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Robert H. McMichael Jr.
University of Southern Mississippi

Stephen T. Ross
University of Southern Mississippi

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THE RELATIVE ABUNDANCE AND FEEDING HABITS OF JUVENILE KINGFISH (SCIAENIDAE: *Menticirrhus*) IN A GULF OF MEXICO SURF ZONE

Robert H. McMichael, Jr.[1] and Stephen T. Ross[2]

Department of Biological Sciences
University of Southern Mississippi
Hattiesburg, MS 39406-5018

ABSTRACT: We describe seasonal and diel occurrence patterns, density, dietary progressions, and trophic relationships of *Menticirrhus littoralis, M. americanus* and *M. saxatilis* collected from the Horn Island, Mississippi, surf zone. *Menticirrhus littoralis* was the most abundant species (62.7%), followed by *M. americanus* (21.8%) and *M. saxatilis* (15.5%). Densities were highest during spring and summer and decreased markedly during the winter. Species showed diel changes in abundance, with abundance increasing during dusk and dawn for *M. littoralis,* and during the day for *M. americanus* and *M. saxatilis.* All three species showed ontogenetic progressions in diet, with siphon tips from *Donax* spp., cumaceans and mysids being most important to smaller (<80 mm SL) *M. littoralis* and *M. americanus;* cumaceans, mysids and amphipods were most important to smaller *M. saxatilis.* Larger individuals of all three species fed more on whole *Donax,* polychaetes, *Emerita talpoida,* brachyurans, and fishes. Both intra- and interspecific dietary overlap was greatest for the smaller size groups of juveniles and declined with growth. Dietary overlap between 20 mm size classes was greatest for intra- compared to interspecific comparisons.

The *Menticirrhus* complex of the northern Gulf of Mexico consists of three species, *M. americanus* (southern kingfish), *M. saxatilis* (northern kingfish), and *M. littoralis* (gulf kingfish). Juveniles of these species occur in various inshore marine habitats (Springer and Woodburn 1960; Irwin 1970; Crowe 1984) and may co-occur in surf zones (Naughton and Saloman 1978; Modde and Ross 1981). Juvenile gulf kingfish are strongly associated with surf zones of moderate to high salinities (Modde and Ross 1981), and adults apparently remain in relatively shallow water (<36 m) near such areas (Gunter 1945; Irwin 1970; Christmas and Waller 1973; Darovec 1983). Juvenile northern kingfish also occur primarily in outer surf zone habitats (Irwin 1970; Johnson 1978), although various studies have reported them from estuaries as well (Bearden 1963; Schaefer 1965). Adult northern kingfish move into deeper water with increasing age (Schaefer 1965; Irwin 1970). Southern kingfish are less restricted to surf zones as juveniles, often occurring in low salinity estuaries. Adult southern kingfish are thought to leave the inner coastal and surf zone areas for deeper, more saline water, especially with the onset of cold weather (Bearden 1963; Irwin 1970; Crowe 1984). Recently, Smith and Wenner (1985) found that southern kingfish from the South Atlantic Bight moved south during the winter, rather than simply moving into deeper water at the same latitude.

Surf zones in the Gulf of Mexico are important as nursery areas for many fish species (Modde and Ross 1981; Ross 1983; Ross *et al.* 1987b), even though such areas are physically dynamic. Modde and Ross (1983) found that certain species from the Horn Island surf

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[1] Present Address: Florida Department of Natural Resources, Bureau of Marine Research, 100 Eighth Ave., S.E., St. Petersburg, FL 33701-5095.
[2] Authorship decided by a coin toss.

zone showed partitioning of food resources by prey kind and size, as well as through temporal separation of food and habitat use. Such "resource partitioning" may be due to coevolution of surf zone species, but may also be due to historical or environmental effects (Wiens 1977; 1984; James *et al.* 1984; Ross *et al.* 1987a). Thus, while it is generally not possible to understand causation from observational field studies (e.g. Connor and Simberloff 1986), it is important to document patterns of resource use so that there is a basis for formulating testable hypotheses regarding the underlying mechanisms (Ross 1986).

Due to the increasing habitat divergence associated with growth, the early juvenile stage is the period of greatest potential ecological overlap of the three kingfish species in the northern Gulf of Mexico. However, most ecological studies of *Menticirrhus* have either emphasized only late juvenile to adult forms (e.g. Bearden 1963), or have only considered a single species (e.g. Schaefer 1965; Crowe 1984). As recently summarized by Ross (1986), an understanding of resource requirements and interactions within a taxocene ideally requires an examination of all life history stages. Our purpose in this paper is to expand the knowledge of resource differences of these species by examining resource use of the co-occurring juvenile forms. Specifically, we describe seasonal and diel occurrence patterns, densities, trophic relationships and dietary progressions.

METHODS AND MATERIALS

The study sites were in the surf zone on the south shore of Horn Island, Mississippi. Horn Island lies approximately 14 km offshore and is 19 km long by no more than 1.2 km wide. The center of the island is located at 30°14'N, 88°40'W. The Horn Island surf zone is characterized by a sand substratum, moderate wave activity and no rooted vegetation.

We sampled monthly from March, 1978 through September, 1979 at Stations 1 and 4 of Modde and Ross (1981). The April, 1978 and March, 1979 sampling periods were omitted due to adverse weather. We made diel collections over a 24 h period in July, August and October, 1978, and April, May and June, 1979. All other collections were between 0900 and 1600 CST. During the day we took two samples at each station and time period; at night we made only one sample per time period at a single station.

We used three types of sampling gear; 1) A 9.1 x 1.8 m, 3.2mm bar mesh bag seine — used from March, 1978 through June, 1978 and periodically thereafter; 2) A 50 x 1.8m, 3.2mm bar mesh, block seine, with a $1.83 m^2$ bag located 7.6 m from one end — used from July, 1978 through September, 1979; and 3) An 18m experimental gill net — used periodically during the study to collect larger fishes. The 50 m block seine was set around poles to enclose a $300 m^2$ area. Procedures for using this net are described in Ross *et al.* (1987b).

Fishes were fixed in 10% formalin and larger specimens were injected intraperitoneally to halt digestion. In the laboratory, specimens were identified, weighed (to the nearest 0.1 g), and grouped into 20 mm standard length (SL) intervals. For food analyses, the portion of the alimentary tract between the esophagus and the pylorus, hereafter called the stomach, was removed. All contents were identified to the lowest taxonomic level possible. The fullness of each stomach was estimated based on a subjective scale from 0 (empty) to 5 (full).

Diets were described by percent occurrence (F), total number (N) and total volume (V) of each prey item. These methods have been reviewed by Hynes (1950), Windell (1971) and Hyslop (1980). Prey volume was measured by a displacement technique, or by a squash technique (Hellawell and Abel 1971; Ross 1974) when prey volume was visually estimated as $<.05$ cm^3. Specimens with empty stomachs were not used in computing measures of dietary importance of prey kinds.

As a criterion for sample size in food habit analyses, we plotted cumulative new prey taxa against cumulative stomachs examined. A minimal sample size, sufficient for description of prey taxa, is indicated when the curve reaches a horizontal asymptote. When all sizes were combined approximately 35 gulf kingfish (excluding fish with empty stomachs), and 15 southern and northern kingfish were required to meet our criterion. Because adequate sample size changes as the diet varies, or as the size distribution of the predators changes, we tested each size class where comparisons were made. All dietary comparisons met our criterion for adequate sample size unless so specified.

Comparisons of food habits between species were made using Schoener's (1968) index of proportional overlap based on mean food volume, following recommendations of Wallace (1981) and Linton *et al.* (1981). The index ranges from 0 (no overlap) to 1 (total overlap). While there is not a simple statistical test of what constitutes a significant value, we followed current practice (e.g. Galat and Vucinich 1983) in considering overlap index values > 0.60 to indicate substantial overlap. Use of mean prey volume lessens the bias which results when a few individuals consume very large prey items (Mathur 1977; Wallace 1981). Because of the effect of small samples on the reliability of overlap measures (Wallace and Ramsey 1983), we grouped fishes into 20 mm SL intervals to retain sufficient sample sizes, while still keeping size groups fairly homogeneous.

RESULTS

Seasonal Occurrence

During the 17 month study period we collected 1,192 kingfish. *Menticirrhus littoralis* was the most abundant of the three species, comprising 62.7% of the kingfish catch by number, followed by *M. americanus* (21.8%) and *M. saxatilis* (15.5%). *Menticirrhus littoralis* also had the greatest frequency of occurrence in seine hauls (66.7%), again followed by *M. americanus* (29.7%) and *M. saxatilis* (24.6%).

Kingfish abundance varied seasonally, with the highest abundance from June through October (Fig. 1). Both frequency of occurrence and abundance decreased rapidly during the fall and winter months, and no kingfish were taken in December, 1978, or January, 1979.

Gulf kingfish first appeared in the surf zone as juveniles (10-20 mm) in May, 1979, and density increased during spring and early summer reaching 14 per $100 m^2$ by August, 1979. Specimens taken during summer collections ranged from 5-270 mm SL (fish >150 mm were captured primarily during qualitative sampling by the gill net), but most were less than 50 mm, with 21-30 mm fish making up 60%, 70% and 84% of the individuals collected for May, June, and July, 1979, respectively. Recruitment into the surf zone by 10-20 mm fish continued through

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the summer, with 5-10 mm fish occurring as late as October. The minimum size for the November, 1978, collection was 20 mm, suggesting that recruitment into the surf zone had ended.

Data for both *M. americanus* and *M. saxatilis* suggest that abundances were highest in June, 1979, preceding the peak density of gulf kingfish (Fig. 1). Southern kingfish first appeared in the surf as juveniles (10-20 mm) in May, 1978 and June 1979 and recruitment of early juveniles continued into October. Fish were between 10-225 mm, and all fish > 80 mm were collected with the gill net. Southern kingfish were not collected between November, 1978 and May, 1979. The recruitment period for northern kingfish was more limited with juvenile fish (10-20 mm) only being collected in May, 1978 and June-July, 1979. Northern kingfish ranged from 10-130 mm, with fish less than 50 mm most common.

Diel Occurrence Patterns

Diel estimates of density for *M. littoralis* in July and October, 1978, and

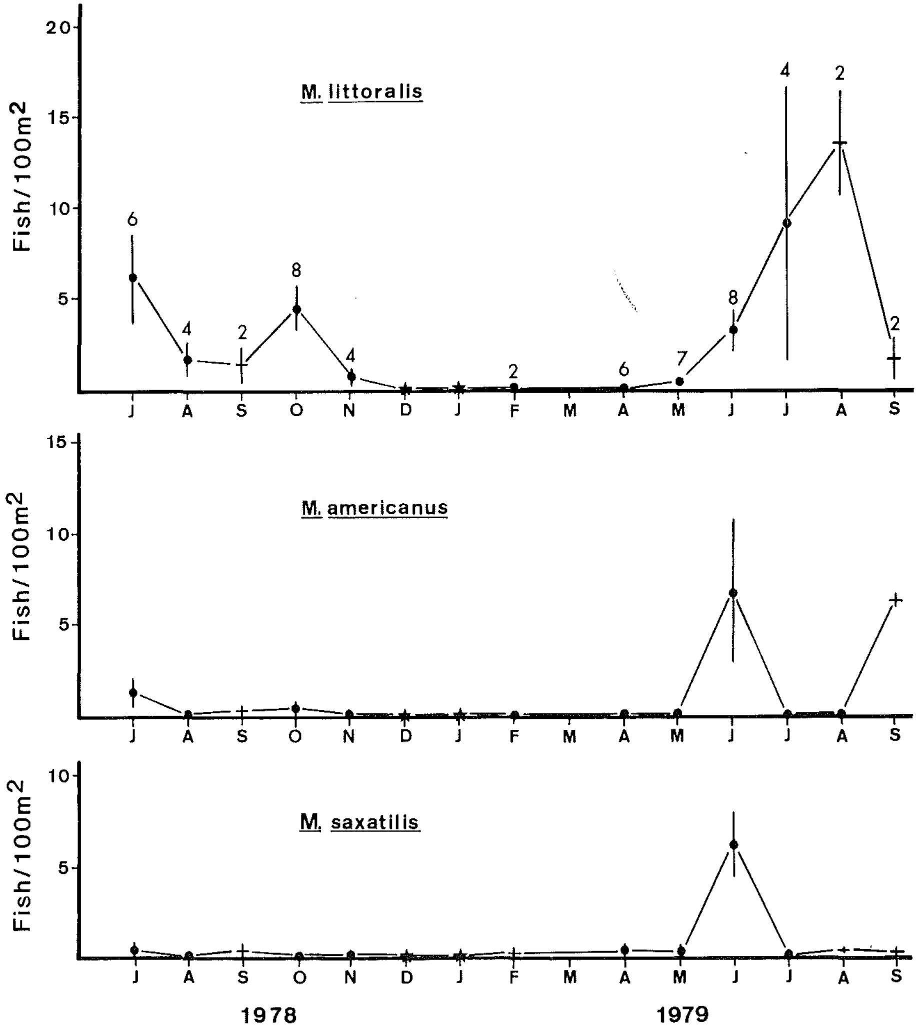

Figure 1. Mean number (+/− 1 SE) of *Menticirrhus littoralis, M. americanus* and *M. saxatilis* collected from Horn Island, July, 1978-Sept., 1979. Asterisks indicate the time period of samples taken with the 9.1 m net (catch = 0); all other samples were taken with the 50 m net. For dates with only two samples, the vertical line is the range, the horizontal line the midpoint. Number above the ranges are seine hauls.

Table 1. Percent occurrence, number and volume of prey organisms of *Menticirrhus littoralis* collected between March, 1978 and June, 1979 (N = 423).

PREY CATEGORY	% OCCURRENCE	% NUMBER	% VOLUME
Pelecypoda (siphon tubes)	50.7	64.00	15.40
Polychaeta	34.7	7.90	17.90
Cumacea (*Oxyurostylis* sp.)	18.4	9.90	4.20
Emerita talpoida	16.3	3.10	19.70
Mysidacea (*Metamysidopsis* sp.)	9.7	5.60	3.30
Calanoidea	7.3	4.00	0.70
Pelecypoda (entire)	3.8	3.30	17.90
Brachyura (*Callinectes* sp.)	3.5	1.00	17.40
Gammaridea	2.8	0.50	0.60
Isopoda	2.6	0.40	0.40
Vegetation	0.9	0.10	0.30
Fishes	0.7	0.10	0.20
Caligoidea	0.5	0.10	0.03
Brachyuran megalops	0.5	0.10	0.03
Caprellidea	0.2	0.03	0.03
Unidentified material	—	—	0.90
Crustacean remains	—	—	0.30

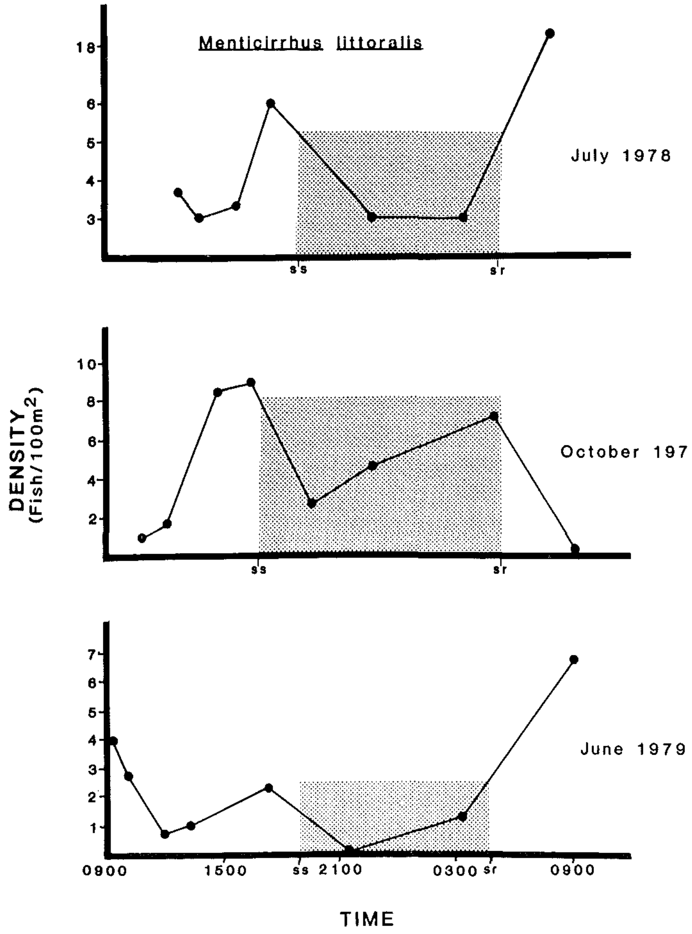

Figure 2. Densities of *Menticirrhus littoralis* collected at different times (CST) during July and October, 1978, and June, 1979. Shading indicates night samples; ss = sunset, sr = sunrise.

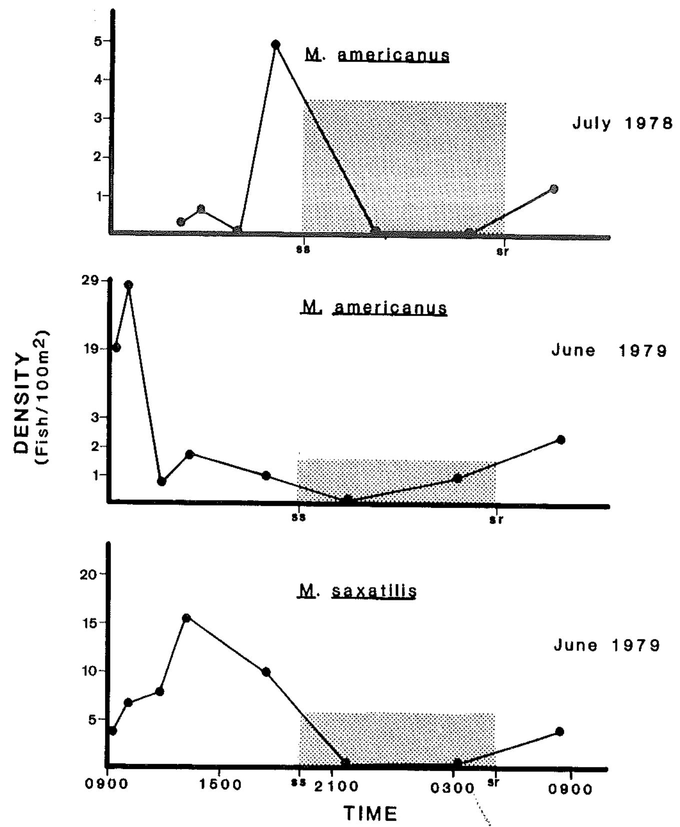

Figure 3. Densities of *Menticirrhus americanus* and *M. saxatilis* collected at different times (CST) during July, 1978 and June, 1979. Shading indicates night samples; ss = sunset, sr = sunrise.

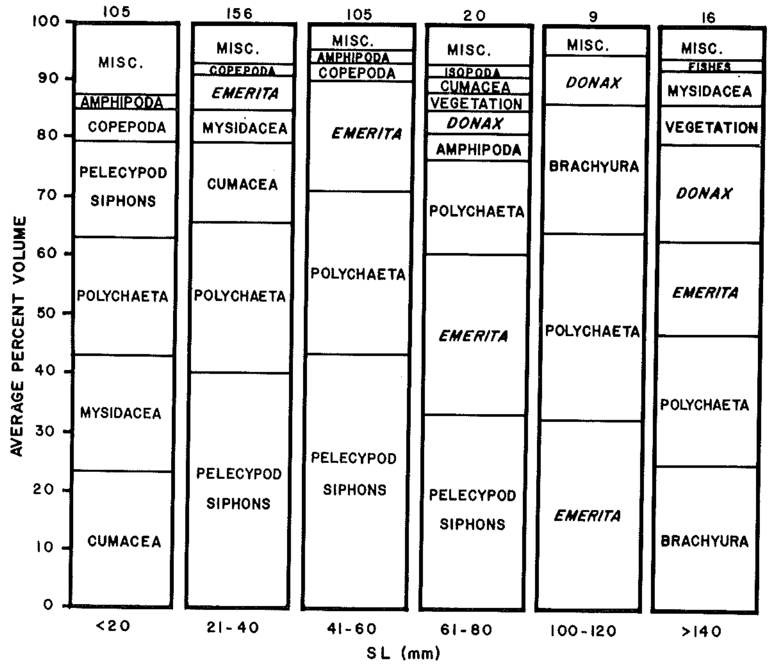

Figure 4. Average proportional volume of major (> 2% volume) food items from *Menticirrhus littoralis*, in 20 mm SL size classes, collected from the Horn Island surf, March, 1978- June, 1979. N = number of stomachs examined which contained food. Misc. = prey taxa contributing < 2% proportional volume.

June, 1979 (months of their greatest 24 h representation), showed significant increases during times of astronomical sunset and sunrise (+/− 1h; Mann-Whitney U-Test, $P<.05$) (Fig. 2). However, total densities did not differ between day and night, either when tested separately for each month or for the three diel sample months combined (Mann-Whitney U-Test, $P>.05$).

Numbers of *M. americanus* and *M. saxatilis* collected over any 24 h period were relatively low. However, diurnal densities for July, 1978 and June, 1979 (months of greatest 24 h representation of these species) significantly exceeded night densities for *M. americanus* (Mann-Whitney U-Test, $P<.05$), and approached significance for *M. saxatilis* (Mann-Whitney U-Test, $.1>P>.05$) (Fig. 3). Peak abundance of these species fell within our regular monthly sampling times so that monthly samples should be representative of maximal abundance.

Food Habits

Menticirrhus littoralis

Overall, pelecypod siphon tips (predominantly *Donax* spp.) were the most important prey on the basis of number and percent occurrence, and fifth in importance on the basis of volume (Table 1). Other important prey (on the basis of percent occurrence, number or volume) were polychaetes (primarily Nephtyidae), *Emerita talpoida* and cumaceans (*Oxyurostylis* sp.).

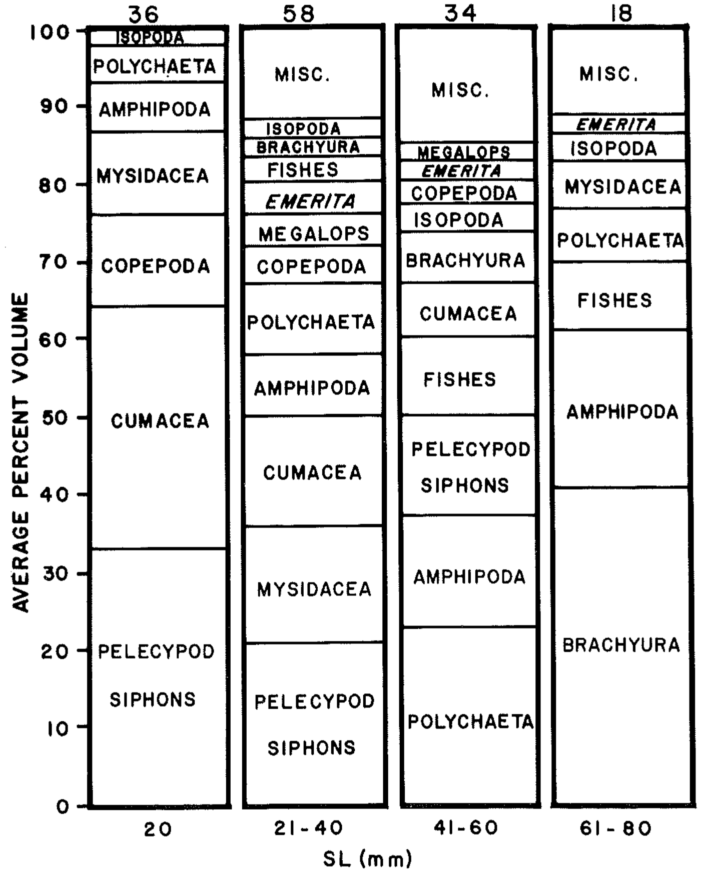

Figure 5. Average proportional volume of major (> 2% volume) food items from *Menticirrhus americanus*, in 20 mm SL size classes, collected from the Horn Island surf, March, 1978- June, 1979. See Fig. 4 for further information.

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Table 2. Overlap based on average proportional volume of prey items for 20 mm SL size classes of *Menticirrhus*. Sample sizes are shown in parentheses for each group which met our criterion of minimum sample size. L = *Menticirrhus littoralis;* A = *M. americanus;* S = *M. saxatilis.* 1 = <20 mm; 2 = 21-40 mm; 3 = 41-60 mm; 4 = 61-80 mm; 5 = 81-100 mm; 6 = 101-120 mm; 8 = >141 mm. Values ≥ 0.60 are underlined; long dashed lines undersore intraspecific comparisons.

	(105) L-1	(156) L-2	(105) L-3	(20) L-4	(9) L-6	(14) L-8	(36) A-1	(58) A-2	(34) A-3	(18) A-4	(68) S-3	(24) S-4	(15) S-5
L-2	.64	--											
L-3	.46	.77	--										
L-4	.45	.63	.74	--									
L-6	.24	.33	.51	.50	--								
L-8	.30	.39	.42	.45	.73	--							
A-1	.65	.61	.46	.48	.06	.11	--						
A-2	.68	.61	.43	.49	.18	.28	.64	--					
A-3	.52	.52	.44	.47	.35	.39	.36	.61	--				
A-4	.21	.20	.15	.23	.34	.47	.21	.42	.51	--			
S-3	.65	.40	.20	.30	.23	.33	.51	.61	.60	.53	--		
S-4	.44	.31	.12	.21	.21	.31	.33	.59	.49	.52	.68	--	
S-5	.36	.28	.35	.46	.54	.56	.23	.47	.43	.54	.54	.66	--

Gulf kingfish showed strong evidence of an ontogenetic dietary progression. A feeding transition occurred at about 60-80 mm SL, with smaller fish obtaining most of their prey volume from pelecypod siphons, polychaetes, cumaceans and mysids, and larger fish obtaining most of their prey volume from *Emerita talpoida,* polychaetes, brachyurans and whole pelecypods (*Donax* spp.) (Fig. 4). Polychaetes were volumetrically important prey over all size groups. Fragments of seagrass blades also were consumed by larger fish. The highest overlap between 20 mm SL size classes generally occurred among adjacent size groups, providing further evidence of dietary changes with increasing length (Table 2).

Menticirrhus americanus

Pelecypod siphon tips were important prey on the basis of percent occurrence and number, and ranked sixth in importance by volume (Table 3). However, unlike gulf kingfish, siphon tips occurred in less than one-third of the southern kingfish stomachs, reflecting the broader food spectrum of this species. Cumaceans, brachyurans, amphipods, polychaetes, mysids and fishes were also important prey taxa (on the basis of percent occurrence, number or volume).

An ontogenetic dietary progression is apparent with smaller southern kingfish (<41 mm) obtaining the largest food volume from pelecypod siphons, cumaceans, copepods and mysids (Fig. 5). Diets of fish between 21-60 mm were more varied, but showed a decline in the volumetric importance of siphon tips, cumaceans and mysids, and increased importance of polychaetes and amphipods. Larger fish (61-80 mm SL) obtained the bulk of their prey volume from brachyurans, amphipods, fishes and polychaetes. Dietary overlap was again highest between adjacent 20 mm SL size groups (Table 2).

Table 3. Percent occurrence, number and volume of prey organisms of *Menticirrhus americanus* collected between March, 1978 and June, 1979 (N = 147).

PREY CATEGORY	% OCCURRENCE	% NUMBER	% VOLUME
Pelecypoda (siphon tubes)	28.6	37.40	6.80
Cumacea (*Oxyurostylis* sp.)	24.5	19.20	4.70
Mysidacea (*Metamysidopsis* sp.)	16.3	5.40	7.90
Polychaeta	15.0	6.20	8.40
Brachyura (*Callinectes* sp.)	12.9	11.90	29.00
Gammaridea	12.9	4.00	13.80
Isopoda	8.2	2.80	3.00
Fishes	7.5	2.20	16.40
Calinoidea	6.8	7.20	1.10
Emerita talpoida	2.7	1.60	1.70
Brachyuran megalops	2.7	1.00	0.90
Caligoidea	2.7	1.00	0.70
Caprellidea	0.7	0.20	0.30
Unidentified material	—	—	4.40
Crustacean remains	—	—	1.10

Menticirrhus saxatilis

Cumaceans were the most important prey on the basis of percent occur-

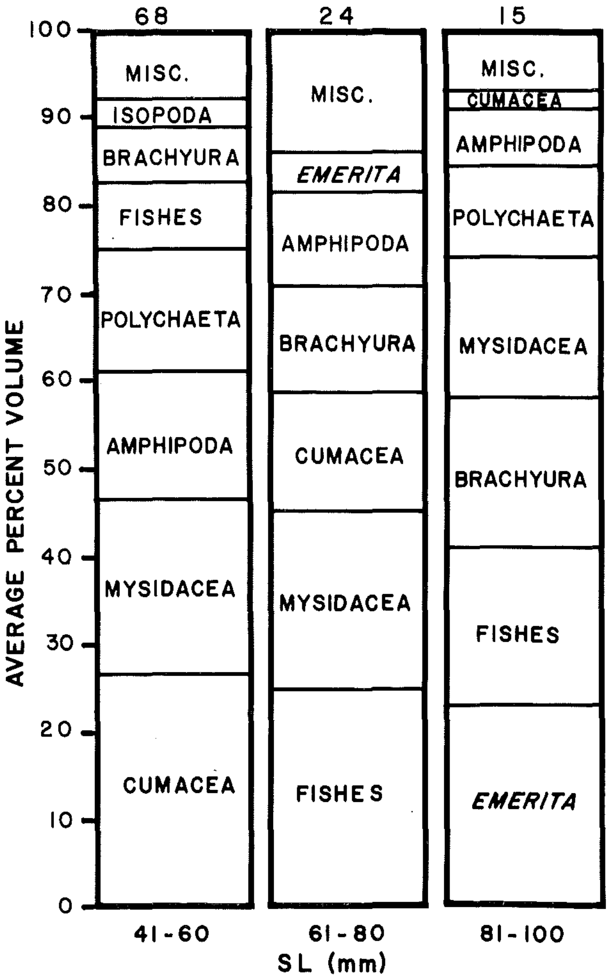

Figure 6. Average proportional volume of major (> 2% volume) food items from *Menticirrhus saxatilis,* in 20 mm SL size classes, collected from the Horn Island surf, March, 1978- June, 1979. See Fig. 4 for further information.

Table 4. Percent occurrence, number and volume of prey organisms of *Menticirrhus saxatilis* collected between March, 1978 and June, 1979 (N = 129).

PREY CATEGORY	% OCCURRENCE	% NUMBER	% VOLUME
Cumacea (*Oxyurostylis* sp.)	37.2	72.40	9.40
Mysidacea (*Metamysidopsis* sp.)	24.8	11.10	13.60
Pelecypoda (siphon tubes)	22.3	0.60	0.30
Polychaeta	20.9	4.40	31.10
Gammaridea	19.4	2.60	8.50
Fishes	17.8	2.10	18.50
Brachyura (*Callinectes* sp.)	16.3	3.80	9.40
Emerita talpoida	5.4	0.60	3.30
Isopoda	5.4	0.80	1.20
Brachyuran megalops	2.3	0.80	0.40
Calanoidea	1.6	0.80	0.20
Brachyuran zoea	0.8	0.10	0.10
Caligoidea	0.8	0.10	0.11
Unidentified material	—	—	3.50
Crustacean remains	—	—	0.60

rence and number, and ranked fourth in importance by volume (Table 4). Additional food items of importance (on the basis of percent occurrence, number or volume) were polychaetes, mysids, fishes (principally *Anchoa* spp.), gammarids and brachyurans. While pelecypod siphons occurred in 22% of the stomachs, their contribution to the diet in terms of number or volume was low. Few fish (N = 6) larger than 90 mm were captured which contained food, and the sample size was also insufficient to describe the diet of the smallest size class. Thus the diet description is biased towards intermediate sized fish.

While the data are limited, an ontogenetic dietary progression is apparent for fish between 40-100 mm (Fig. 6). The contribution of cumaceans and amphipods to dietary food volume decreased with fish size, while the contribution of fishes, brachyurans and *Emerita* increased. The limited data on intraspecific overlap indicates the greatest dietary similarity between adjacent 20 mm size groups.

Interspecific Overlap

Overall, dietary overlap was significantly greater for intraspecific ($\bar{x}$ = .51) than interspecific comparisons ($\bar{x}$ = .40; Mann-Whitney U-Test, $P < .05$). Thus, the three species showed some divergence in food habits. As occurred with intraspecific comparisons, the highest values of interspecific overlap were among the smaller size groups.

DISCUSSION

The three species of kingfish all are primarily spring and summer inhabitants of the Horn Island surf zone, a pattern typical for many other surf inhabiting species in the Gulf of Mexico (e.g. Ross 1983; Ross *et al.* 1987b). Peak abundance of the numerically dominant *Menticirrhus littoralis* followed peak abundances of *M. saxatilis* and *M. americanus*; however, the three species cooccur in the surf zone from June to October. The difference in timing of peak abundance of kingfish may be meaningful, although times of greatest abundances of kingfish in surf zones are variable for Gulf of Mexico and Atlantic studies (Table 5). Gulf kingfish tend to have their greatest abundance during July and August, while northern kingfish generally show earlier (primarily May-June) peaks, at least for

Table 5. Size range, month (interval from January-August) of earliest occurrence of the smallest size group, and the three months of greatest kingfish abundance for juvenile or adult kingfish in surf zones. Data are arranged by decreasing latitude of collection sites.

Menticirrhus littoralis

Size range (mm)	First Occurrence	Greatest Abundance	Location	Reference
83-145	January	July-September	Folly Beach, NC	Anderson *et al.* (1977)
69-112	March	July-September	exposed beaches, SC	Cupka (1972)
18-22	May	--	Sapelo Beach, GA	Dahlberg (1972)
10-20	May	August	Horn Island, MS	present study
11-15	August, 1975	August-October	Horn Island, MS	Modde (1980)
11-15	May, 1976	August-October	Horn Island, MS	Modde (1980)
16-20	April, 1977	June & September	Horn Island, MS	Modde (1980)
--	January	June-July	St. Andrews Bay, FL	Naughton & Saloman (1978)
--	February	July-September	Mustang Island, TX	Gunter (1945)
--	February	July-August	Mustang Island, TX	McFarland (1963)
9-25	June	July	Pinellas Co., FL	Springer and Woodburn (1960)
24-193	January	July-September	Pinellas Co., FL	Saloman and Naughton (1979)

Menticirrhus saxatilis

Size range (mm)	First Occurrence	Greatest Abundance	Location	Reference
13-26	July	July-August	Morris Cove, CN	Warfel & Merriman (1944)
220-410*	May	May-June	Fire Island, NY	Schaefer (1967)
33-50	June	June	Folly Beach, NC	Anderson *et al.* (1977)
18-88	June	June	exposed beaches, SC	Cupka (1972)
17-50	April	--	Sapelo Beach, GA	Dahlberg (1972)
10-20	May	June	Horn Island, MS	present study
6-10	April	--	Horn Island, MS	Modde (1980)
--	January	December	St. Andrews Bay, FL	Naughton & Saloman (1978)
--	March	June	Mustang Island, TX	McFarland (1963)
47-93	January	May-July	Pinellas Co., FL	Saloman & Naughton (1979)

Menticirrhus americanus

Size range (mm)	First Occurrence	Greatest Abundance	Location	Reference
24	June	--	exposed beaches, SC	Cupka (1972)
11-15	May	May-July	Sapelo Beach, GA	Dahlberg (1972)
10-20	May	June	Horn Island, MS	present study
--	July	August-October	St. Andrews, Bay, FL	Naughton & Saloman (1978)
--	July	July	Mustang Island, TX	Gunter (1945)
--	March	May	Mustang Island, TX	McFarland (1963)
25-45	July	July, August	Pinellas Co., FL	Springer and Woodburn (1960)
--	June	June-July	Pinellas Co., FL	Saloman & Naughton (1979)

*fork length

more southern localities. Studies of southern kingfish indicate peak densities between May and August, dates generally overlapping with gulf kingfish. Modde and Ross (1981) found that water temperature was the dominant parameter affecting the frequency of gulf kingfish in the surf zone, so differences between the three species, if real, might reflect differing temperature preferences.

The spring (May) initiation of recruitment of the three juvenile kingfish species reported in this study generally agrees with other work done in the Gulf of Mexico, with times ranging from April to August for fishes < 50 mm SL (Table 5). These data corroborate the reported spring-summer spawning seasons for kingfish in the northern Gulf of Mexico (Irwin 1970; Darovec 1983). However, spawning seasons of *Menticirrhus* are often protracted and may vary with latitude (Smith and Wenner 1985).

Minor diel changes in abundance occurred among the three kingfish, with gulf kingfish being most abundant in the morning and evening, and southern and northern kingfish (although to a lesser extent) more abundant during the day. These results differ from Modde and Ross (1981) who did not find a distinct diel abundance pattern for gulf kingfish, although their data showed a tendency for early afternoon and evening abundance peaks.

Previous studies of gulf kingfish have listed small crustaceans, molluscs, fishes and polychaetes as important prey items (Gunter 1945; Breder 1948; Viosca 1959; Springer and Woodburn 1960; Irwin 1970). Juvenile northern kingfish (13-30 mm) are known to feed on copepods, mysids, crabs and gammarid amphipods while larger individuals feed on mole crabs, amphipods, mysids, hermit crabs, polychaetes and larval fishes (Springer and Woodburn 1960; Irwin 1970; Chao and Musick 1977). The food habits of *M. americanus* have been studied in more detail than the other two species (e.g. Smith 1907; Hildebrand and Schroeder 1928; Hildebrand and Cable 1934; Miles 1949; Pew 1954; Reid 1954; Viosca 1959; Irwin 1970; Fritzche and Crowe 1981). However, only Springer and Woodburn (1960) examined southern kingfish from a surf zone area. Major food items included polychaetes, crabs, mysids and *Emerita.* Our findings generally agree with the published information on food habits of the three species, except for the importance of pelecypod siphons in gulf and southern kingfish. Seagrass fragments in gulf kingfish were likely consumed incidentally to ingestion of epiphytes.

The primary prey of juvenile gulf kingfish were pelecypod siphon tips. While other studies on the food habits of this species have reported the presence of pelecypods (e.g. Springer and Woodburn 1960), only Modde (1979) and Modde and Ross (1983) listed siphon tips as important food items. Pelecypod siphons were also an important dietary component of southern kingfish. Browsing on infaunal invertebrates by fishes has been observed in other systems (e.g. Woodin 1982; Peterson and Quammen 1982; de Vlas 1985), and may be an important energy pathway from particulate organic matter and primary production to higher consumer levels in the surf zone environment.

Although it is difficult to assign water column positions to prey in the turbulent surf zone, adults of the three kingfish species appear to be demersal feeders, as reported by previous studies (e.g. Trewavas 1964; Chao and Musick 1977). However, we observed strong ontogenetic shifts in food habits, with smaller fishes using more epibenthic, or even planktonic prey. Modde (1979) and Modde and Ross (1983) also found small juvenile *M. littoralis* (<20 mm) to be planktivores, feeding almost exclusively on mysids, but shifting to pelecypod siphons, polychaetes and mole crabs with growth. Joseph (1962), working with the eastern Pacific *M. undulatus,* reported a similar size related diet progression in that fish less than 50 mm fed primarily on mysids and amphipods, while fish between 50 and 100 mm fed primarily on pelecypod siphon tips (*Donax gouldi*). Individuals larger than 100 mm fed mainly on *Emerita analoga* and smaller fishes.

In part, ontogenetic changes in food habits may be functionally related to the presence of a swimbladder. Smaller individuals of *M. americanus* and *M. saxatilis* have swimbladders, fascilitating movements into the water column (Bearden 1963; Irwin 1970). With increasing fish size the swimbladders of southern and northern kingfish become less functional and the fishes apparently forage less in the water column. Gulf kingfish lack swimbladders even as juveniles (Irwin 1970; N = 50, size <60 mm; Ross pers. obs., N = 28, size 18-86 mm SL).

The three species of kingfish showed the greatest dietary overlaps as juveniles. However, overlap of size groups was greater within than between size groups of species. The average interspecific overlap was only 40%, a level that Ross (1986) used as the cutoff point for indicating the presence of substantial resource separation. While we did not attempt to measure food abundance, it seems unlikely that food is often limiting in the surf zone environment. Prey of planktonic origin would be continually brought into the surf zone by longshore currents, and benthic prey dislodged by wave action. Because of the physical harshness of the habitat, the dietary separation and tendencies for seasonal and diel separation in habitat use may more likely reflect events mediated primarly by anti-predation responses and/or reproductive biology than present or historical selection for resource separation during periods of lower food abundances. For instance, Ross *et al.* (1985) summarized studies showing greater biological control of fish assemblages in benign compared to harsh environments. Thorman and Wiederholm (1983; 1984; 1986) also found fish assemblages in the environmentally harsh Bothnian Sea to be controlled more by abiotic than biotic interactions. Because of the difficulty of conducting controlled field experiments in the surf zone, choosing between the alternatives of primarily biotic versus abiotic assemblage control will be difficult at best. Perhaps, as pointed out by Conner and Simberloff (1986), the best approach lies in the use of null hypotheses and models.

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