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George R. Sedberry
South Carolina Marine Resources Research Institute

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FEEDING HABITS OF SHEEPSHEAD, *Archosargus probatocephalus*, IN OFFSHORE REEF HABITATS OF THE SOUTHEASTERN CONTINENTAL SHELF

George R. Sedberry

South Carolina Marine Resources Research Institute
P.O. Box 12559, Charleston, South Carolina 29412

ABSTRACT: The feeding habits of sheepshead, *Archosargus probatocephalus*, were studied by examining contents of digestive tracts from fish collected on offshore live bottom reefs in the South Atlantic Bight. Sessile invertebrates were the most important prey for sheepshead. Smaller sheepshead (<350 mm standard length) had a diet dominated by bryozoans. Larger sheepshead also fed heavily on bryozoans, but included more bivalves, echinoderms and ascidians in the diet. Barnacles and decapods were consumed in lesser amounts by both size classes. Foraminiferans, cnidarians, polychaetes, gastropods and small arthropods were also eaten. The sessile species utilized as prey by sheepshead are common colonial organisms found on offshore reefs. Motile epifaunal species consumed by sheepshead were common species associated with hard substrates or sessile species. Predation by sheepshead may be important in regulating the structure of epifaunal communities in reef habitats.

The sheepshead, *Archosargus probatocephalus* (Walbaum), is distributed from Nova Scotia to Rio de Janeiro and is commonly associated with hard substrates such as piers and jetties in estuarine and shallow inshore waters (Johnson, 1978; Ogburn, 1984). Sheepshead are also found on the continental shelf of the South Atlantic Bight where they are associated with artificial and natural "live bottom" reefs (Struhsaker, 1969; Sedberry and Van Dolah, 1984). Although the sheepshead is common and constitutes a recreationally important species (Randall and Vergara, 1978), little is known of its life history. Johnson (1978) summarized existing information on the early life history, during which sheepshead spend their time in shallow-water grass beds, feeding on soft-bodied invertebrates. Darnell (1958) reviewed early reports on feeding habits, provided additional data on the food of sheepshead, and concluded that vegetation and hard-shelled invertebrates were the most important foods for sheepshead in shallow waters. Springer and Woodburn (1960) reported some plant material in addition to the mollusks, crustaceans (mainly amphipods) and polychaetes they found in stomachs collected in Tampa Bay. Overstreet and Heard (1982) reported a great diversity of invertebrates (mainly polychaetes, mollusks and crustaceans) and fishes from sheepshead collected in Mississippi Sound, and Ogburn (1984) reported that sheepshead fed primarily on intertidal algae and mollusks on North Carolina jetties. Little is known, however, of the ecology of sheepshead in offshore reef habitats, and the food of sheepshead in those reef areas is unknown. The purpose of this report is to describe the feeding habits of sheepshead collected from offshore live bottom reefs and to relate feeding habits to the ecology of live bottom reefs.

METHODS

Fish stomachs analyzed for feeding habits were collected during seasonal cruises in 1980 (two cruises, one in winter (January-March) and one in summer

(August-September) and 1981 [four cruises, one each winter, spring (May-June), summer, and fall (October-November)] from seven live bottom stations. Stations were located in two depth zones representing the inner (16-22 m depth, three sites) and middle (23-37 m, four sites) shelf. Inner shelf stations were located off of Charleston, South Carolina, Sapelo Island, Georgia (in Gray's Reef National Marine Sanctuary) and Jacksonville, Florida; the middle shelf stations were located off of South Carolina and Georgia. Delineation of depth zones was based on distribution of fish assemblages as noted in previous studies and on community analysis of catches in the present study (Struhsaker, 1969; Miller and Richards, 1980; Sedberry and Van Dolah, 1984; Sedberry, MS). Fish were collected primarily from standard-distance tows with a roller-rigged 40/54 high rise trawl (Hillier, 1974). This net is very effective in sampling fishes on rough bottom (Smith, 1977). Some larger fish were collected with speargun. Sampling for fishes was conducted on reef habitat which was mapped for each station using underwater television and diver observations. Detailed descriptions of station locations and fish sampling techniques are described elsewhere (Sedberry and Van Dolah, 1984; Sedberry, MS).

Sheepshead were measured (standard length, SL) at sea and their entire gastrointestinal tracts removed, individually labeled, and preserved in 10% seawater-formalin. In the laboratory, the contents of the anterior fourth of the digestive tract (to avoid bias due to differential digestion in the more posterior sections of the gut) were examined in the laboratory, sorted by taxa, counted and measured volumetrically. Colonial forms were counted as one organism. Because of the bias inherent in some methods of quantifying food habits, (Hynes, 1950; Pinkas *et al.*, 1971; Windell, 1971), the relative contribution of food items to the diet was determined using three methods: (1) percent frequency occurrence (F), (2) percent numerical abundance (N), and (3) percent volume displacement (V). Percent frequency, number and volume were calculated for prey species and for prey items grouped into higher taxonomic groups for two length categories.

RESULTS

Sheepshead were caught only occasionally by trawl at inner (1.7 per tow) and middle shelf (0.2 per tow) stations. Underwater television and diver observations (Sedberry and Van Dolah, 1984; pers. obs.), however, indicate that they are common at the stations that were sampled. Their low abundance in trawl catches probably reflects trawl avoidance or their cryptic habits.

The 42 sheepshead guts examined contained a diversity (approximately 125 species) of sessile and motile organisms. Bryozoans, pelecypod mollusks, and barnacles (Cirripedia) were the most frequently consumed taxa and each occurred in more than 70 percent of stomachs with food (Table 1). Amphipods and ascidians were also frequently consumed and several other taxa occurred in more than 50% of the stomach samples. Amphipods and barnacles were the most abundant prey; however many colonial organisms could not be counted. Bryozoans, ascidians, echinoids, and pelecypods made up most of the prey volume. Most organisms eaten by sheepshead were sessile or tubicolous forms that are firmly attached to the substrate or to other sessile animals. These included all hydroids and anthozoans, some polychaetes (e.g. *Filograna*

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Table 1. Percent frequency (F), percent number (N), and percent volume (V) of prey items found in sheepshead (*Archosargus probatocephalus*) stomachs.

PREY ITEM	F	N	V
Foraminifera			
Puteolina pseudodiscoida	12.9	0.4	<0.1
Pyrgo subsphaerica	3.2	0.1	<0.1
Quinqueloculina lamarkiana	9.7	0.3	<0.1
Trochammina inflata	6.4	0.2	<0.1
Total Foraminifera	22.6	1.0	<0.1
Cnidaria			
Hydrozoa			
Aglaophenia sp.	3.2	0.1	<0.1
Aglaophenia latecarinata	12.9	0.3	<0.1
Dynamena cornicina	25.8	0.6	<0.1
Dynamena quadrindentata	3.2	0.1	<0.1
Halecium sp. A	9.7	0.2	0.6
Monostaechas quadrindens	6.4	0.2	<0.1
Sertularella sp. A	6.4	0.2	0.1
Sertularella conica	9.7	0.2	<0.1
Sertularella pinnigera	3.2	0.1	<0.1
Sertularia marginata	3.2	0.1	<0.1
Synthecium tubitheca	6.4	0.2	<0.1
Thyroscyphus marginatus	3.2	0.1	<0.1
Total Hydrozoa	54.8	2.3	0.8
Anthozoa			
Leptogorgia virgulata	3.2	0.1	0.1
Telesto fruticulosa	48.4	1.2	1.4
Total Anthozoa	51.6	1.3	1.5
Annelida			
Polychaeta			
Arabellidae undetermined	3.2	0.1	<0.1
Ceratonereis mirabilis	3.2	0.1	<0.1
Chaetopteridae undetermined	3.2	0.1	<0.1
Cistenides gouldii	3.2	0.2	<0.1
Crucigera websteri	3.2	0.1	<0.1
Exogone dispar	3.2	0.2	<0.1
Filograna implexa	6.4	1.4	<0.1
Hydroides sp. A	9.7	0.2	<0.1
Hydroides sp. D	3.2	0.1	<0.1
Lumbrineris sp.	3.2	0.1	<0.1
Lysidice ninetta	6.4	0.2	<0.1
Maldanidae undetermined	3.2	0.1	<0.1
Nereidae undetermined	3.2	0.1	<0.1
Nereis sp.	6.4	0.3	<0.1
Nichomache trispinata	3.2	0.1	<0.1
Owenia fusiformis	3.2	0.1	<0.1
Potamilla sp. B	3.2	0.1	<0.1
Sabellaria vulgaris	6.4	0.2	<0.1
Syllis gracilis	3.2	0.1	<0.1
Terebellidae undetermined	3.2	0.1	<0.1
Websterinereis tridentata	3.2	0.1	<0.1
Total Polychaeta	51.6	3.9	0.1
Mollusca			
Gastropoda			
Astyris lunata	22.6	1.9	<0.1
Caecum cooperi	9.7	0.2	<0.1
Calliostoma pulchrum	12.9	1.3	0.1
Colubraria lanceolata	3.2	0.1	<0.1
Costoanachis avara	29.0	1.8	0.1
Crepidula aculeata	3.2	0.1	<0.1
Diodora cayenensis	3.2	0.1	0.1
Gastropoda undetermined	3.2	0.1	<0.1
Marginella sp.	3.2	0.2	<0.1
Natica canrena	3.2	0.1	<0.1
Total Gastropoda	45.2	5.9	0.3
Pelecypoda			
Anadara transversa	3.2	0.1	<0.1
Arca imbricata	3.2	0.2	7.4
Arca zebra	3.2	0.1	<0.1
Brachiodontes modiolus	3.2	0.1	<0.1
Cerithiopsis emersoni	6.4	0.2	<0.1
Chama sp.	3.2	0.1	0.1
Chama macerophylla	6.4	0.2	0.2
Chione grus	6.4	0.2	<0.1
Chione intapurpurea	3.2	0.1	<0.1
Chione latilirata	3.2	0.1	<0.1
Crassinella lunulata	3.2	0.1	<0.1
Ervilia concentrica	6.4	0.2	<0.1
Macrocallista maculata	3.2	0.2	<0.1
Mactridae undetermined	3.2	0.1	<0.1
Musculus lateralis	29.0	1.0	<0.1
Payridea soleniformis	3.2	0.1	<0.1
Pteria colymbus	41.9	2.2	2.6
Total Pelecypoda	74.2	5.0	10.4
Arthropoda			
Pycnogonida			
Anoplodactylus petiolatus	3.2	0.1	<0.1
Crustacea			
Cirripedia			
Balanus trigonus	48.4	5.1	1.8
Balanus venustus	45.2	7.6	1.2
Total Cirripedia	71.0	12.6	3.0
Isopoda			
Carpias bermudensis	3.2	0.1	<0.1
Erichsonella filiformis	3.2	0.1	<0.1
Total Isopoda	6.4	0.2	<0.1

Table 1. Cont.

PREY ITEM	F	N	V
Amphipoda			
Ampelisca sp.	9.7	0.2	<0.1
Ampelisca schellenbergi	9.7	0.4	<0.1
Caprella equilibra	25.8	3.4	<0.1
Caprella penantis	3.2	0.2	<0.1
Ceradocus sp. A	3.2	0.1	<0.1
Cerapus tubularis	32.3	3.9	<0.1
Erichthonius brasiliensis	58.1	18.0	0.1
Luconacia incerta	38.7	11.0	0.1
Lysianopsis alba	3.2	0.2	<0.1
Melita appendiculata	9.7	0.4	<0.1
Photis pugnator	51.6	11.6	0.1
Phtisica marina	3.2	0.1	<0.1
Podocerus sp.	9.7	0.4	<0.1
Stenothoe georgiana	12.9	0.3	<0.1
Total Amphipoda	64.3	50.3	0.4
Decapoda			
Batrachonotus fragosus	6.4	0.3	0.1
Brachyuran megalopae	3.2	0.1	<0.1
Hypoconcha sabulosa	3.2	0.2	0.2
Macrocoeloma camptocerum	3.2	0.2	0.2
Megalobrachium soriatum	3.2	0.2	<0.1
Metoporhaphis calcarata	6.4	0.4	1.3
Mithrax forceps	3.2	0.1	<0.1
Mithrax pleuracanthus	9.7	0.3	0.2
Neopanope sayi	3.2	0.1	<0.1
Osachila tuberosa	3.2	0.1	<0.1
Paguristes sp.	3.2	0.1	0.1
Pagurus carolinensis	9.7	0.3	<0.1
Pagurus hendersoni	3.2	0.1	<0.1
Pagurus piercei	3.2	0.1	<0.1
Pelia mutica	3.2	0.2	0.2
Pilumnus sp.	6.4	0.5	0.1
Pilumnus dasypodus	9.7	0.6	<0.1
Pilumnus sayi	9.7	0.6	0.5
Pinnotheres maculatus	6.4	0.2	<0.1
Synalpheus townsendi	3.2	0.1	<0.1
Total Decapoda	45.2	4.5	2.9
Sipunculida			
Golfingia sp.	3.2	0.1	<0.1
Bryozoa			
Aeverrillia setigera	9.7	0.2	<0.1
Amathia alternata	3.2	0.1	<0.1
Amathia distans	3.2	0.1	<0.1
Antropora leucocypha	12.9	0.3	<0.1
Bugula turrita	9.7	0.2	<0.1
Celleporaria albirostris	3.2	0.1	<0.1
Celleporaria magnifica	12.9	0.3	1.5
Chaperia galeata	3.2	0.1	<0.1
Crisia sp. A	71.0	1.8	2.6
Ctenostomata undetermined	6.4	0.2	0.3
Cupuladria doma	9.7	0.2	<0.1
Diaperoecia floridana	12.9	0.3	<0.1
Discoporella umbellata	9.7	0.2	0.2
Hippaliosina rostrigera	6.4	0.2	<0.1
Microporella ciliata	19.4	0.5	0.1
Nellia tenella	29.0	0.7	<0.1
Petraliella bisinuata	3.2	0.1	<0.1
Schizoporella cornuta	58.1	1.4	32.3
Schizoporella errata	3.2	0.1	<0.1
Schizoporella floridana	3.2	0.1	<0.1
Scrupocellaria regularis	6.4	0.2	<0.1
Stylopoma informata	3.2	0.1	<0.1
Sundanella sibogae	29.0	0.7	0.1
Turbicellepora dichotoma	41.9	1.0	0.2
Total Bryozoa	80.6	9.2	37.5
Echinodermata			
Echinoidea			
Arbacia punctulata	6.4	0.2	<0.1
Clypeasteroida undetermined	9.7	0.2	12.7
Total Echinoidea	16.1	0.4	12.7
Ophiuroidea			
Axiognathus squamatus	6.4	0.2	<0.1
Ophiothrix angulata	9.7	0.2	<0.1
Total Ophiuroidea	16.1	0.4	<0.1
Holothuroidea			
Ocnus pygmeaus	6.4	0.2	0.4
Chordata			
Ascidiacea			
Aplidium sp.	3.2	0.1	3.0
Ascidia sp.	6.4	0.9	1.5
Ascidiacea undetermined	9.7	0.2	0.6
Didemnum candidum	12.9	0.3	4.4
Molgula sp.	6.4	0.2	0.7
Molgula (?) sp.	6.4	0.2	1.4
Molgula occidentalis	3.2	0.1	0.9
Perophora sp.	3.2	0.1	<0.1
Pyura vittata	3.2	0.1	0.3
Styela plicata	19.4	0.5	17.5
Total Ascidiacea	61.3	2.6	30.2
Number of stomachs examined:		42	
Examined stomachs with food:		31	

implexa, *Hydroidea* spp.), some pelecypods (e.g. *Pteria colymbus*, *Arca* spp.), barnacles, some amphipods (e.g. *Cerapus tubularis*), and all bryozoans and ascidians. It is apparent that sheepshead are heavy grazers on live bottom reefs. Most fishes had full guts at all times of the day and a large volume of food was usually present in the entire gut.

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Attached sessile fauna dominated the volume of prey in both size groups of sheepshead examined, though larger attached pelecypods (e.g., *Arca* spp.) made up a greater portion of the diet of larger fish than that of smaller sheepshead and bryozoans were much more important in the diet of smaller sheepshead (Table 2). Barnacles were consumed in nearly the same frequency, number, and volume in both size classes. Amphipods were consumed in large numbers by both size classes, and gastropods were consumed more by smaller fish.

DISCUSSION

Previously published studies of the food of sheepshead in inshore habitats reveals striking differences in the prey of this fish between inshore and offshore habitats. Darnell (1958) found that filimentous algae and submerged aquatic tracheophytes dominated the prey volume in stomachs of 11 fish (218-410mm long) he examined. Mollusks, especially bivalves, sponges, crabs and fishes were also found. Amphipods, copepods, and polychaetes were found in 11 stomachs of small juvenile sheepshead (<50 mm) from inshore seagrass beds around Tampa Bay (Springer and Woodburn, 1960). Springer and Woodburn (1060) found that larger juveniles (51-100 mm) fed mainly on mollusks and barnacles, and some small crustaceans and algae were also noted. Wardle (1980) reported digeneic trematodes, whose intermediate host is a mussel (*Ischadium recurvum*) often consumed by sheepshead in shallow Gulf of Mexico waters (Darnell, 1958; Overstreet and Heard, 1982), from the hindgut of sheepshead from Texas. Overstreet and Heard (1982) found over 113 species of plants and animals in 125 sheepshead guts from Mississippi Sound. In contrast to the present study, they found a relatively low frequency of bryozoans and ascidians, and a greater frequency of plant material and fishes. Fishes, which were not consumed by sheepshead in the present study, were most frequent in the diet of sheepshead >350mm SL. Ogburn (1984) noted a diet dominated by intertidal algae and mussels (*Brachidontes exustus*) in sheepshead (<350mm SL) collected from jetties in North Carolina, and small sheepshead (<300mm SL, N = 4) collected from inshore waters of South Carolina (1 m depth) fed on algae and mollusks (*B. exustus*) that were abundant on the rock jetty where they were collected (Van Dolah *et al.*, 1984). Smaller sheepshead that occur in inshore waters feed heavily on algae and mollusks and apparently move to offshore reefs as they become adults, where algae become less important in their diet. Benthic algae are not common on live bottom reefs off of South Carolina, Georgia and Florida (South Carolina Wildlife and Marine Resources Department, 1981), and sheepshead found in these habitats apparently switch their diet to more abundant organisms such as bryozoans and ascidians. Although cordgrass (*Spartina alterniflora*), a source of food for many estuarine detritus feeding fishes, including sheepshead (Darnell, 1958; Overstreet and Heard, 1982), accumulates under rock outcrops and in crevices in some inner shelf live bottom areas (Office of Coastal Zone Management, 1980), vascular plant detritus was not found in any sheepshead guts in the present study.

Randall (1967) examined the stomach contents of 212 species of West Indian reef fishes and grouped species into the following categories: 1) plant and detritus feeders, 2) zooplankton feeders, 3) sessile animal feeders, 4) "shelled" in-

Table 2. Percent frequency occurrence (F), percent number (N) and percent volume (V) of higher taxonomic groups of food in the diet of *Archosargus probatocephalus*, by length interval.

	Length Intervals (mm SL)					
	<350			≥350		
Prey	F	N	V	F	N	V
Foraminifera	22.2	0.9	<0.1	23.1	1.3	<0.1
Cnidaria						
Hydrozoa	55.6	2.3	0.3	53.8	2.4	1.1
Anthozoa	66.7	1.7	2.6	30.8	0.7	0.6
Annelida						
Polychaeta	50.0	4.8	0.3	53.8	2.8	0.1
Mollusca						
Gastropoda	44.4	7.0	0.4	46.2	4.4	0.2
Pelecypoda	72.7	5.3	2.4	76.9	4.6	16.4
Arthropoda						
Pycnogonida	5.6	0.1	<0.1			
Cirripedia	77.8	14.4	3.0	61.5	10.3	3.0
Isopoda	5.6	0.1	<0.1	7.7	0.2	<0.1
Amphipoda	61.1	44.9	0.4	69.2	57.2	0.3
Decapoda	38.9	5.0	2.2	53.9	3.9	3.4
Sipunculida	5.6	0.1	<0.1			
Bryozoa	83.3	9.3	76.2	76.9	9.2	8.5
Echinodermata						
Echinoidea	11.1	0.3	<0.1	23.1	0.6	22.1
Ophiuroidea	22.2	0.6	0.1	7.7	0.2	<0.1
Holothuroidea	5.6	0.3	0.7	7.7	0.2	0.2
Chordata						
Ascidiacea	55.6	2.8	11.4	69.2	2.2	44.2
Number of stomachs examined:		26			18	
Examined stomachs with food:		18			13	
Mean length of fish with food:		304.7			410.5	

vertebrate feeders, 5) generalized carnivores on motile invertebrates and fishes, 6) ectoparasite feeders, and 7) fish feeders. Sheepshead apparently function in two of Randall's (1967) feeding guilds, being omnivorous but feeding primarily on plant material in inshore habitats and functioning as sessile animal feeders in offshore reef habitats. Sessile invertebrates dominated the volume of prey in sheepshead guts by far, and included some of the most frequently occurring species found in live bottom habitats (i.e. *Microporella ciliata, Crisia* sp. A, *Schizoporella cornuta, Balanus trigonus*) (Wenner *et al.*, 1983). Many individuals of motile crustaceans that are associated with the sessile prey of sheepshead were incidentally consumed, but they made up little of the prey volume. These motile species were mainly abundant live bottom species of amphipods that build tubes on sessile organisms (*Erichthonius brasiliensis, Cerapus tubularis*) or that cling to and feed on sessile organisms (*Caprella*

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equilibra) (Wenner *et al.,* 1983; Wenner *et al.,* 1984; Knott *et al.,* in prep.)

Predation can be an important factor in regulating the structure of sessile communities (Peterson, 1979). Because sheepshead feed heavily on live bottom sessile invertebrates, they may be important in contributing to the high diversity (Wenner *et al.,* 1983, Wenner *et al.,* 1984) found in the live bottom sessile fauna. Sutherland (1978) reported that *Schizoporella unicornis* (= *S. errata* of later authors), an encrusting bryozoan very similar in form and functional role to *S. cornuta*, and the ascidian *Styela plicata* are able to colonize available space to the exclusion of other species. *Styela plicata* is also capable of invading space occupied by other species. Both of these species serve to stabilize the fouling community at a low diversity level (Sutherland, 1978). *Styela plicata* and *S. cornuta* (similar to *S. unicornis*) may function in a similar manner if left undisturbed in hard bottom habitat, i.e. they may monopolize and stabilize the community at a low diversity level. However, these two species were the top ranking prey, by volume, for sheepshead. If these species function in live bottom areas as they do in shallow water fouling communities (Sutherland, 1978) then sheepshead are probably very important in controlling the structure of sessile invertebrate communities in live bottom habitats by reducing the abundance of these competitively superior species.

Predation by sheepshead may also be a contributing factor in the regulation of the structure of live bottom motile epifauna communities. Some of the most abundant motile prey species found in sheepshead guts are species that are prolific and opportunistic [as indicated by their early colonizing ability (Knott *et al.,* in prep.)] inhabitants of live bottom communities, such as *Erichthonius brasiliensis* and *Caprella equilibra.* By cropping off these opportunistic species, predation by sheepshead may allow more motile epifaunal species to co-exist (Dayton and Hessler, 1972; Virnstein, 1977; Peterson, 1979).

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