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Foods of Juvenile Spotted Seatrout in Seagrasses at Seahorse Key, Florida

William T. Mason, Jr., and Scott A. Zengel

Early juvenile [<1 yr; 10–100 mm total length (TL)] spotted seatrout in the shallow seagrasses at Seahorse Key, Florida, in the Northeast Gulf of Mexico, fed on 12 kinds of foods. Although the total diversity of major food items of juvenile seatrout is about the same as 50 years ago, for some unexplained reasons, the juvenile diets have apparently switched to other invertebrate species and to small fish. The 10–30 mm TL seatrout ate small Crustacea, e.g., amphipods and grass shrimps, and fed mostly in the *Halodule* seagrass zone (average depth 0.5 m). In addition to these species, the 50–80 mm TL seatrout, feeding primarily in the *Halodule* and *Thalassia* (average depth 0.8 m) zones, consumed copepods, a combination of decapod shrimps (*Mysidopsis bahia, Palaemonetes pugio, P. vulgaris, Periclimenes longicaudatus, Penaeus duorarum*), and small fish. Seatrout of 80–100 mm TL appeared to feed only in *Thalassia,* and larger juveniles (not collected) probably fed in the mixed-grass zone beyond our study area (>1 m depth). Seatrout food resources at the Keys were robust. Peak densities and diversities of hyperbenthic invertebrates in the seagrasses were inversely proportional (maximum average number of individuals = 12,000/sled trawl, Sep.; maximum average number of taxa = 35 spp., March).

The spotted seatrout *Cynoscion nebulosus:* Sciaenidae (Cuvier) remains one of the prime fish of commercial and recreational importance in the Northeast Gulf of Mexico. During the 1940s and the 1950s, this seatrout was second only to the mullet in pounds of harvest at the Cedar Keys, Florida (Reid, 1954). Although many factors contribute to a successful seatrout population, the presence of littoral submerged aquatic vegetation (SAV) is a major one (Moody, 1950; Reid, 1954; Joseph and Yerger, 1956; Klima and Tabb, 1959; Carr and Adams, 1973; Moffett, 1961; Tabb, 1961; McMichael and Peters, 1989). Seagrass meadows provide natural spawning ground for adult seatrout, protection and living space for the young, and unpolluted, warm-water estuaries of the southeastern United States usually contain an abundance of benthic foods.

Juvenile seatrout feeding is highly influenced by major habitat differences, especially in the transitional ecotone between SAV and open water (Lorio and Schafer, 1966; Minello and Zimmerman, 1984; Ruiz et al., 1993). Microscale habitat changes in seagrass meadows are known to greatly affect the composition and distribution of hyperbenthic organisms (Stoner, 1980a, 1980b, 1983; Lewis, 1984; Schneider and Mann, 1991), and, in extreme cases, changes undoubtedly affect seatrout feeding.

In coastal areas with limited SAV or denuded bottom substrates, seatrout depend on marginal emergent vegetation for feeding and nursery habitat (Peterson, 1986; Baltz et al., 1993; Ruiz et al., 1993). The coastal shelf in the vicinity of the Cedar Keys, Florida, is extensive and the slope from shore is quite gradual. Luxuriant stands of three dominant species of shallow-water SAV are present. Thus, the spotted seatrout and other finfish populations at the Keys have benefited from a stable, productive habitat for life activities.

Adult spotted seatrout are present in the seagrass meadows at the Keys from late March to Oct., preferentially at depths of 1–2 fathoms. Spawning begins as early as April and lasts through Oct. (Moody, 1950; Reid, 1954). Juveniles occupy the most shallow beds (Moody, 1950) and feed almost exclusively on shrimps and marine fish. They mostly eat small, free-living crustaceans found in the "hyperbenthos," or those organisms that dwell above the bottom substrate and are closely associated with submerged objects in the water column (Mees and Hamerlynck, 1992; Mason et al., 1994).

Our purposes were to determine the diet of early juvenile (<100 mm TL) spotted seatrout at Seahorse Key, Florida, and to compare our results, if possible, with those of Moody (1950) and Reid (1954). Thirdly, we wanted to determine the status (distribution, abundance, and composition) and health of the seatrout's food resources.

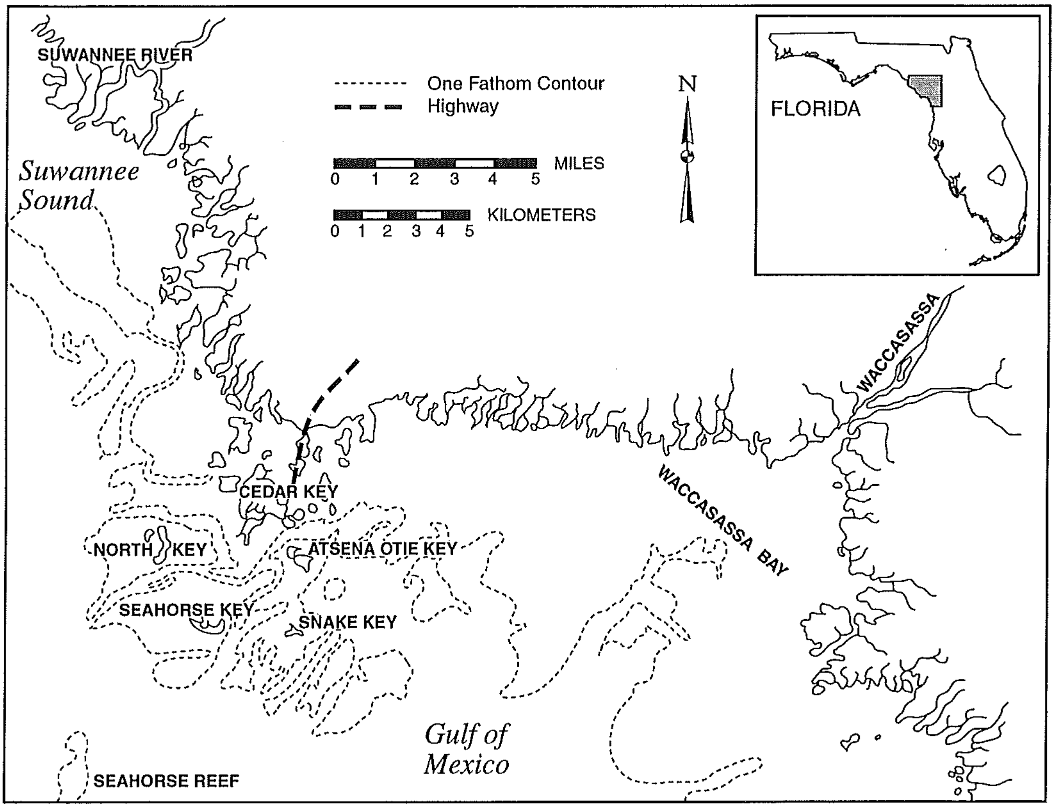

Fig. 1. Map of the Cedar Keys, Florida.

Materials and Methods

Study Area.—The five islands composing the Cedar Keys (Fig. 1) are just south of the "Big Bend" area in the northeast Gulf of Mexico and in the path of the Gulf stream's southward flow. Seahorse Key is a crescent-shaped, outermost island that lies about 5 km offshore and about 10 km south of the mouth of the Suwannee River. The waters at Seahorse Key are usually clear, except after local storms, and are well mixed by the winds and tides.

Table 1. Habitat characteristics in three habitat zones at Seahorse Key, Florida, Sep. 1992–Sep. 1993. Averages of physicochemical measurements (ranges in parentheses) taken at midpoint of study area: transect 16, *Halodule.*

	Bare sand zone	Seagrass zones	
		Halodule	*Thalassia*
Depth (m)	0.4	0.5	0.7
Seaward distance (max. m)	7	28	63–107
Bottom slope (m)	0.021	0.005	0.003
Temperature (C)	36 max.	21 (11–31)	
Salinity (ppt)		25 (17–28)	
Dissolved oxygen (mg/liter)		7.5	

Seahorse Key is part of the U.S. Fish and Wildlife Service's Cedar Keys National Wildlife Refuge. A brown pelican rookery is part of the wildlife management area, and part of the University of Florida's estuarine research is conducted from a renovated lighthouse.

The study site lies along the southwestern beach and is bounded to the north by a high embankment, to the northwest by stands of *Spartina* and *Typha,* and to the southeast by palmetto-scrub (island's primary vegetative cover). The narrow beach (25–30 m wide) is windswept and bare and gradually slopes onto the coastal shelf (Table 1). A broad seagrass meadow, extending 1.5 km from shore, stabilizes the sand bottom substrate (average depth <1 m). Three habitat zones proceed from the shoreline: 25–50-m-wide bare sand (average depth 0.3 m); 25–50-m-wide shoal grass *Halodule* *wrightii* (average depth 0.5 m); and a 75–400-m-wide band of turtle grass *Thalassia testudinum* (average depth 0.8 m). The mixed stand of *Thalassia* and *Syringodium filiforme,* extending beyond 400 m from shore (>1 m depth), was not included in our study.

Climatic conditions were normal during the study, except for a localized torrential storm during the week preceding the March 1993 collections. Prior to sampling, however, conditions returned to near normal.

Physicochemical methods.—The waters at the site were well mixed and little variation among the seagrass zones was encountered. Measurements of water temperature, salinity, pH, and dissolved oxygen (DO) were taken monthly in the *Halodule* zone (representative zone). Nightly conditions were recorded only during the March, May, Aug., and Sep. invertebrate collections.

Seatrout and food collections.—A quad-grid sampling design was selected for the study. It was formed by 32 transects, perpendicular to shore and 30 m apart, each bisecting the three habitat zones. Due to relatively uniform bottom substrate type (coarse sand) and contours, the quads within each major habitat zone were spatially and volumetrically about equal. Junctures at each habitat zone were delineated by PVC rods (2.54 cm diameter) driven into the substrate. Floats, attached to the tips of rods, marked the junctures at high tide and facilitated their recognition during night sampling.

Attempts to collect spotted seatrout and other finfish (Zengel 1993) were made monthly (June 1992 to Oct. 1993) with a 15-m-wide pole seine (3-mm mesh nylon bag and 3-m-long wing panels of 6-mm mesh). Seining was conducted parallel to shore for 20 m. Fish catches were rough sorted in the field and later identified and enumerated in the laboratory.

Sampling for invertebrate foods of the seatrout was conducted from Sep. 1992 through Sep. 1993 at randomly selected points within each of the habitat zones: two quads each for the bare sand zone and *Halodule* zone, and four quads for the *Thalassia* zone (total = 8 samples/mo). To check on diel periodicities of the hyperbenthos, day sampling (0900–1300 h) and night sampling (2000–0100 h) were taken within the same 24-h period; March, May, July, and Sep. 1993 only.

Seatrout stomach content analysis.—to avoid possible contamination of stomach contents with other fish tissues, the entire belly of the fish (anus to opercle) was cut from the body and placed in a petri dish filled with 95% ethanol preservative. The alimentary canal was then removed intact and placed in a watch glass, and the stomach was dissected away from the canal. After the stomach was opened, materials were flushed from the lining and food items were identified and tallied.

Heads of partially digested foods were counted as whole organisms. Dry weights (103 C; 4 h) and ash-free dry weights (500 C; 1 h) of total food materials in the stomachs were recorded on electronic balance (nearest 0.01 mg). Biomass estimates for highly fragmented stomach contents (e.g., parts of amphipods and remains of shrimps) were based on average weights (2–4 replicate samples of six whole specimens each) of representative life-stage specimens of the species (W. T. Mason, 1989–1993, unpubl. data).

Plankton analysis of stomach contents was performed by randomly withdrawing 10-ml subsamples of intestinal fluids (four reps/stomach). Dense materials in the extracts were concentrated by centrifugation (140 × *g*; 3 min) and then the top 8 ml of supernatant was withdrawn by pipette and discarded. The remaining centrifugate was remixed and 1 ml was placed in a Sedgwick-Rafter counting cell and scanned (3 strip counts at ×200 magnification). In addition, a 0.5-ml aliquot of the remix was permanently slide-mounted in CMC-10 medium (Mention of manufacturers and their products does not necessarily constitute endorsement by the U.S. Department of the Interior or of the authors and their firms.) and 10 random field counts were examined (×400 magnification).

Invertebrate sample collection and analysis.—Pullen et al.'s (1968) "marsh net," referred to as "sled trawl," was used to collect the hyperbenthic foods of the seatrout. The trawl (weight 5 kg), made of two heavy-guage stainless steel runners (5-cm wide) held apart by steel rods (collection aperture 18 high × 53 cm wide), is fitted with a 1-m-long drift net (450-μm pore mesh).

To minimize organism avoidance during the collection process, the boat motor (and auxiliary lights at night) was turned off during approach to the sampling point, so that the boat drifted into position. First the trawl was placed gently on the seagrass bed and its tether was played out as the boat was poled in an arc to a point 14 m away and parallel to shore. After the boat was staked into place, the trawl was winched in at a rate of 0.3 mps. Inside the boat, the sample collection bag was inverted and its contents were emptied into a shallow tub partially filled with water. Materials were thoroughly flushed from the bag. Easily recognizable large organisms (e.g., adult tunicates, mussels, and crabs) were immediately counted and replaced in the water. Remaining small clinging organisms that required identification in the laboratory were flushed from the bag using a strong stream of 95% ethanol-rose bengal stain preservative (Mason and Yevich, 1967) provided by a pressurized sprayer (4-liter cap.). As most trawl samples netted about 500 cc of sample that contained hundreds to thousands of organisms, those samples containing >200 organisms were halved using the sieve sample splitter (Mason, 1991a).

Although use of the trawl removed some epibenthos on sand windrows, overall the device was gentle on the bottom substrate and left it relatively undisturbed after sampling. Blades of the seagrasses flexed as the trawl slid over. A performance trial for the sled trawl in *Halodule,* conducted in August 1992 prior to initiation of benthic sampling, yielded an SEM for individuals and taxa of about 40% each, which is acceptable for semiquantitative benthological sampling (Elliott, 1993).

Data interpretive methods.—General descriptive statistics (Zar, 1984) (e.g., Student's t-test) were applied to the data through computer software (Hintze, 1987). The total diversity of the trawl-captured macrofauna was determined as a bioindicator of community health as was *d,* the community diversity index (Zar, 1984). The latter index is Florida's only legal measure of "biological balance" for class I–III surface waters [Florida Surface Water Quality Standards, 1992; Sec. 17-302.540(8), 550(7), and 560(9)]. It is calculated based on the total number of individuals and the number of invertebrates in the *i*th species occupying a U.S. EPA standard hardboard multiplate sampler after incubation for 30 consecutive days. Although the error for *d* is known to be high in samples containing <200 individuals (Zar, 1984), our sled trawl samples, usually >500 individuals/trawl, likely minimized the error.

Sled trawl sampling highly favors capture of organisms in the hyperbenthos and some epibenthos (surface-dwelling organisms). Sled trawls collect little of the embenthos (partially buried organisms) and hardly any hypobenthos (tunneling organisms living well below the substrate). Thus, we did not feel justified in expressing our sled trawl data in traditional benthological sampling units for epibenthos and embenthos (no./m^2), or in volumetric units (no./m^3) for pelagic and drift organisms. Instead, we used counts per trawl (sample). Enumeration of organisms on a "per-sampler basis" has precedence in other kinds of benthological sampling, e.g., of artificial substrates as conducted in the nearby Suwannee River (Mason, 1991b; Mason et al., 1994).

Experience shows that, excluding large-bodied individuals, benthic bioassessments using individual counts of organisms/taxon produce similar results to those using individual weights (biomass). Individual tallies have a distinct advantage over weight measurements, especially when small organisms are encountered (such as amphipods and highly fragmented organisms), and permit comparisons of species-specific food preferences of fish and other wildlife, e.g., as used for waterfowl by Johnson (1980). Nonetheless, counts of small food organisms (e.g., amphipods) may distort their importance among other food items. For example, it requires 5–10 mysid shrimps, 2–4 *Palaemonetes* shrimps, and just 1–2 *Penaeus* shrimp to fill the stomach of a 60-mm-TL juvenile seatrout. Therefore, we elected to determine both individual counts and biomass, but relied mostly on individual counts for reporting results in figures and text.

RESULTS

Physicochemical conditions.—Annual average daytime water temperature in *Halodule* was 21 C (range 11 to 31 C), and was stable at 25 C. A synoptic survey of water temperatures in the habitat zones in Sep. 1992 revealed a day temperature of 36 C (0.1-m depth) in the shoreline bare sand zone. The lowest salinity measurement (17 ppt) occurred in winter and maximum salinity was during late summer (Table 1). Salinity during May–Sep. averaged 25–26 ppt. Values for pH were uniform at 8 standard units (SU). DO concentrations averaged 7.5 mg/liter (Table 1) and ranged narrowly between 7–8 mg/liter. DO concentrations for each quarterly night sampling revealed little variation within the habitat zones or by water depth.

Juvenile seatrout diet.—Of the 62 juvenile seatrout <100 mm TL in 1992–93 (Table 2), 95% of the stomachs contained foods. During the year, the juveniles consumed 12 major foods in the seagrasses at Seahorse Key (Table 3) averaging 1.4 food items/stomach. On average combined, the seatrout ate 28 food items in *Halodule* and 66 food items in the *Thalassia.*

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TABLE 2. Number of spotted seatrout collected for stomach content analysis in two seagrass zones at Seahorse Key, Florida, 1992–93 (none collected in the bare sand zone).

	Halodule zone		*Thalassia* zone	
	n	Average TL mm (range)	n	Average TL mm (range)
June 1992	4	49 (33–55)	0	
July 1992	1	63	0	
Aug. 1992	7	37 (16–61)	8	55 (30–86)
Sep. 1992	10	41 (32–56)	4	75 (44–92)
June 1993	1	32	0	
July 1993	0		2	36 (22–49)
Aug. 1993	4	45 (38–51)	2	36 (18–53)
Sep. 1993	7	60 (49–72)	12	41 (25–71)
Total	34	46 (16–61)	28	49 (18–92)

For both SAV zones combined, the primary foods of juveniles were; Copepoda (28%), *P. duorarum* (22%), *H. pleuracanthus* (16%), *Palaemonetes* (2 spp.) (10%), free-living Amphipoda (9%), Osteichthyes (7%), *M. bahia* (5%), and *Periclimenes longicaudatus* (3%).

Average gut fullness for the 62 fish was estimated at 68%. Examination of stomach fluids of the seatrout revealed only an occasional diatom that could have been inadvertently ingested or secondarily ingested as part of the foods consumed by the invertebrate prey. All five of the 20–30-mm-TL seatrout and two of the four 50–60-mm-TL seatrout in *Thalassia* had consumed copepods (Table 3).

Invertebrate food densities.—The abundance of hyperbenthic food resources in the seagrass meadows was greatest in May–June and Aug.–Dec. (Figs. 3 and 4a) and closely mirrored the densities of the most abundant crustacean at the site, the caridean shrimp *H. pleuracanthus* (Fig. 4b). It alone averaged 84% of the individuals/trawl, or 77% dry weight/trawl.

Decapods exhibited two density peaks; a minor one in April–June and a major one in Aug.–Sep. (Table 4 and Fig. 4a). Other abundant crustaceans were (in descending order); decapod *Tozeuma carolinense,* cumacean *Oxyurostylis smithi* and *Almyracuma* sp. A (Heard 1982), decapods *Palaemonetes pugio* and pink shrimp *Penaeus duorarum,* and the tanaid isopod *Hargeria rapax.* Amphipods were most abundant in Jan.–March, decapods were most abundant in April–Dec., and mysids were most abundant in Jan. only (Fig. 4a).

The diversities and densities of invertebrates were inversely proportional. Generally, lowest densities occurred in winter when diversities peaked, and greatest densities in late summer–fall were marked by low diversities (Table 4 and Figs. 3, 4a–b).

We found that invertebrate densities between the two adjacent seagrass zones varied considerably. For example (Fig. 3), the average density in Sep. 1992 *Halodule* was twice as great as in *Thalassia,* but the Sep. 1993 densities in both seagrass zones were about equal.

A single trawl collected in *Halodule* during Sep. 1992 contained about 14,000 individuals.

TABLE 3. Average number of food items in stomachs of juvenile spotted seatrout in seagrasses at Seahorse Key, Florida, Aug. 1992–Sep. 1993. Co = Copepoda; Amphipoda-Amphithoidae, Cc = *Cymadusa compta,* Cr = Corophiidae, Gm = Gammaridae spp., Mn = *Monoculodes* n. sp.; Tanaidacea, Hr = *Hargerian rapax*; Decapoda, Hp = *Hippolyte pleuracanthus,* Mb = *Mysidopsis bahia,* Pd = *Penaeus duorarum,* Pl = *Periclimenes longicaudatus,* Pp = *Palaemonetes pugio,* and Os = Osteichthyes. * = Actual numbers/stomach.

	Halodule zone												*Thalassia* zone									
TL (mm)	Seatrout (n)	Hr	Cc	Cr	Gm	Mn	Hp	Mb	Pd	Pl	Pp	Os	Seatrout (n)	Co	Cc	Gm	Hp	Mb	Pd	Pl	Pp	Os
10–20	2								1				1*			1						
20–30	1*	1		1	1		1						5	25		1	1		1			1
30–40	5						1	1		1	1	1	5		1			1				1
40–50	11						1	1	1	1	2	1	5			1	1				2	
50–60	10		1		1	1	1		1		1	1	4	1			1	1	1	1	1	1
60–70	4						2		2		1		2				1		1			1
70–80	1*						1						3				4		1			
80–90	0												2								2	
90–100	0												1*					1	10		1	
Totals																						
Fish	34												28									
Food items		1	1	1	2	1	7	2	5	2	5	3		26	1	3	8	3	14	1	6	4

TABLE 4. Monthly average total number of individuals and percent of primary (i.e., >10% of total individuals) hyperbenthic invertebrates/trawl in day (D) and night (N) collections from combined zones; bare sand, shoal grass *Halodule wrightii,* and turtle grass *Thalassia testudinum,* Sep. 1992–Sep. 1993, Seahorse Key, Florida.

	Year:	1992				1993								
	Month:	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.
						Average total individuals/trawl								
	D	4,860	3,498	2,436	3,099	1,251	1,293	1,190	1,318	3,796	3,871	1,428	5,752	6,311
	N							1,146		4,469		1,958		5,052
						Average % individuals/trawl								
Taxa														
Crustacea														
Amphipoda	D				14	45	30	21	13	12				
	N							28		16		18		
Decapoda	D	94	92	60	64	10	16	14	51	53	74	23	92	94
	N							32		66		33		81
Mysidacea	D					11								
	N													
Mollusca														
Bivalvia	D											13		
	N													
Gastropoda	D			26	12	32	29	37	20	24	20	42		
	N							18		11		37		13

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This peak was confirmed by 12,000 individuals/trawl in fall 1993. The cyclic abundance of dominant decapod crustaceans paralleled the growth of seagrasses from spring through fall. Lowest densities coincided with winter low water temperature (minimum 11 C) and salinity (minimum 17 ppt) and natural seagrass dieback and reduced habitat.

Invertebrate food diversities.—The total inventory of 198 hyperbenthic invertebrate taxa at Seahorse Key (Table 5) was split almost evenly among Arthropoda, Mollusca, and Annelida. Seasonal diversity became evident (Fig. 2) from fall (about 13–17 taxa) to the March night collections (37 taxa) (Fig. 5). Thereafter, the diversity gradually tailed off during summer and early fall.

Values of $\bar{d}$ ranged from 1 to 2.5 in summer and fall, and from 3 to 4 in winter and early spring. These $\bar{d}$ values are comparable to those for the macrobenthos of lower Suwannee River and Estuary system, Florida, collected during the previous 5 yr (Mason, 1991b; Mason et al., 1994). Values of $\bar{d}$ for the seagrass hyperbenthic community (Figs. 3 and 4b) reflected the increase in diversity during winter and peak in number of individuals in fall (Jan., 5.37; Sep., 0.92).

Diel food patterns.—The differences between day and night densities and diversities of hyperbenthos in each habitat zone for each of the four quarterly collections were minor (Fig. 5a–b and Table 4). However, seasonal differences were obvious. For example, the combined day and night March diversities (average total taxa–day = 30; average total taxa–night = 38) were about 26% greater than for May (not significantly different $P \leq 0.05$) and May densities were significantly greater than for March (t = 4.5, 14 df).

DISCUSSION

Fish–food habit studies are difficult because of the variables encountered for fish, e.g., seasonal migrations and competition with other species for habitat and foods, and, on the food side, cyclic periods of food abundance and local environmental and habitat conditions. For both, sampling biases are major problems. Thus, most fish–food habit studies, although well designed, are seldom quantitative. We encountered most of these problems. However, our study provides a good basis for comparison with the food habits of juvenile spotted seatrout at the Keys 50 yr ago.

Food resources.—The gradual decline in total density of hyperbenthic invertebrates in *Halodule* traced from May to Aug. 1993 (Fig. 3) was primarily due to fewer *H. pleuracanthus.* This reduction might reflect predation on the food stock by juvenile finfish, including the spotted seatrout, and large epibenthic decapod crustaceans, e.g., the blue crab *Callinectes sapidus* (Fig. 4a), then in the beds. Heavy foraging by blue crab on the benthos in the denuded intertidal zone of the Chesapeake Bay, Maryland, was also recorded by Ruiz et al. (1993).

The diversity of hyperbenthic invertebrates (taxonomic richness) is considered one of the best measures of "biological balance." Our findings show a highly diverse and, therefore, healthy hyperbenthic community (Table 5). Usually in freshwaters, $\bar{d}$ values of <1 reflect an "unbalanced" situation, i.e., few taxa, but each taxon represented by a large population. Values of 1–3 are indicative of normal communities, and $\bar{d}$ values of >4 are seldom encountered in natural situations. Based on our survey where $\bar{d}$ values ranged from 3.75 to 5 from Jan. through July (Fig. 2), Florida's biological classification of surface waters needs modification for use in estuarine waters. The "clean water" indicator level may need elevation and the "polluted water" category may need to be lowered.

During Jan.–March, free-swimming amphipods *Cymadusa compta* and *Gammarus* spp., adapted for solitary life in the water column, were numerically dominant crustaceans. Conversely, densities of epibenthic Corophiidae amphipods, dense at the mouth of the Suwannee River (Mason, 1991b), contributed <10% to densities in the Seahorse Key trawls. Corophiids depend on detrital materials for tubemaking and some protection from strong tidal currents and shifting sediments, contrary to site conditions.

Densities of mysid populations were relatively even compared to other crustacean groups during the winter and early spring cool-water, low-salinity, and reduced-seagrass habitat. These small crustaceans, intermediate in size between the amphipods and decapods, occupied 11% of the average total densities in Jan. (Table 4). Thereafter, mysid densities declined to <10% of the average total of hyperbenthos and did not recover until Nov.–Dec. (Fig. 4a). Mysid seasonal abundance at Seahorse Key was thus similar to some species of estuarine zooplankton and amphipods.

In other northeastern Gulf estuaries, such as the Apalachicola River Estuary (Livingston, 1976) and Apalachee Bay, Florida (Ryan,

TABLE 5. Benthic invertebrates and allied macrofauna in seagrass meadows during Sep. 1992–Sep. 1993 at Seahorse Key, Florida.

Taxa

Taxa

Surface-dwelling fauna

- Cnidaria—Coelenterates
  - Siphonophora—Portuguese man-of-war
    - Physaliidae
      - *Physalia physalia* (Linnaeus)
- Scyphozoa—Scyphozoans
  - Rhizostomeae—jellyfishes
    - Stomolophidae—cannonball jellyfish
      - *Stomolophus meleagris* L. Agassiz

Hyperbenthos

- Arthropoda
  - Crustacea
    - Amphipoda—free-living amphipods
      - Ampelscidae
        - *Ampleisca vadorum* Mills
        - *A. verrilli* Mills
      - Ampithoidae
        - *Ampithoe longiamanna* Smith
        - *Cymadusa compta* (Smith)
      - Aoridae
        - *Grandidierella bonnieroides* Myers
        - *Unicola dissimilis* Shoemaker
      - Dexaminidae
        - *Polycheria*
      - Gammaridae
        - *Gammarus mucronatus* Say
        - *G.* nr. *tigrinus*
      - Haustoriidae
        - *Parahaustorius* cf. *longimerus* Bousfield
      - Hyalidae
        - *Hyale plumosa* (Stimpson)?
      - Lynassidae
        - Unidentified 2 spp.
      - Melitidae
        - *Melita nitida* Smith
      - Oedicerotidae
        - *Monoculodes nyeri* Schoemaker
        - *M.* n. sp.
    - Decapoda—decapods, shrimps, shellfish
      - Dendrobranchiata
        - Penaeidae—penaeid shrimps
          - *Penaeus duorarum* Burkenroad—pink shrimp
          - *P. setiferus* (Linnaeus)—white shrimp
        - Sergestidae
          - *Acetes americanus carolinae* Hansen
        - Pleocyemata: Caridea—caridean shrimps
        - Alpheidae—snapping shrimps
          - *Alpheus heterochaelis* Say
        - Hippolytidae—grass shrimps
          - *Hippolyte pleuracanthus* (Stimpson)
          - *Latreutes fucorum* (Fabricius)
          - *L. parvulus* (Stimpson)
          - *Thor dobkini* Chace
          - *Tozeuma caroliense* Kingsley
        - Palaemonidae—prawns, grass shrimps
          - *Palaemon floridanus* Chace
          - *Palaemonetes vulgaris* Say
          - *P. paludosus* (Gibbes)
          - *Periclimenes iridescens* Lebour
          - *P. longicaudatus* (Stimpson)
        - Processidae—deep water shrimps
          - *Ambidexter symmetricus* Manning and Chace
        - Pleocyemata: Brachyura
        - Portunidae—swimming crabs
          - *Callinectes sapidus* Rathbun—blue crab
          - *Portunus* sp. Weber
      - Mysidacea
        - Mysidae—mysid shrimps
          - *Mysidopsis almyra* Bowman
          - *M. bahia* Molenock
          - *Taphromysis bowmani* Bacescu
          - *T. louisianae* Banner

Epibenthos—Section I

- Porifera—sponges
  - Demospongiae
  - Calcarea—purse sponges
- Tunicata (=Urochordata)—tunicates
  - Didemnidae
    - *Didemnum duplicatum* F. Minniot
  - Perophoridae
    - *Ecteinascidia turbanata* Herdman
  - Polyclinidae
    - *Aplidium constellatum* Verrill
  - Polycitoridae
    - *Clavelina*
    - *Distaplia bermudensis* van Name
    - *Eudistoma hepaticum*
    - *E. carolinense* van Name
- Nemertea—nemerteans
  - *Prostoma* Duges
- Mollusca
  - Bivalvia—mussels and oysters (part)
    - Dreissenidae
      - *Ischadium recurvum* (Rafinesque)
      - *Parastarte triquetra* Conrad
    - Ostreidae
      - *Crassostrea virginica* (Gmelin)—eastern oyster

TABLE 5. Continued.

Taxa | Taxa

Epibenthos—Section II

- Echinodermata
  - Holothuroidea—sea cucumbers
      - *Leptosynapya parvipatina*
      - *Sclerodastyla brairens*
  - Stelleroidea—starfishes
    - Ophiuridae
      - Ophiactidae
        - *Ophiactis rubropoda* Singletary
      - Amphiuridae
        - *Amphioplus abditus*
        - *A. pulchella*
        - *A. thrombiodes*
        - *Ophiothrix angulata* (Say)
- Mollusca
  - Gastropoda—snails
      - Acteonidae
        - *Acteon punctostriatus* (C. B. Adams)
      - Atyidae
        - *Haminoea succinea* (Conrad)
      - Bullidae
        - *Bulla striata* Bruguiere
      - Caecidae
        - *Caecum pulchellum* Stimpson
        - *C. vestitum* Folin
      - Cerithiidae
        - *Cerithium muscarum* Say
        - *Cerithiopsis greeni* (C. B. Adams)
      - Columbellidae
        - *Anachis semiplicata* Abbott
        - *Mitrella lunata* (Say)
      - Conidae
        - *Conus stearnsi* Conrad
      - Crepidulidae
        - *Crepidula maculosa* Conrad
      - Ellobiidae
        - *Detracia floridana* (Pheiffer)
      - Epitoniidae—wentletraps
        - *Epitonium angulatum* (Say)
      - Fasciolariidae—tulip shells
        - *Fasciolaria hunteria*
      - Littorinidae—periwinkles
        - *Littorina irrorata* (Say)
      - Marginellidae
        - *Granulina ovuliformis* (d'Orbigny)
        - *Hyalina veliei* (Donovan)
        - *Marginella apicina* Menke
        - *M. lavalleeana* Orbigny
      - Melongenidae—conchs, whelks
        - *Busycon* sp. Roding—whelk
        - *B. spiratum* (Lam.)—fig whelk
        - *Melongena corona* (Gmelin)—crown conch
      - Modulidae—button snails
        - *Modulus modulus* (Linnaeus)
      - Nassariidae—mudsnails, nassas
        - *Nassarius albus* (Say)
        - *N. vibex* (Say)
      - Naticidae—moonsnails
        - *Polinices duplicatus* (Say)
      - Olividae—olive snails
        - *Olivella mutica* (Say)
      - Neritidae—nerites
        - *Neritina reclivata* (Say)
      - Pyramidellidae
        - *Sayella hemphilli* (Dall)
      - Retusidae
        - *Retusa sulcata* (Orbigny)
      - Siphonodentaliidae
        - *Cadulus carolinensis* Bush
      - Siphonariidae—false limpets
        - *Siphonaria pectinata* (Linnaeus)
        - *S. alternata* (Say)
      - Terebridae—auger snails (part)
        - *Terebra floridana* Dall?
      - Turbinidae—turban snails
        - *Turbo castanea* Gmelin
      - Turridae—auger snails (part)
        - *Mangelia biconica* C. B. Adams
        - *M.* cf. *ceroplasta* Bush
  - Nudibranchia—sea slugs
- Arthropoda
  - Arachnoidea
    - Xiphosura—horseshoe crabs
        - *Limulus polyphemus* Linnaeus
  - Crustacea
  - Malacostraca
    - Amphipoda—amphipods, scuds
      - Corophiidae—tube-dwelling amphipods
        - *Corophium* cf. *insidiosum* Crawford
        - *C.* cf. *tuberculatum* Shoemaker
        - *C.* cf. *lacustre* Vanhoffen
        - *Cerapus* cf. *tubularis* Say
      - Ischyroceridae—tube-dwelling amphipods
        - *Erichthonius brasiliensis*
        - *Jassa falcata* Smith
    - Isopoda—isopods, aquatic sow bugs
      - Asellota
        - Gnathiidea
          - Anthuridae
            - *Cyathura polita* Stimpson

TABLE 5. Continued.

Taxa | Taxa

Epibenthos—Section II (Continued)
Nudibranchia—sea slugs (Continued)

- Valvifera
  - Idoteidae
    - *Chiridotea* Harger
    - *Edotea* cf. *montosa* (Stimpson)
    - *Erichsonella attenuata*
    - *Idotea baltica* (Pallas)
- Flabellifera
  - Sphaeromidae
    - *Sphaeroma quadridentatum* Say
    - *Cassidinidea ovalis* (Say)
- Tanaidacea (=Chelifera)
  - Paratanaidae
    - *Hargeria rapax* (Harger)
- Decapoda—shellfish, decapods
  - Grapsidae—wharf crabs
    - *Sesarma cinereum* (Bosc)
  - Ocypodidae—fiddler crabs
    - *Uca minax* LeConte
  - Paguridae—hermit crabs
    - *Pagurus* Say
  - Pinnotheridae—commensal crabs
    - *Pinnixa chaetopterana* Stimpson
    - *P. cylindrica* (Say)
    - *P. pearsi* Wass
    - *P. retinens* Rathbun
    - *P. sayana* Stimpson
  - Xanthidae—mud crabs
    - *Panopeus texana* (Stimpson)
    - *Rhithropanopeus depressus*
    - *R. harrisii* (Gould)
- Cumacea—Cumaceans
  - Nannasticidae
    - *Almyracuma* sp. A Heard
    - *Oxyurostylis smithi* Calman
- Cirripedia—barnacles
  - Thoracica—acorn barnacles
    - Balanidae
      - *Balanus eburneus* Gould?

Embenthos

- Brachiopoda (lamp shells)
  - Inarticulata
    - Lingulida
      - Lingulidae
        - *Glottidia pyramidata* (Stimpson)
- Polychaeta—polychaetes, marine bloodworms
  - Ampharetidae
    - *Hobsonia florida* (Hartman)
    - *Isolda pulchella* Muller
    - *Melinna* Malmgren
    - *Sabellides* Milne
  - Capitellidae
    - *Capitella capitata* (Fabricius)
    - *Heteromastus filiformis* (Claparede)
    - *Mediomastus* Hartman
    - *Notomastus* Sars
    - *Polydora* Bosc
  - Cirratulidae
    - *Tharyx* Webster et Benedict
  - Dorvilleidae
    - *Schistomeringos rudolphii* (delle Chiaje)
  - Eunicidae
  - Glyceridae
    - *Glycera* Savigny
    - *Glycinde* Muller
  - Hesionidae
    - *Gyptis* Marion et Bobretzky
    - *Hesione* Savigny
    - *Parahesione* Pettibone
  - Lumbrineridae
    - *Lumbrineris* Blainville
  - Magelonidae
    - *Magelona* Muller
  - Maldanidae
    - *Maldane* Grube
    - *Axiothella* Verrill
    - *Clymenella torquatus* (Leidy)
  - Nephtyidae
    - *Aglaophamus* Kinberg
    - *Nephtys* Cuvier
  - Nereidae
    - *Kinbergonuphis* Pettibone
    - *Laeonereis culveri* (Webster)
    - *Nereis succinea* (Frey & Leuckart)
    - *N. occidentalis*
    - *Platynereis* Kinberg
  - Onuphidae
    - *Diopatra* Audouin et Milne-Edwards
    - *Onuphis eremita* Audouin et Milne-Edwards
  - Opheliidae
    - *Polyophthalmus pictus*
  - Orbiniidae
    - *Haploscoloplos* Monro
    - *Orbinia* Quatrefages
    - *Scoloplos* Blainville
  - Oweniidae
    - *Myriochele* Malmgren
  - Paraonidae
    - *Aricidea* Webster
  - Phyllodocidae
    - *Eteone* Savigny
    - *Eumida sanguinea* (Orsted)
    - *Phyllodoce* Savigny

TABLE 5. Continued.

Taxa | Taxa

Epibenthos—Section II (Continued)
Embenthos (Continued)

- Pilargidae
  - *Loandalia* Monro
  - *Parandalia* Emerson et Fauchild
  - *Sigambra* Muller
- Polynoidae
  - *Halosydna* Kinberg
  - *Harmothoe* Kinberg
  - *Lepidonotus* Leach
  - *Phyllohartmania taylori* Pettibone
- Sabellidae
  - *Fabricia sabella* (Ehrenberg)
  - *Jasmineira* Langerhans
- Serpulidae
  - *Hydroides dianthus* (Verrill)
- Spionidae
  - *Paraprionospio pinnata* (Ehlers)
  - *Prionospio* Malmgren
  - *Scolelepis squamatus* (O. F. Muller)
  - *Spiophanes* Grube
  - *Sterblospio benedicti* Webster
- Spionidae
  - *Polydora* Bosc/*Boccardia* Carazzi complex
  - *Pseudopolydora* Czerniavsky
- Spirorbidae
- Syllidae
  - *Syllis* Savigny

- Mollusca
  - Bivalvia—clams and mussels
    - Carditidae
      - *Carditamera floridana* Conrad
    - Corbiculidae—marsh clams
      - *Polymesoda caroliniana* (Bosc)—Carolina marsh clam
    - Donacidae
      - *Donax variabilis* Say
    - Mactridae
      - *Rangia cuneata*
    - Nuculanidae
      - *Nuculana acuta* (Conrad)
    - Tellinidae
      - *Macoma tenata* (Say)
    - Veneridae—quahogs
      - *Mercenaria campechiensis* (Gmelin)
- Cephalochordata—lancelets
  - Branchiostomidae
    - *Branchiostoma caribaeum* Sundevall
- Hemichordata
  - Enteropneusta—acorn worms
    - Harrimaniidae
      - *Saccoglossus kowalevskii* (A. Agassiz)
  - Sipuncula—peanut worms

Hypobenthos

- Arthropoda
  - Crustacea
    - Decapoda
      - Callianassidae—mud shrimps, ghost shrimps
        - *Lepidophthalmus louisianensis* (Schmitt)

Epizoos/parasites

- Arthropoda
  - Crustacea
    - Branchiura: Arguloidea—fish lice
      - *Argulus japonicus* Thiele

1981), where the littoral substrate is nearly devoid of SAV, diel periodicities of the hyperbenthos may be extreme. The lack of diel rhythms in abundance of hyperbenthos in seagrass meadows at Seahorse Key fits Ledoyer's Class(a) ecological grouping for Madagascar where caridean shrimps occur in equal densities both day and night. This was also true of the hyperbenthos in seagrass meadows of coastal southwest Japan (Kikuchi and Peres, 1977).

Juvenile seatrout diet.—The overall findings on juvenile seatrout foods of the 1940s and 1950s (Moody, 1950; Reid, 1954), i.e., reliance on decapod crustaceans, is supported by the results of our 1992–93 survey. Our survey showed that the seatrout selected 12 kinds of foods from a total menu of 199 items. Copepods and amphipods are still key foods of <60-mm-TL-stage juvenile spotted seatrout and are not usual food items of >60-mm-TL seatrout. Further, the largest juvenile seatrout had gorged on

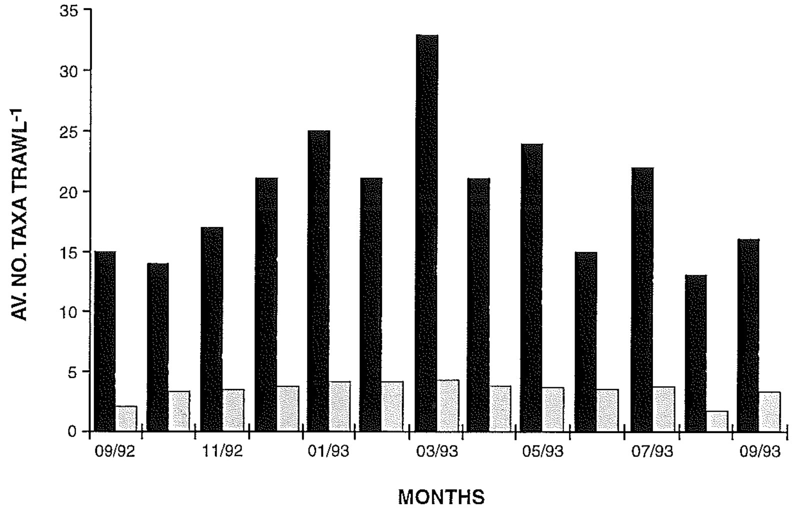


Fig. 2. Total taxa (solid bar) and community diversity index *d* (gray bar) for hyperbenthic communities for combined shoreline bare sand, *Halodule,* and *Thalassia* habitats at Cedar Keys, Florida, Sep. 1992–Sep. 1993.

adult pink shrimp, usually found in deeper water.

We found that the 10–100-mm-TL fish in the *Thalassia* zone consumed about double the number of food of an almost equal number of fish in the *Halodule* zone (Table 3). This significant difference (based on individual food items) was due to a total of 127 copepods in five seatrout in *Thalassia* during June 1993. Minimizing the importance of this perhaps anomalous event and considering the capture of 80–100-mm-TL fish only in *Thalassia,* we suspect that >100-mm-TL juvenile seatrout, as 50 yr ago (Moody, 1950), feed in the stands of mixed seagrasses beyond >1 m average depth.

Moody (1950) did not find small fish of major importance in the diet of 50–150-mm-TL juvenile seatrout. However, our findings reveal that that large decapods, *Penaeus* and *Palaemonetes,* and also small fish are important foods of the 20–30-mm-TL juvenile seatrout. Also, we found that *Hippolyte* was not the prime food item of the juveniles, as was reported by Moody (1950). This is unusual considering its overwhelming dominance in the seagrasses. In fact, *Hippolyte* was absent from juveniles >80 mm TL

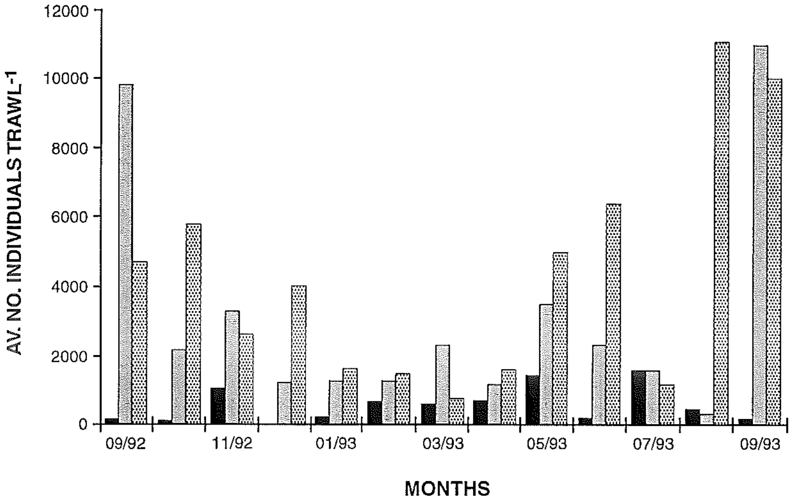
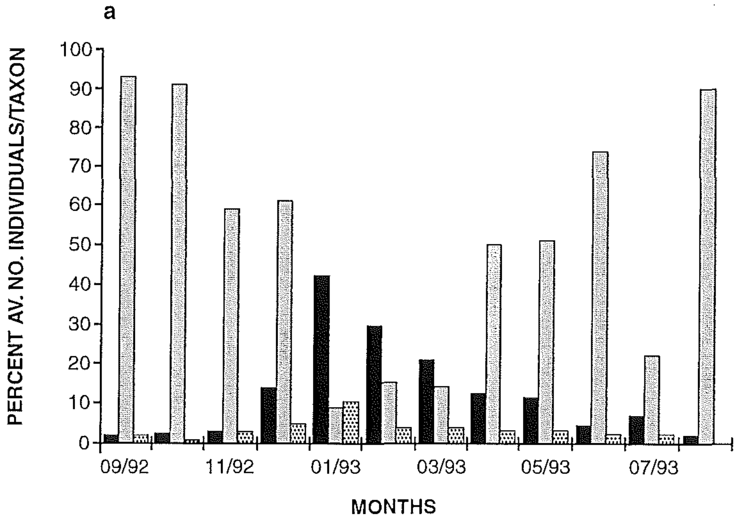


Fig. 3. Average number of hyperbenthic individuals in day sled trawls from bare sand (solid bar), *Halodule* (gray bar), and *Thalassia* (stippled bar) zones during Sep. 1992–Sep. 1993, Seahorse Key, Florida.



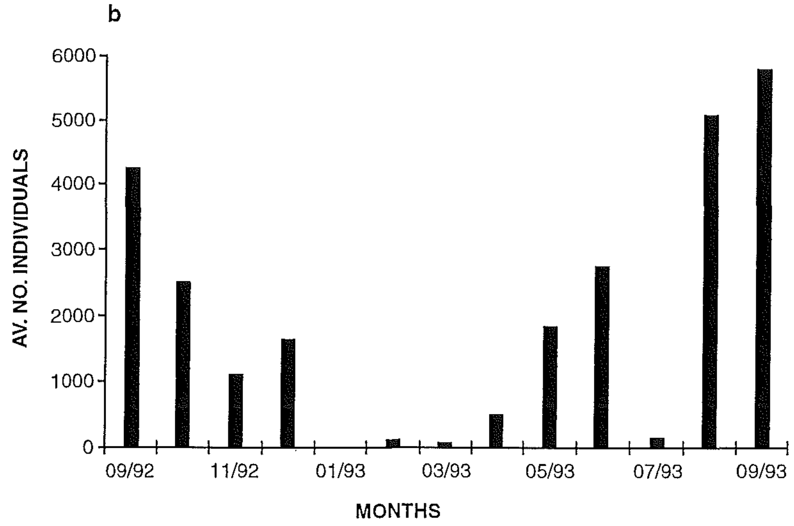


Fig. 4. (a) Average percent of crustacean individuals/sled trawl: Amphipoda (solid bar), Decapoda (gray bar), and Mysidacea (stippled bar); and (b) average number of individuals of *Hippolyte pleuracanthus*/sled trawl, Sep. 1992–Sep. 1993, Seahorse Key, Florida.

(Table 3). Although other epibenthic and sedentary crustaceans were present in the seagrasses (i.e., *Tozeuma carolinense,* tanaid *Hargeria rapax,* cumaceans *Oxyurostylis smithi* and *Almyracuma* sp.) (Table 5), <100-mm-TL juvenile seatrout did not prey on them. The lack of *T. caroliense* as another prominent member of the diet of juvenile seatrout reported by Moody (1950) is unexplainable. The shrimp's greenish color and long rostrum, giving it a bladelike appearance on the grasses, is good camouflage. Also, the importance of the decapod *P. longicaudatus,* a primary seatrout food of the 1940s and 1950s, was not confirmed by us.

Populations of several dozen species of epibenthic organisms, e.g., mollusks, hermit crab, and mud crab (often comprising 20% of total individuals/trawl), were not included in the diet of juvenile spotted seatrout. This may be due to hard body armature that would make ingestion by early juvenile seatrout more difficult.

Average gut fullness for adult and juvenile seatrout reported by Moody (1950) was somewhat lower (54%) than our finding of 68%, but

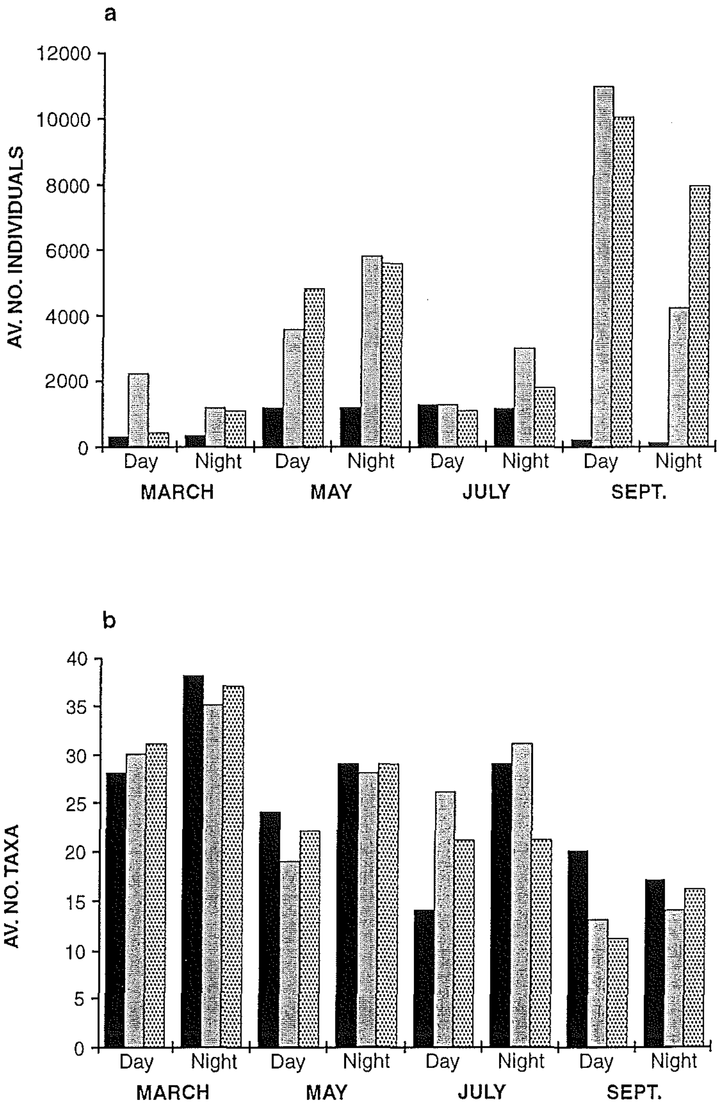


Fig. 5. (a) Average number of individuals/trawl and (b) average number of total taxa in quarterly day and night sled trawls from bare sand (solid bar), *Halodule* (gray bar), and *Thalassia* (stippled bar), Sep. 1992–Sep. 1993, Seahorse Key, Florida.

is within the range of sampling error. Based on the evidence at hand, we suspect that the food habits of early juvenile spotted seatrout at the Cedar Keys have not changed appreciably in the past half century.

Moody's (1950) extensive survey of the entire Cedar Keys area compared to our localized study at Seahorse Key and his focus on larger individuals in deeper water and our relatively low n for juvenile seatrout makes us cautious about reporting real dietary changes. However, in terms of food quality, i.e., reliance on crustacean diet, there has been little change in the diet of the juveniles in the past 50 yr. It is apparent that the juvenile seatrout <100 mm TL have switched to feeding on large hyperbenthic invertebrates. These larger organisms are abundant in the seagrasses at Seahorse Key and their use by the seatrout would represent an energy conservation measure. Habitat management to protect the SAV and the invertebrate foods at the Key bodes well for continuance of a healthy spotted seatrout community.

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