Feeding Habits of Whitebone Porgy, *Calamus leucosteus* (Teleostei: Sparidae), Associated with Hard Bottom Reefs off the Southeastern United States[1]

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ABSTRACT: The feeding habits of whitebone porgy, *Calamus leucosteus*, were investigated by examining stomachs of specimens collected from hard bottom reef habitat on the southeastern continental shelf and by comparing stomach samples with benthic samples and with stomach samples from four other sparids collected from the same habitat. Whitebone porgy were found to feed mainly on small hard-shelled species of gastropods, pagurid decapods, and sipunculids. Polychaetes, pelecypods, barnacles, and fishes were also eaten. Fishes and echinoderms were consumed by larger individuals. Whitebone porgy selected invertebrate species that were not abundant in benthic samples from the reef, suggesting that these fish forage on sand bottom fauna. Patterns of diet overlap with other reef-associated sparids appeared to be related to feeding morphology and feeding habitat. Overlap in diet between whitebone porgy and southern porgy, *Stenotomus aculeatus*, was low, although both species forage on sand bottom organisms. Pinfish, *Lagodon rhomboides*, fed mainly on a sessile reef amphipod that was rarely consumed by whitebone porgy. Whitebone porgy had a higher diet overlap with sheepshead, *Archosargus probatocephalus*, and with red porgy, *Pagrus pagrus*, because all three species fed on barnacles not consumed by other sparids examined.

The whitebone porgy, *Calamus leucosteus*, distributed from the Carolinas through the Gulf of Mexico (Randall 1978), is an abundant sparid fish on the continental shelf of the South Atlantic Bight, where it is an important component of trawl and hook-and-line fisheries (Huntsman 1976; Waltz et al. 1982). Whitebone porgy are found in depths of 11–88 m on the continental shelf of the southeastern coast of the United States, but they are most abundant in depths < 30 m (Waltz et al. 1982). The continental shelf at these depths consists primarily of sandy bottom, with occasional scattered outcrops of sedimentary rock (Struhsaker 1969), and, although whitebone porgy frequently occur on sand bottom, they are much more abundant in rocky reef habitats (Wenner et al. 1980; Waltz et al. 1982). These hard bottom habitats support a greater abundance and biomass of large sessile invertebrates (e.g., sponges, corals, tunicates) and associated motile organisms than do sand bottom areas of the shelf (Struhsaker 1969; Wenner 1983; Wenner et al. 1983; Sedberry and Van Dolah 1984; Wenner et al. 1984; Wendt et al. 1985). Many of these invertebrates serve as prey for fishes that are closely associated with the reef habitat (Manooch 1977; Sedberry 1987, 1988). Other species of fishes are less closely associated with hard bottom reefs, and, while living on or in proximity to these reefs, do much of their foraging in sand bottom habitats on the shelf (Sedberry 1985). Although whitebone porgy appear to be a reef-associated species, their dependence on reef habitat and the abundance of prey provided by these habitats are unknown. Although hard bottom reefs support a high biomass of potential prey for fishes, many species of predatory fish are concentrated in these habitats (Sedberry and Van Dolah 1984), and competition for prey may be intense, particularly among closely related species. Several other sparids are abundant in hard bottom reef communities and competition for food among these species could be as intense. Although the food habits of some of these more common sparids have been reported from offshore reef habitats (Manooch 1977; Sedberry 1987), overlap in diet among the species has not been investigated.

The purpose of this study is to describe the food habits of whitebone porgy, to determine the importance of hard bottom reef habitat as foraging grounds for this species, and to determine diet overlap between whitebone porgy and some

[1]Contribution No. 281 from the South Carolina Marine Resources Center.

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Manuscript accepted April 1989.
Fishery Bulletin, U.S. 87: 935–944.

other abundant sparid fishes from the same habitat.

METHODS

Stomachs of fish analyzed for food habits were collected during six trawl cruises on the continental shelf in 1980 and 1981. Stomachs of whitebone porgy were taken at 11 hard bottom stations distributed among 3 depth zones representing the inner shelf (16–22 m depth, three stations), middle shelf (23–37 m depth, four stations), and the outer shelf (46–69 m depth, four stations). Delineation of depth zones was based on distribution of fish and invertebrate species assemblages as noted in previous studies and on community analysis of trawl catches used in the present study (Struhsaker 1969; Miller and Richards 1980; Sedberry and Van Dolah 1984; Wenner et al. 1984). Fishes were collected primarily in trawl tows as described elsewhere (Sedberry and Van Dolah 1984; Wenner et al. 1984; Sedberry 1985). A few specimens were collected with trap or hook and line. Sampling for fishes was conducted on hard bottom habitat, which was mapped for each station using underwater television (Sedberry and Van Dolah 1984).

Whitebone porgy were measured (standard length, SL) at sea, and their stomachs were preserved in 10% seawater formalin. Contents of individual stomachs were then sorted in the laboratory by taxa, counted, and measured volumetrically. The relative contribution of food items to the diet was described by percent frequency occurrence (F), percent numerical abundance (N), and percent volume displacement (V). F, N, and V were calculated for prey species and for prey items grouped into higher taxonomic categories, for 50 mm intervals of SL.

In order to determine the selectivity or dependence of demersal fishes on hard bottom prey organisms, stomach samples were compared with benthic samples using Ivlev's index of electivity (Ivlev 1961). Electivity values range from -1 to $+1$. Negative values imply that the prey species is avoided by the predator or that it is unavailable to the predator. Positive values imply that the predator prefers the prey species or that it is feeding on prey species that occur in a different habitat than that sampled by the benthic sampler. A value near zero implies no selectivity by the predator; i.e., the fish is feeding on the prey in proportion to the prey's relative abundance in samples taken in the habitat.

The electivity index was calculated for species that were numerically dominant in benthic samples or in fish stomach samples which were pooled by depth zone (inner, middle, and outer shelves) for comparison. Benthic samples were obtained at the 11 hard bottom sites during 1980 and 1981 with a suction device (inner and middle shelves) or a grab (outer shelf). Divers obtained five replicate suction samples at each inner and middle shelf station by scraping the hard substrata enclosed by a 0.1 m^2 quadrat box, while simultaneously sucking with an airlift device similar to that described by Chess (1979). Suction samples were collected in 1.0 mm mesh bags. At the outer shelf stations where water depth precluded the use of the suction device operated by divers, quantitative samples (five copies) were collected with a 0.1 m^2 Smith-McIntyre grab. After retrieval, each sample was placed into a 1.0 mm sieve and washed to remove the finer sediment.

Sampling motile benthic invertebrates with the suction sampler proved to be a very simple, yet effective, technique. Samples were quantitative because suctioning effectively collected everything within the confines of the walled box placed on the substratum. The Smith-McIntyre grab, which was substituted for the suction sampler at deeper stations, was somewhat less quantitative because the sampler is not as effective on hard substrate, and the actual area sampled was unknown. In spite of these limitations, the grab sampler was the only feasible means of sampling the benthos at outer shelf stations and provided the only benthic collections with which to calculate electivity.

Similarity in diet between whitebone porgy and four other co-occurring and frequently collected sparids was also investigated. Stomach samples of these additional species were collected at the same time as the whitebone porgy stomachs and were analyzed in a similar manner (South Carolina Wildlife and Marine Resources Department 1984; Sedberry 1987). These other sparids were sheepshead, *Archosargus probatocephalus;* pinfish, *Lagodon rhomboides;* red porgy, *Pagrus pagrus*; and southern porgy, *Stenotomus aculeatus.*

Similarity in diet between these sparids was measured using the Bray-Curtis measure (Bray and Curtis 1957). Because sample sizes of predators were unequal, abundance of prey items was standardized as percent numerical abundance for each predator, resulting in values of percent similarity in composition of diet between pairs of predator species (Clifford and Stephenson 1975; Boesch 1977). Only prey items that were identified to species were included in the similarity analyses. To reduce the data matrix to a size that could be accommodated by the computer program and to eliminate very rare prey species that were not important in the diet of any sparid, only prey species that occurred more than once were included in the analysis.

RESULTS

Whitebone porgy were common in all three depth zones, but they were more abundant at middle and outer shelf stations (5.6 and 5.8 fish per tow, respectively) than on the inner shelf (2.6 fish per tow). Other sparids examined overlapped in depth distribution with whitebone porgy. Sheepshead occurred at inner (1.7 fish per tow) and middle (0.2 per tow) shelf stations. Pinfish (6.2, 1.1, and < 0.1 fish per tow for inner, middle, and outer shelf stations, respectively) and southern porgy (376.8, 562.8, and 0.9 fish per tow) occurred in all three depth zones; red porgy was collected only on the middle (1.4 fish per tow) and outer (5.6 fish per tow) shelf stations.

Whitebone porgy stomachs (N = 219) contained at least 135 species of invertebrates and fishes. Decapods were the most important prey and ranked high in frequency, number, and volume (Table 1). Very small hermit crabs (*Pagurus* spp., *Dardanus* spp., *Paguristes* spp., *Pylopagurus* spp., other Paguroidea) were the dominant decapods in whitebone porgy stomachs, and they sometimes were found along with their gastropod shells, which were usually very damaged. Gastropods were important prey and sipunculids, especially the species *Aspidosiphon gosnoldi* which occupies gastropod shells, were frequently consumed. Gastropods and *Aspidosiphon* sipunculids were often found without their shells. Because mollusk shells were infrequently swallowed by whitebone porgy, many gastropods and pelecypods could not be identified. The gastropod *Costoanachis avara* was the most abundant identifiable mollusk in whitebone porgy stomachs. Other important prey for whitebone porgy included polychaetes, pelecypods, barnacles, and fishes.

TABLE 1.—Percentage of frequency occurrence (F), percentage of number (N), and percentage of volume (V) of prey items and higher taxonomic groups of food in the diet of whitebone porgy, *Calamus leucosteus*.

Taxon Prey item	F	N	V
Algae undetermined	1.3	0.2	<0.1
Porifera undetermined	0.6	0.1	0.2
Cnidaria			
Hydrozoa			
Dynamena sp.	0.6	0.1	<0.1
Halecium sp.	1.3	0.2	<0.1
Total Hydrozoa	1.9	0.2	<0.1
Anthozoa			
Actiniaria undetermined	5.7	0.7	1.5
Athenaria undetermined	8.2	2.4	4.5
Renilla reniformis	1.3	0.2	2.6
Total Anthozoa	15.1	3.3	8.6
Nemertinea undetermined	1.3	0.4	2.0
Annelida			
Polychaeta			
Aglaophamus verrilli	0.6	0.1	<0.1
Ampharete acutifrons	1.3	0.2	<0.1
Amphinomidae undetermined	0.6	0.1	<0.1
Arabella iricolor	0.6	0.1	0.2
Arabella mutans	1.9	0.2	1.0
Arabellidae undetermined	0.6	0.1	0.2
Armandia maculata	0.6	0.2	<0.1
Capitellidae undetermined	0.6	0.1	0.1
Cirratulidae undetermined	1.9	0.2	0.3
Polychaeta—*Con.*			
Diopatra cuprea	1.9	0.2	0.5
Dodecaceria corallii	0.6	0.1	<0.1
Eunice vittata	1.3	0.2	<0.1
Eunicidae undetermined	0.6	0.1	<0.1
Glycera americana	0.6	0.1	<0.1
Glycera sp.	0.6	0.2	0.1
Hydroides crucigera	0.6	0.1	<0.1
Leiochrides pallidior	0.6	0.2	<0.1
Lumbrineris coccinea	0.6	0.1	0.2
Lumbrineris inflata	0.6	0.1	<0.1
Lumbrineris latreilli	0.6	0.1	<0.1
Maldanidae undetermined	5.0	0.7	0.5
Nephtyidae undetermined	2.5	0.3	<0.1
Nephtys incisa	0.6	0.1	<0.1
Nereidae undetermined	0.6	0.1	<0.1
Nichomachinae undetermined	0.6	0.1	0.2
Onuphidae undetermined	1.3	0.2	1.5
Onuphis eremita	2.5	0.4	0.6
Onuphis nebulosa	1.3	0.6	0.4
Onuphis pallidula	0.6	0.1	<0.1
Onuphis sp.	1.3	0.2	<0.1
Opheliidae undetermined	0.6	0.1	<0.1
Paranaitis polynoides	0.6	0.1	<0.1
Petaloproctus socialis	0.6	0.1	<0.1
Phyllodoce longipes	0.6	0.1	<0.1

TABLE 1.—*Continued.*

Taxon Prey item	F	N	V
Annelida—*Con.*			
Polychaeta—*Con.*			
Phyllococe sp.	0.6	0.1	<0.1
Phyllodocidae undetermined	1.3	0.2	<0.1
Polychaeta undetermined	22.6	3.1	1.4
Polydora commensalis	0.6	0.1	<0.1
Psammolyce ctenidophora	0.6	0.1	0.3
Scalibregmidae undetermined	1.3	0.2	0.1
Sigalionidae undetermined	1.3	0.2	<0.1
Spionidae undetermined	0.6	0.1	<0.1
Sthenelais boa	0.6	0.1	<0.1
Sthenelais sp.	1.3	0.2	0.1
Syllidae undetermined	1.3	0.2	0.1
Syllis sp. F	0.6	0.1	<0.1
Terebellidae undetermined	0.6	0.1	0.4
Travisia parva	0.6	0.1	<0.1
Websterinereis sp.	1.3	0.2	<0.1
Total Polychaeta	46.5	9.6	8.6
Mollusca			
Gastropoda			
Buccinidae undetermined	1.3	0.2	0.1
Caecum pulchellum	0.6	0.1	<0.1
Calliostoma baridi	1.9	0.4	0.2
Cerithidea sp.	0.6	0.1	<0.1
Cymatium krebsii	0.6	0.2	<0.1
Costoanachis avara	6.9	2.1	0.2
Costoanachis sp.	0.6	0.1	<0.1
Diodora cayenensis	0.6	0.1	0.5
Epitonium sp.	3.1	2.0	0.4
Epitonium multistriatum	0.6	0.1	<0.1
Fissurellidae undetermined	0.6	0.1	0.2
Gastropoda undetermined	46.5	13.8	7.7
Marginella sp.	1.3	0.2	0.1
Marginella hartleyanum	3.8	1.8	0.9
Marginellidae undetermined	1.9	0.3	0.2
Natica canrena	1.9	0.4	0.2
Naticidae undetermined	4.4	1.1	0.8
Trochidae undetermined	0.6	0.1	<0.1
Total Gastropoda	58.5	23.0	11.4
Pelecypoda			
Americardia media	0.6	0.1	<0.1
Anadara sp.	0.6	0.1	0.7
Brachidontes sp.	0.6	0.1	<0.1
Chione latilirata	1.3	0.2	<0.1
Corbula contracta	3.1	0.5	0.3
Corbula dietziana	0.6	0.2	0.2
Dinocardium robustum	1.9	0.2	0.3
Ervilia concentrica	2.5	0.4	0.3
Glycymeris pectinata	0.6	0.1	<0.1
Laevicardium sp.	0.6	0.2	0.2
Laevicardium laevigatum	3.1	0.5	0.4
Laevicardium pictum	2.5	0.4	0.4
Pectinidae undetermined	1.9	0.2	0.2
Pelecypoda undetermined	11.3	2.0	4.9
Pitar fulminatus	0.6	0.1	<0.1
Pleuromeris tridentata	0.6	0.1	<0.1
Solemya velum	0.6	0.1	0.2
Pelecypoda—*Con.*			
Solenidae undetermined	0.6	0.1	<0.1
Tellina sp.	1.9	0.3	0.1
Total Pelecypoda	21.4	5.6	8.4
Cephalopoda undetermined	0.6	0.1	<0.1
Crustacea			
Ostracoda undetermined	0.6	0.2	<0.1
Copepoda undetermined	0.6	0.1	<0.1
Cirripedia			
Balanoidea undetermined	1.3	0.4	0.5
Balanus sp.	1.9	0.2	<0.1
Balanus trigonus	10.7	5.0	2.6
Balanus venustus	6.3	3.4	1.8
Total Cirripedia	14.5	9.0	5.0
Stomatopoda undetermined	2.5	0.4	0.2
Mysidacea			
Bowmaniella portoricensis	1.9	0.4	<0.1
Mysidae undetermined	0.6	0.1	<0.1
Total Mysidacea	2.5	0.4	<0.1
Cumacea			
Bodotriidae undetermined	0.6	0.1	<0.1
Cyclaspis varians	0.6	0.1	<0.1
Oxyurostylis smithi	4.4	0.7	<0.1
Total Cumacea	5.7	0.8	<0.1
Isopoda			
Apanthura magnifica	0.6	0.1	<0.1
Total Isopoda	0.6	0.1	<0.1
Amphipoda			
Ampelisca sp.	2.5	0.3	<0.1
Ampelisca cristoides	1.3	0.2	<0.1
Ampelisca schellenbergi	0.6	0.1	<0.1
Ampelisca vadorum	1.9	0.3	0.1
Ampelisca venetiensis	0.6	0.2	0.1
Carinobatea carinata	0.6	0.1	<0.1
Caprellidae undetermined	0.6	0.1	<0.1
Corophiidae undetermined	0.6	0.2	<0.1
Elasmopus sp. A	0.6	0.1	<0.1
Erichthonius sp. A	1.3	0.2	<0.1
Erichthonius brasiliensis	2.5	0.3	<0.1
Gammaridea undetermined	3.8	0.6	<0.1
Haustoriidae undetermined	1.9	0.2	<0.1
Lembos smithi	0.6	0.1	<0.1
Lembos spinicarpus inermis	0.6	0.1	<0.1
Lembos unicornis	0.6	0.1	<0.1
Melita appendiculata	0.6	0.1	<0.1
Metharpinia floridanus	1.9	0.4	0.1
Photis sp.	0.6	0.1	<0.1
Phtisica marina	1.9	0.2	<0.1
Podocerus sp. A	0.6	0.1	<0.1
Rhepoxynius epistomus	0.6	0.1	<0.1
Tiron tropakis	0.6	0.1	<0.1
Total Amphipoda	21.4	3.8	0.4

TABLE 1.—*CONTINUED.*

Taxon Prey item	*F*	*N*	*V*
Crustacea—*Con.*			
Decapoda			
Albunea sp	1.3	0.2	0.4
Alpheidae undetermined	1.3	0.3	0.2
Anomura undetermined	0.6	0.2	<0.1
Automate sp.	0.6	0.1	<0.1
Brachyura undetermined	17.0	2.3	3.0
Calappidae undetermined	0.6	0.1	0.1
Callianassa sp.	0.6	0.1	<0.1
Callianassa atlantica	1.3	0.2	0.4
Caridea undetermined	0.6	0.1	<0.1
Dardanus sp.	1.9	0.4	0.1
Diogenidae undetermined	0.6	0.1	<0.1
Dissodactylus mellitae	0.6	0.1	<0.1
Euceramus praelongus	0.6	0.1	0.1
Hepatus epheliticus	1.3	0.2	0.8
Hippidae undetermined	0.6	0.1	<0.1
Hypoconcha arcuata	3.1	0.5	1.3
Iridopagurus dispar	3.1	1.1	0.3
Leptochela sp.	1.9	0.2	<0.1
Leptochela papulata	3.1	1.1	0.4
Majidae undetermined	2.5	0.3	0.4
Mithrax pleuracanthus	0.6	0.1	0.7
Munida irrasa	0.6	0.1	<0.1
Natantia undetermined	5.7	0.7	0.6
Natantia undetermined zoea	0.6	0.1	<0.1
Osachila sp.	0.6	0.2	2.8
Osachila tuberosa	0.6	0.4	0.2
Paguridae undetermined	13.2	2.8	0.7
Paguridea undetermined	8.8	1.2	0.2
Paguristes sp.	1.3	0.2	0.1
Paguristes tortugae	1.3	0.2	<0.1
Pagurus sp.	12.6	3.4	0.8
Pagurus carolinensis	17.0	3.3	0.7
Pagurus hendersoni	17.0	5.1	0.9
Pagurus longicarpus	0.6	0.1	<0.1
Pagurus piercei	2.5	0.3	0.2
Panulirus sp. larvae	0.6	0.1	<0.1
Parthenope sp.	0.6	0.1	0.3
Parthenopidae undetermined	1.3	0.2	0.1
Penaeidae undetermined	0.6	0.2	0.5
Periclimenaeus sp.	0.6	0.1	<0.1
Pilumnus dasypodus	0.6	0.1	<0.1
Pinnixa sp.	0.6	0.1	<0.1
Pinnotheres sp.	0.6	0.1	<0.1
Podochela gracilipes	0.6	0.1	0.1
Portunidae undetermined	2.5	0.3	0.5
Portunus spinicarpus	0.6	0.1	0.1
Pseudomedaeus agassizii	0.6	0.1	0.1
Pylopagurus sp.	0.6	0.1	<0.1
Pylopagurus corallinus	0.6	0.1	<0.1
Pylopagurus discoidalis	0.6	0.1	<0.1
Pylopagurus holthuisi	1.9	0.4	0.1
Synalpheus townsendi	0.6	0.1	0.1
Xanthidae undetermined	1.9	0.2	0.1
Total Decapoda	70.4	27.8	17.3
Crustacea undetermined	1.9	0.2	<0.1
Sipunculida			
Aspidosiphon gosnoldi	17.6	6.2	0.6
Phascolopsis gouldi	1.3	0.2	0.9
Sipunculida undetermined	3.1	0.4	1.5
Sipunculus nudus	0.6	0.1	2.7
Total Sipunculida	22.6	7.0	5.8
Brachiopoda			
Glottidia pyramidata	2.5	0.6	0.1
Total Brachiopoda	2.5	0.6	0.1
Bryozoa			
Antropora tincta	0.6	0.1	<0.1
Bryozoa undetermined	0.6	0.1	<0.1
Diaperoecia floridana	0.6	0.1	<0.1
Hippoporidra janthina	2.5	0.3	0.1
Schizoporella cornuta	3.8	0.4	0.1
Total Bryozoa	6.3	1.0	0.2
Echinodermata			
Asteroidea			
Asteroidea undetermined	0.6	0.1	0.1
Astropecten sp.	3.8	0.4	3.2
Astropecten articulatus	1.9	0.2	1.4
Astropecten duplicatus	1.3	0.3	0.7
Echinaster sp.	1.9	0.3	0.5
Luidia sp.	0.6	0.1	0.5
Luidia alternata	1.9	0.2	2.1
Total Asteroidea	12.0	1.6	8.4
Echinoidea			
Clypeasteroida undetermined	0.6	0.1	<0.1
Echinoidea undetermined	3.1	0.4	1.7
Total Echinoidea	3.8	0.4	1.8
Ophiuroidea undetermined	17.6	2.0	1.2
Holothuroidea			
Holothuroidea undetermined	1.9	0.2	1.4
Thyone sp.	1.3	0.2	4.4
Total Holothuroidea	2.5	0.4	5.8
Chordata			
Ascidiacea undetermined	0.6	0.1	1.8
Pisces			
Bothidae undetermined	0.6	0.1	0.8
Decapterus punctatus	0.6	0.1	0.6
Ogcocephalus parvus	0.6	0.1	1.2
Synodus sp.	0.6	0.1	3.6
Teleostei undetermined	9.4	1.4	6.6
Fish scales	0.6	0.1	<0.1
Total Pisces	12.0	1.8	12.8
Number of stomachs examined		219	
Examined stomachs with food		159	

Whitebone porgy (99–315 mm SL) demonstrated slight changes in feeding habits with increasing size (Table 2). Anthozoans and barnacles (Cirripedia) appeared to be more frequent in the smallest size class, but this may be a result of the small sample of fish < 151 mm SL. Decapods were frequently consumed by all size classes; however, because most decapods eaten were tiny species of hermit crabs, this taxon contributed a much smaller proportion of the prey volume for fish larger than 150 mm SL. Gastropods and sipunculids were also consumed by all size classes. Fishes increased in volumetric importance in the diet of fish up to a length of 250 mm but were not frequently consumed by the largest fish. Echinoderms were more important in the diet of larger whitebone porgy.

Suction and grab samples from the hard bottom stations were dominated by tube-reef building polychaetes, such as *Filograna implexa*, *Phyllochaetopterus socialis*, and *Pista palmata*, as well as epifaunal amphipods (*Erichthonius brasiliensis*, *Luconacia incerta*) that cling to or build tubes on hard substrates or other epibenthic organisms. These species were generally not consumed by whitebone porgy in any

TABLE 2.—Percentage of frequency occurrence (*F*), percentage of number (*N*), and percentage of volume (*V*) of higher taxonomic groups of food in the diet of whitebone porgy, by length interval.

	Length intervals (mm SL)											
	<151			151–200			201–250			>250		
Prey	*F*	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*
Algae							3.2	0.3	<0.1			
Porifera										2.3	0.3	0.3
Cnidaria												
Hydrozoa				4.4	0.6	<0.1				2.3	0.3	<0.1
Anthozoa	37.5	9.8	10.0	10.9	4.4	14.8	14.5	2.4	5.8	16.3	2.9	9.2
Nemertinea				2.2	1.1	12.7	1.6	0.2	0.3			
Annelida												
Polychaeta	25.0	9.8	6.9	47.8	9.4	11.6	48.4	8.8	6.8	46.5	11.1	9.3
Mollusca												
Gastropoda	12.5	2.4	0.2	58.7	26.9	16.2	66.1	24.9	11.2	55.8	17.9	10.4
Pelecypoda	12.5	9.8	14.4	21.7	4.2	12.0	22.6	5.8	7.6	20.9	6.4	7.8
Cephalopoda				2.2	0.3	0.1						
Crustacea												
Ostracoda										2.3	0.6	<0.1
Copepoda							1.6	0.2	<0.1			
Cirripedia	37.5	17.1	17.2	8.7	2.5	2.5	14.5	10.4	5.0	16.3	12.3	5.3
Stomatopoda	12.5	2.4	1.0				1.6	0.2	0.2	4.6	0.9	0.2
Mysidacea				8.7	1.7	0.2						
Cumacea				8.7	1.1	0.1	3.2	0.6	<0.1	7.0	0.9	<0.1
Isopoda							1.6	0.2	<0.1			
Amphipoda				17.4	4.2	0.8	29.0	4.3	0.5	18.6	2.9	0.2
Decapoda	50.0	26.8	43.3	71.7	31.7	14.2	71.0	23.0	11.4	72.1	32.8	22.8
Crustacea undetermined				6.5	0.8	0.1						
Sipunculida	12.5	17.1	6.9	23.9	6.7	4.2	33.9	9.5	11.4	7.0	1.5	1.2
Brachiopoda				2.2	0.8	0.2	3.2	0.6	0.1	2.3	0.3	<0.1
Bryozoa							14.5	1.8	0.4	2.3	0.6	0.2
Echinodermata												
Asteroidea				4.4	0.6	5.7	12.9	1.6	7.6	20.9	2.9	10.4
Echinoidea							4.8	0.5	0.4	7.0	0.9	3.6
Ophiuroidea	12.5	2.4	<0.1	15.2	1.9	0.8	21.0	2.1	2.4	16.3	2.0	0.4
Holothuroidea										9.3	1.5	13.1
Chordata												
Ascidiacea										2.3	0.3	4.0
Pisces	12.5	2.4	0.1	8.7	1.1	4.0	19.4	2.7	28.9	4.6	0.6	1.5
Number of stomachs examined		11			62			86			60	
Examined stomachs with food		8			46			62			43	
Mean length of fish with food		125.2			183.7			223.5			272.2	

of the three depth zones (Table 3). Rather, whitebone porgy fed selectively on hard-shelled invertebrate species that were collected only occasionally, or not at all, in suction and grab samples. Many of these prey species are apparently more common in sand bottom habitat (see Discussion).

Whitebone porgy displayed a relatively high similarity in diet to red porgy and sheepshead; overlap in diet with pinfish and southern porgy was low (Table 4).

DISCUSSION

Published information on the diet of *Calamus leucosteus* is lacking. Randall (1967) and Darcy (1986) reported on the food habits of several other Atlantic species of *Calamus* and noted a high incidence of shelled invertebrates such as mollusks, crabs, and echinoids in their diets. Randall (1967) also noted that those *Calamus* spp. which fed on hermit crabs were largely gastropod feeders as well and that sipunculids

TABLE 3.—Relative abundance (percentage of total number of individuals) and electivity values (E) for dominant benthic species in suction and grab samples and in whitebone porgy stomachs. Dominant species include those that ranked in the five most abundant species within stomach or benthic samples in any depth zone for collections pooled for all seasons and years.

	Inner shelf			Middle shelf			Outer shelf		
	Fish stomachs	Benthic samples	E	Fish stomachs	Benthic samples	E	Fish stomachs	Benthic samples	E
Dominant species—benthic samples									
Chone americana	—	0.33	−1.00	—	0.81	−1.00	—	0.59	−1.00
Erichthonius brasiliensis	0.20	2.89	−0.87	0.18	0.30	−0.25	0.66	0.13	−0.66
Erichthonius sp. A	—	0.08	−1.00	—	—	—	0.66	3.75	−0.70
Exogone dispar	—	3.71	−1.00	—	0.47	−1.00	—	0.01	−1.00
Filograna implexa	—	20.42	−1.00	—	63.87	−1.00	—	21.90	−1.00
Luconacia incerta	—	3.27	−1.00	—	1.03	−1.00	—	0.18	−1.00
Malacoceros glutaeus	—	0.41	−1.00	—	0.81	−1.00	—	0.02	−1.00
Phyllochaetopterus socialis	—	0.21	−1.00	—	0.12	−1.00	—	12.40	−1.00
Pista palmata	—	0.09	−1.00	—	0.08	−1.00	—	8.60	−1.00
Podocerus sp. A	—	2.87	−1.00	0.18	0.27	−0.19	—	0.14	−1.00
Spiophanes bombyx	—	0.39	−1.00	—	0.46	−1.00	—	5.81	−1.00
Syllis spongicola	—	2.14	−1.00	—	1.90	−1.00	—	1.38	−1.00
Total	0.20	36.81		0.36	70.12		1.32	54.92	
Dominant species—stomachs									
Costoanachis avara	2.15	0.02	0.98	3.27	<0.01	0.99	—	—	—
Aspidosiphon gosnoldi	12.13	1.63	0.76	3.99	0.46	0.79	0.33	0.09	0.57
Glottidia pyramidata	0.20	0.01	0.88	—	0.01	−1.00	2.31	0.07	0.94
Iridopagurus dispar	—	—	—	0.36	0.01	0.97	4.29	0.07	0.97
Leptochela papulata	—	0.04	−1.00	2.54	0.09	0.93	0.33	0.12	0.46
Marginella hartleyanum	4.70	0.14	0.94	0.18	0.01	0.87	—	0.03	−1.00
Onuphis nebulosa	—	0.01	−1.00	—	0.05	−1.00	2.64	0.56	0.65
Osachila tuberosa	—	<0.01	−1.00	—	<0.01	−1.00	1.98	0.02	0.98
Pagurus carolinensis	2.35	0.40	0.71	4.36	0.30	0.87	2.97	0.07	0.96
Pargurus hendersoni	6.46	0.26	0.92	5.81	0.11	0.96	1.65	0.11	0.88
Total	27.99	2.51		20.51	1.05		16.50	1.14	

TABLE 4.—Percentage of similarity in diet (Bray-Curtis index) between sparid fishes collected from hard bottom habitats.

Species	*C. leucosteus*	*L. rhomboides*	*P. pagrus*	*S. aculeatus*
A. probatocephalus	0.182	0.369	0.125	0.207
C. leucosteus		0.053	0.264	0.060
L. rhomboides			0.037	0.249
P. pagrus				0.076

(*Aspidosiphon* spp.) were occasionally consumed by West Indian *Calamus*. Fishes of the genus *Calamus* have broad molariform teeth (Gregory 1933) that are used to crush the shells of gastropods, hermit crabs, and other invertebrates equipped with hard protective shells, and this is reflected in the food of *C. leucosteus* in the South Atlantic Bight. The motile gastropod shell is apparently a visual stimulus to whitebone porgy, which results in ingestion of the shell regardless of its inhabitant. Gastropods, hermit crabs, and sipunculids that were eaten consisted of very small species. All occupied similarly sized shells, and collumbellid shells (e.g., *Costoanachis avara* and *C. avara* shells occupied by other organisms) were the most frequently found shells in stomach samples.

Whitebone porgy demonstrated a relatively small change in food habits with increasing fish size. This is unusual for sparid fishes, many species of which switch between a herbivorous habit and an omnivorous or carnivorous habit during different life history stages (Christensen 1978; Ogburn 1984; Stoner and Livingston 1984; Darcy 1985a, b; Sedberry 1987). Many of these other sparids occupy grass beds or intertidal waters at certain life history stages and feed on tracheophytes and algae that are common on those shallow-water habitats. Whitebone porgy, like other sparids found in offshore habitats where algae are uncommon, do not feed on plant material (Manooch 1977; Sedberry 1983, 1987).

Most of the invertebrate species that dominated in benthic collections from the hard bottom habitat were not important in the diet of whitebone porgy. Most of these were polychaetes and amphipods that may have been too small to be consumed by a generalized predator like whitebone porgy; however, whitebone porgy probably does not forage directly on hard-bottom reef species, regardless of their size. Dominant prey species such as *Aspidosiphon gosnoldi*, *Glottidia pyramidata*, and *Onuphis nebulosa* are inhabitants of sandy bottoms (Wells and Gray 1964; Cutler 1973; Gardiner 1975; Cooper 1977; Fauchald and Jumars 1979), and *Leptochela papulata* is also commonly found in sandy habitats (Williams 1984).

Calamus leucosteus had a relatively high overlap in diet with *Pagrus pagrus* and *Archosargus probatocephalus*. Pagurid decapods and especially the barnacle *Balanus trigonus* were common in the diet of these three predators but were not consumed by the other sparids examined (South Carolina Wildlife and Marine Resources Department 1984). Aside from a sessile barnacle species, however, few other sessile organisms were consumed by whitebone porgy or red porgy. Red porgy fed mainly on motile decapods and fishes and can be classified as a generalized predator of motile organisms. *Archosargus probatocephalus* appeared to depend more on hard bottom habitat for feeding (Sedberry 1987); whereas, *Calamus leucosteus* fed on a combination of motile invertebrates and fishes, in addition to some hard bottom epifaunal species.

Stenotomus aculeatus had a low overlap in diet with whitebone porgy. Southern porgy, like whitebone porgy, are frequently taken in trawls over sand bottoms (Wenner et al. 1980), but they are not nearly as abundant as they are in hard bottom habitats (Sedberry and Van Dolah 1984). Southern porgy had a diet dominated by a pelecypod (*Ervilia concentrica*) and a cumacean (*Oxyurostylis smithi*) that are infaunal sand dwelling species (Van Engel 1972; Porter 1974); by planktonic species (copepods, *Calanopia americana*, and the caprellid *Phtisica marina*); and by an epifaunal amphipod (*Erichthonius brasiliensis*) that were rarely consumed by whitebone porgy (South Carolina Wildlife and Marine Resources Department 1984; this study). Since these two sparids feed heavily on sand dwelling benthos or near-bottom plankton, they are apparently not dependent on hard bottom habitat for food, although they are found in higher densities in hard bottom areas. Because they feed on different kinds of organisms (infaunal sedentary or planktonic species for southern porgy versus motile epifaunal species for whitebone porgy), there is little overlap in diet between these two species.

Overlap in diet between pinfish and whitebone porgy was very low. Pinfish examined in the present study ate primarily a hard-bottom, sessile, tube-dwelling amphipod, *Erichthonius brasiliensis*, (36% of prey items) that was rarely consumed by whitebone porgy. Pinfish are apparently more closely associated with substrates from which they can browse on attached organisms, as has been noted in previous studies (Stoner and Livingston 1984). Because pinfish fed on attached epifauna, this species was similar in diet to sheepshead, a heavy grazer on attached epifauna (Sedberry 1987). Whereas *Calamus* spp. possess conical teeth in the anterior of the jaws for grasping motile prey and strong molariform teeth on the sides for crushing shells (Gregory 1933; Randall and Caldwell 1966; Randall 1967), the anterior of the jaws of pinfish are provided with incisors that are suited to scraping epifauna (Stoner and Livingston 1984).

Predation by fishes and other organisms can be an important factor in regulating the structure of sessile invertebrate communities (Peterson 1979; Sedberry 1987); however, it is obvious from the present results that whitebone porgy have little impact on hard-bottom epifaunal communities. While they are an abundant and a dominant member of the predatory fish community (Sedberry and Van Dolah 1984), whitebone porgy do not function as keystone predators (Paine 1969) in hard bottom reefs of the South Atlantic Bight.

ACKNOWLEDGMENTS

For their help in identification and confirmation of prey items, I thank the following scientists: D. M. Knott, amphipods; C. B. O'Rourke and E. R. Hens, polychaetes; and E. L. Wenner, decapods. D. M. Knott, R. F. Van Dolah, P. H. Wendt, and E. L. Wenner provided the data on invertebrate distribution and abundance for the electivity analyses. P. H. Wendt and C. J. Moore provided helpful reviews of the manuscript. This work was supported with funds provided by the Bureau of Land Management (Contract No. AA551-CT9-27) and the Minerals Management Service (Contract Nos. AA551-CT1-18 and 14-12-0001-29185), U.S. Department of the Interior; and the National Marine Fisheries Service (South Carolina MARMAP contract No 50-WCNF-7-06004).

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