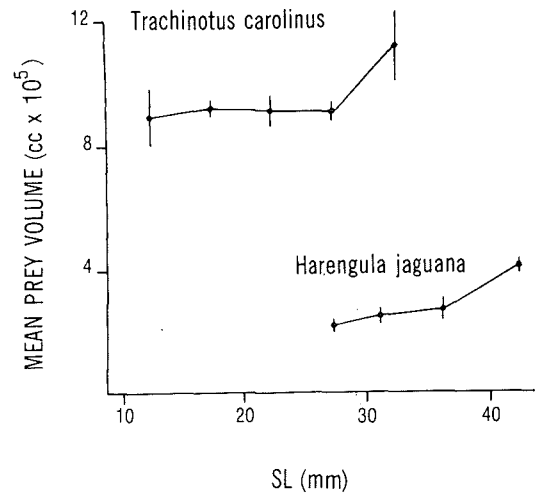


Figure 9. Average volume of calanoid copepods ( $\pm 1$  SE) consumed per length group by *Harengula jaguana* and *Trachinotus carolinus* collected from Horn Island.

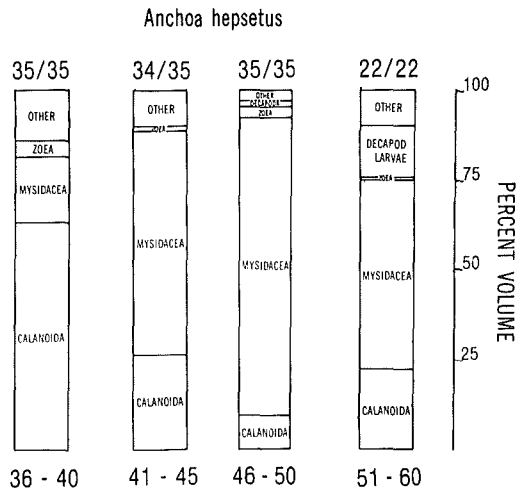


Figure 10. Percent volume of the major food items from *Anchoa hepsetus* stomachs collected from the surf zone of Horn Island in May 1976. Upper number = N; lower numbers = SL (mm).

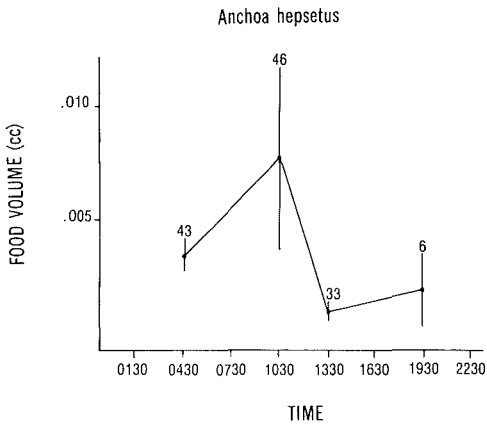


Figure 11. Mean stomach volume per time period ( $\pm 1$  SE) of juvenile and sub-adult *Anchoa hepsetus* collected in May 1976.

calanoid copepods and mysids (Fig. 10). Calanoids were volumetrically important for fish between 36 and 40 mm while mysids were utilized more by larger individuals. Despite volumetric differences, the frequency of occurrence of food items within all length groups were not significantly different. Spearman rank correlation coefficients ranged from  $r_s = .78$  ( $P < .05$ ) for the length groups 41 to 45 mm with 51 to 60 mm, to  $r_s = .86$  ( $P < .05$ ) for the length groups 46 to 50 mm with 51 to 60 mm. Cluster analysis of *A. hepsetus* supports the diet similarity between size groups (Fig. 3). All intervals linked at greater than 82% similarity.

*Anchoa hepsetus* fed primarily during early to mid-morning (Fig. 11). Stomachs from fish collected between 0300 and 0600 were dominated by calanoid copepods. Fish captured during the late morning exhibited a high but variable quantity of food items, consisting primarily of mysids.

***Anchoa lyolepis***

*Anchoa lyolepis* used in stomach analysis were obtained in both May and September 1976. May fish were juveniles ranging between 31 and 45 mm. Only

seven individuals during this month were collected outside the 0900 to 1200 h CST interval and digested organic matter and large numbers of unicellular diatoms were characteristic of the stomachs. Those fish collected in September had a somewhat greater length range and were captured during most time intervals. The majority of identifiable prey items were recovered from stomachs of fish collected in September.

Fish between 26 and 30 mm fed primarily on mysids (Fig. 12). However, only 46.2% of the individuals examined had food in their stomachs. Stomach

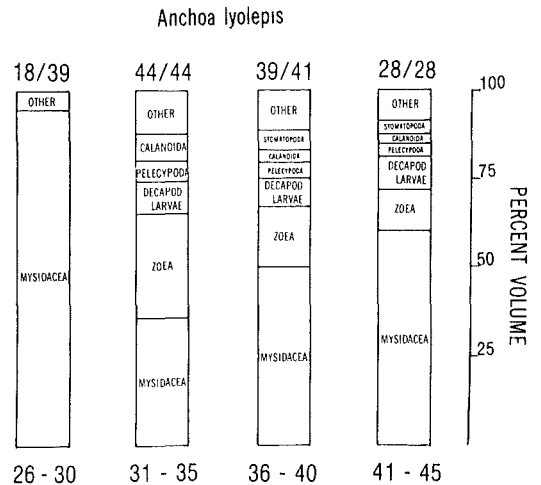


Figure 12. Percent volume of the major food items from *Anchoa lyolepis* stomachs collected from the surf zone of Horn Island in May and September 1976. Upper number = N; lower numbers = SL (mm).

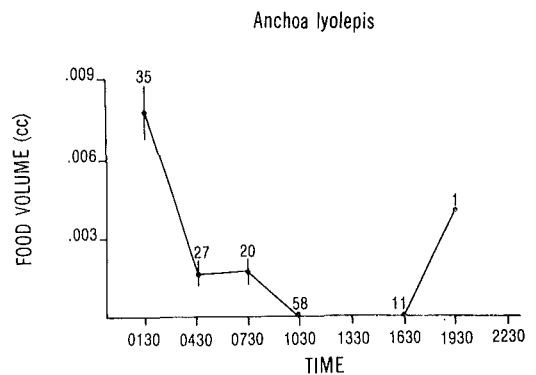


Figure 13. Mean stomach volume per time period ( $\pm 1$  SE) for *Anchoa lyolepis* collected in May and September 1976.



contents of fish 26 to 30 mm were significantly different from the remaining length groups, with coefficients of  $r_s = .54$  ( $P > .05$ ),  $r_s = .13$  ( $P > .05$ ), and  $r_s = -.21$  ( $P > .05$ ) for comparisons with the next three successive 5 mm intervals. Diets of all length groups over 30 mm were correlated, with the lowest coefficient being  $r_s = .9$  ( $P < .05$ ) for the 31 to 55 mm with 41 to 45 mm length groups. Cluster analysis (Fig. 3) also indicates the high diet similarity of *A. lyolepis* over 30 mm. Major prey of fish between 31 and 45 mm were mysids. Zoea also made up a significant portion of the ration while calanoid copepods never comprised over 8.0% of the volume of any length group.

Feeding activity of *Anchoa lyolepis* was exclusively nocturnal. The greatest food volume was between 0000 and 0300 h (Fig. 13) and ration volume decreased rapidly with the onset of daylight. Feeding activity resumed in the evening.

## DISCUSSION

The numerically dominant spring-summer fishes of the Horn Island surf zone are primarily planktivores, with *Harengula jaguana*, *Anchoa hepsetus*, and *A. lyolepis* utilizing calanoid copepods, mysids, and various decapod larvae. Juvenile *Trachinotus carolinus* (< 40 mm) and the smallest size group of *Menticirrhus littoralis* (11-20 mm) also were planktivores, feeding on calanoid copepods and mysids, respectively. Thus, only *M. littoralis* larger than 20 mm, and to a lesser extent *T. carolinus*, fed on benthic prey. McFarland (1963) also found that the most abundant fishes from the Mustang Island, Texas, surf zone were planktivores. Planktivorous fishes were numerically important surf zone inhabitants on a northern Florida beach (Naughton and Saloman 1978) and a mid-Florida Gulf beach (Springer and

Woodburn 1960) as well.

*Menticirrhus littoralis*, the numerically dominant benthic predator on Horn Island, filled the same role on Mustang Island, Texas (McFarland 1963). In both cases the primary prey was the pelecypod *Donax*. Saloman and Naughton (1978) reported that the invertebrate fauna of the St. Andrews, Florida, surf zone was 44% *Donax* by number and that 99% of the benthic macroinvertebrate fauna was comprised of four species, *D. texasianus*, a polychaete (*Scolecopsis squamata*), an amphipod (*Haustorius* sp.), and *Emerita talpoida*. This matches closely with benthic prey of Horn Island fishes which included *E. talpoida* and polychaetes in addition to *Donax*. Leber (1982) also found that *Emerita* and *Donax* composed 98% of the macroinvertebrates on a North Carolina surf zone.

Armitage and Alevizon (1980) found that juvenile pompano from a Florida surf zone consumed primarily *Donax* and *Emerita*, Bellinger and Avault (1971) reported that polychaetes, bivalves, amphipods and penaeid shrimp were important food items for juvenile pompano in Louisiana, while Finucane (1969) reported amphipods, dipterans and whole *Donax* from juvenile pompano in Florida. In contrast, our study indicates a greater use of calanoid copepods, and bivalve (primarily *Donax*) siphon tips, rather than the whole animal. While Armitage and Alevizon (1980) found that whole *Donax* were calorically less desirable than *Emerita*, it seems that *Donax* siphon tips would provide a higher energy yield per unit weight.

*Harengula jaguana* from the Horn Island surf zone utilized calanoid copepods to a much greater extent than reported for the same size classes by Carr and Adams (1973). Carr and Adams found that small *H. pensacolae* (=

*jaguana*) fed primarily on veligers and crab megalops, although Odum (1971) reported copepods as well as zoea and nauplii as being important to 16-30 mm fish.

Diets of all species examined exhibited qualitative changes with increases in length. The greatest variability in diet occurred with *M. littoralis* and *T. carolinus*. Modde and Ross (1981) reported that these two species were closely associated with the surf zone habitat and did not undergo daily off-shore movements as did *H. jaguana*, *A. hepsetus*, and *A. lyolepis*. Greater diversity in prey selection within length groups of fishes spending much of their time within the surf zone habitat may represent a means of reducing the probability of intraspecific competition. The potential of interspecific competition between *M. littoralis* and *T. carolinus* is reduced by differences in the size of prey eaten and by temporal separation in feeding activity. Temporal partitioning of resources, which occurred also for *A. lyolepis* and *A. hepsetus*, may be a viable strategy since wave activity and longshore current movement would likely provide rapid renewal of the zooplankton resource.

Since fish size influences prey utilization we hypothesized that fish size, especially among closely related species, would perhaps be a better indicator of prey type than fish kind. However, when food habits for size groups of all species are compared by clustering prey similarity this was not true (Fig. 3). Length groups of four of the five species clustered first intraspecifically, with the exception of the smallest size intervals of *H. jaguana*, *A. lyolepis*, and *M. littoralis*. *Anchoa hepsetus* and *A. lyolepis* showed the strongest interspecific relationship, linking at approximately 75% similarity. The

three primarily planktivorous clupeoid fishes formed a large cluster linking at the 40% level. Perciform fishes formed a second, less defined, cluster. Only *T. carolinus* did not link intraspecifically; however, this species, more so than the others, was varied in prey type utilizing both planktonic and benthic organisms.

The suggestion of partitioning of food resources by prey kind and size, and the temporal separation of food and habitat use shown by these species is surprising in view of the apparent physical harshness, low spatial heterogeneity, and the temporary use of the habitat. For instance, Matthews and Hill (1980) concluded that habitat partitioning of fishes was less developed in harsh than in environmentally stable streams, and Leviten and Kohn (1980) found that resource partitioning was not important in the gastropod *Conus* inhabiting physically stressed tropical intertidal areas. Whether the patterns shown by the surf zone fishes are persistent responses governed by biotic interaction, or whether they reflect individual or regional variation, or responses to physical factors (sensu Wiens 1977) will require long term studies of trophic and temporal interactions over more surf zone systems.

Three of the five species, *Anchoa lyolepis*, *Harengula jaguana* and *Menticirrhus littoralis* fed at least partially at night, while *Trachinotus carolinus* and *Anchoa hepsetus* were primarily diurnal predators. To find if the surf zone habitat represented an important foraging area we compared diel feeding patterns of the fishes with diel abundance data for the same species from the Horn Island surf zone (Modde and Ross 1981).

The greatest density of *A. lyolepis* and *H. jaguana* in the Horn Island surf zone occurred between 0300 — 0600 h CST. Thus, *A. lyolepis* fed most actively

(cf. Fig. 13) when its density in the surf zone was low. If we assume that feeding periodicity of fish from within the surf zone (where we took all our samples) parallels the feeding pattern offshore, then it follows that most of the *A. lyolepis* population feeds outside of the surf zone area. *Anchoa lyolepis* may concentrate in the shallow surf zone after its nocturnal feeding bout, perhaps as a predator avoidance response.

In contrast, high densities of *H. jaguana* in the surf zone largely coincided with peak feeding (cf. Fig. 6). Thus, if the above assumption holds, the surf zone represents an important feeding area for this species.

Peak abundance of *A. hepsetus* in the surf zone was 0600 - 0900 h CST. Feeding activity (cf. Fig. 11) was highest at the same time, so that the surf zone may also be an important foraging area for this species.

*Trachinotus carolinus* and *M. littoralis* tended to be more abundant in diurnal surf zone samples (Modde and Ross 1981). Feeding activity of *Trachinotus* was greatest in mid-morning to afternoon, while *M. littoralis* fed in the late afternoon and night. The surf zone likely provides an important feeding area for these species, although *M. littoralis* may tend to feed further offshore after dark.

Foraging patterns within length groups of *H. jaguana* changed ontogenetically. Small juveniles fed both diurnally and nocturnally, but switched to primarily nocturnal activity with increased length. Starck and Davis (1966) found that adult *H. jaguana* fed nocturnally. Because most larval fishes are diurnal feeders (Braum 1967), particularly clupeoids (Blaxter 1965; 1966; Arthur 1976), it seems that juvenile *H. jaguana* first reaching the surf zone habitat may be undergoing a transition in foraging

behavior from diurnal to nocturnal activity. A shift in temporal feeding activity with age has been reported for other fishes in both marine and freshwater habitats (Hobson 1968; Hobson and Chess 1976; Helfman 1978; Hobson *et al.* 1981). In species with ontogenetic shifts in foraging, Hobson *et al.* (1981) found that small diurnal predators of zooplankton generally changed with age to nocturnal feeding on larger prey. Manteifel *et al.* (1978) documented a shift from diurnal feeding of *Clupea harengus* larvae to nocturnal feeding of adults. They suggested that predation pressure may be important in this shift. Helfman (1978) also concluded that ontogenetic shifts in foraging may be due to avoidance of intraspecific competition or differential predation pressure on age groups of fish. If larger zooplankton are more abundant at night (as demonstrated by Hobson and Chess 1976 in the eastern Pacific), then the day — night ontogenetic shift in *H. jaguana* may be mediated in part by the increased foraging efficiency gained by utilizing the nocturnally available larger prey.

In summary, the surf zone of Horn Island, Mississippi provides trophic and spatial resources to certain juvenile fishes. Our data suggest that *M. littoralis* and *T. carolinus* utilized this habitat as a nursery in exploiting both resources. *Anchoa hepsetus* and *H. jaguana* also utilized both resources, while *A. lyolepis*, the most abundant species collected by Modde and Ross (1981) perhaps used the area primarily as a refuge and not as a feeding area.

#### ACKNOWLEDGMENTS

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#### LITERATURE CITED

- Armitage, T. M. and W. S. Alevizon. 1980. The diet of the Florida pompano (*Trachinotus carolinus*) along the east coast of central Florida. *Florida Sci.* 43:19-26.
- Arthur, D. K. 1976. Food and feeding of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax* and *Trachurus symmetricus*. *Fish. Bull.* 74:517-530.
- Bellinger, J. W. and J. W. Avault, Jr. 1971. Food habits of juvenile pompano, *Trachinotus carolinus*, in Louisiana. *Trans. Amer. Fish. Soc.* 100:486-494.
- Blaxter, J. H. S. 1965. The feeding of herring larvae and their ecology in relation to feeding. *Calif. Coop. Ocean. Fish. Invest.* 10:79-88.
- \_\_\_\_\_. 1966. The effect of light intensity on the feeding ecology of herring, p. 393-409. *In*: R. Bainbridge, G. C. Evans and O. Rackham (eds.). *Light as an ecological factor*. *Br. Ecol. Soc. Symp.* 6.
- Braum, E. 1967. The survival of fish larvae with reference to their feeding behavior and the food supply, p. 113-141. *In*: S. D. Gerking, (ed.). *The biological basis of freshwater fish production*. Blackwell Sci. Publ., Oxford.
- Carr, W. E. S. and C. A. Adams. 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. *Trans. Amer. Fish. Soc.* 102:511-540.
- Finucane, J. H. 1969. Ecology of the pompano (*Trachinotus carolinus*) and the permit (*T. falcatus*) in Florida. *Trans. Am. Fish. Soc.* 98:478-486.
- Franks, J. S. 1970. An investigation of the fish population within the inland waters of Horn Island, Mississippi, a barrier island in the Gulf of Mexico. *Gulf Res. Rep.* 3:3-104.
- Gunter, G. 1958. Population studies of the shallow water fishes of an outer beach in south Texas. *Publ. Inst. Mar. Sci. Univ. Texas* 5:186-193.
- Helfman, G. S. 1978. Patterns of community structure in fishes: summary and overview. *Env. Biol. Fish.* 3:129-148.
- Hellawell, J. M. and R. Abel. 1971. A rapid volumetric method for the analysis of the food of fishes. *J. Fish Biol.* 3:29-37.
- Hobson, E. S. 1968. Predatory behavior of some shore fishes in the Gulf of California. *U.S. Fish and Wildl. Serv. Res. Rep.* 73. 92p.
- \_\_\_\_\_, and J. R. Chess. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. *Fish. Bull.* 74:567-598.
- \_\_\_\_\_, W. N. McFarland and J.R. Chess. 1981. Crepuscular and nocturnal activities of Californian near-shore fishes, with consideration of their scotopic visual pigments and the photic environment. *Fish. Bull.* 79:1-30.
- Leber, K. M. 1982. Seasonality of macro-invertebrates on a temperate, high wave energy sandy beach. *Bull. Mar.*

- Sci. 32:86-98.
- Leviton, P. J. and A. J. Kohn. 1980. Microhabitat resource use, activity patterns, and episodic catastrophe: *Conus* on tropical intertidal reef rock benches. Ecol. Monogr. 50:55-75.
- Manteifel, B. P., I. I. Girsu and D. S. Paulov. 1978. On rhythms of fish behavior, p. 215-224. *In*: J.E. Thorpe, (ed.). Rhythmic activity of fishes. Academic Press, New York.
- Matthews, W. J. and L. G. Hill. 1980. Habitat partitioning in the fish community of a southwestern river. Southwest. Nat. 25:51-66.
- McFarland, W. N. 1963. Seasonal change in the number and the biomass of fishes from the surf at Mustang Island, Texas. Publ. Inst. Mar. Sci. Univ. Texas 9:91-105.
- McMichael, R., Jr. and S. T. Ross. 1980. Utilization of the surf zone habitat of Horn Island, a barrier island off the Mississippi coast, by the *Menticirrhus* complex (Pisces, Sciaenidae). ASB Bull. 27:50.
- Modde, T. 1980. Growth and residency of juvenile fishes within a surf zone habitat in the Gulf of Mexico. Gulf Res. Rep. 6:377-385.
- \_\_\_\_\_. and S. T. Ross. 1981. Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico. Fish. Bull. 78:911-922.
- Naughton, S. P. and C. H. Saloman. 1978. Fishes of the nearshore zone of St. Andrew Bay, Florida, and adjacent coast. Northeast Gulf Sci. 2:43-55.
- Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner and D. H. Bent. 1975. Statistical package for the social sciences. 2nd ed. McGraw-Hill Book Co.
- Odum, H. T. and B. J. Copeland. 1974. A functional classification of the coastal ecological systems, p. 5-84. *In*: H. T. Odum, B. J. Copeland and E. A. MacMahon, (eds.). Coastal ecological systems of the United States, Vo. 1. The Conservation Foundation, Washington, D.C.
- Odum, W. E. 1971. Pathways of energy flow in a south Florida estuary. Ph.D. Dissertation, Univ. Miami (Sea Grant Tech. Bull. No. 7). 162 p.
- Ross, S. T. 1974. Resource partitioning in searobins (Pisces: Triglidae) on the west Florida shelf. Ph.D. Dissertation, Univ. South Florida, Tampa. 205 p.
- Saloman, C. H. and S. P. Naughton. 1978. Benthic invertebrates inhabiting the swash zone of Panama City Beach, Florida. Northeast Gulf Sci. 2:65-72.
- Sneath, P. H. A. and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco. 573 p.
- Springer, V. G. and K. D. Woodburn. 1960. An ecological study of the fishes of the Tampa Bay Area. Fla. State Board Conser., Mar. Lab. Prof. Pap. Ser., No. 1. 104 p.
- Starck, W. A., II, and W. P. Davis. 1966. Night habits of fishes of Alligator Reef, Florida. Ichthyologia 38:313-356.
- Wiens, J. A. 1977. On competition and variable environments. Amer. Sci. 65:590-597.