TROPHIC RELATIONSHIPS AMONG DEMERSAL FISHES IN A COASTAL AREA OF THE GULF OF MAINE[1]

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ABSTRACT

Food resource utilization was investigated among eight demersal fish species (longhorn sculpin, *Myoxocephalus octodecemspinosus*; winter flounder, *Pseudopleuronectes americanus*; windowpane, *Scopthalmus aquosus*; yellowtail flounder, *Limanda ferruginea*; little skate, *Raja erinacea*; Atlantic cod, *Gadus morhua*; red hake, *Urophycis chuss*; ocean pout, *Macrozoarces americanus*) over a 13-month period in an area of Johns Bay, Maine. Despite the dominance of polychaetes and mollusks in the benthos, crustaceans composed the major prey group in all predators. There was considerable trophic similarity among the fishes and the amphipods *Unciola* sp. and *Leptocheirus pinguis* were the most important prey in seven of the eight predators. The results indicate that resource partitioning by prey size is related to different mouth morphologies for closely related species (winter flounder, yellowtail flounder, windowpane), and that unrelated species with similar mouth morphologies may overlap in prey size use (longhorn sculpin, Atlantic cod).

Recent studies have revealed the complexity of feeding relations among marine organisms (Isaacs 1972; Lange and Hurley 1975). The concept of unstructured food webs necessitates a detailed knowledge of the food habits of component species in order to establish their trophic connections and to determine energy flow pathways through the ecosystem. Fish food habit studies are helpful in deciphering some of the higher level trophic relations in an ecosystem. From a practical standpoint, information on the quantity and quality of food consumed by fish is needed for estimating fish production (Paloheimo and Dickie 1970; Mills and Fournier 1979). In addition, knowledge of the feeding ecology of noncommercial, as well as commercial species, is essential for implementing a multispecies approach to fishery management (Gulland 1977; Larkin 1978).

Studies of the food habits of fish communities in the marine environment are becoming increasingly popular. Most of the early effort was centered on freshwater fish communities (e.g., Nilsson 1967; Keast 1970; Zaret and Rand 1971), but there is now a growing literature on marine systems (e.g., Tyler 1972; Hobson and Chess 1976; Kislalioglu and Gibson 1977; Langton and Bowman 1980; Hunter[3]). These fish population studies are part of a broader area of research in modern ecology concerned with the question of how closely related species coexist in communities. Patterns of resource utilization by cooccurring species have been studied to assess interspecific competition and gain insight into community organization (see review by Schoener 1974).

The purpose of the present study is to examine feeding relationships among demersal fishes in a coastal area of the Gulf of Maine. Specifically, the objectives are 1) to determine quantitatively the principal prey species of the demersal fishes, 2) to examine food resource division and interrelationships among the predator species, and 3) to compare predator diets with food resources potentially available in the benthic infauna.

METHODS

I made monthly trawl collections of demersal fishes in Johns Bay, Maine, from April 1978 through April 1979. A 5.5 m otter trawl was used during the initial 3 mo of sampling. For the remainder of the study I used a 9.1 m otter trawl. The trawl had a 50.8 mm #15 nylon mesh with a 38.1 mm cod end. Trawls were made in approximately

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30 m of water along the eastern side of Johns Bay (Figure 1). Two or three 15-min trawls were made during each sampling trip to obtain a sufficient number of fish. I measured temperature and salinity at the surface (1 m and at a depth of 30 m) using a Beckman[4] RS5-3 salinometer.

Immediately after capture I sorted the trawl catch by species. Total length (TL to nearest millimeter), weight (to nearest gram), sex, and maturity determinations were made for each specimen. By cutting at the esophagus and pyloric constriction stomachs were removed from a maximum of 20 specimens (>15 cm TL) of each species (a subsample of the total size range), fixed in 10% Formalin, later preserved in 70% isopropanol, and then, contents were sorted and identified to the lowest possible taxon. Prey items were damp dried on bibulous paper, and the number of individuals and total wet weight (to nearest 0.01 g) of each prey category were recorded. Total weight included shell weight for mollusks, crustaceans, and echinoderms.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

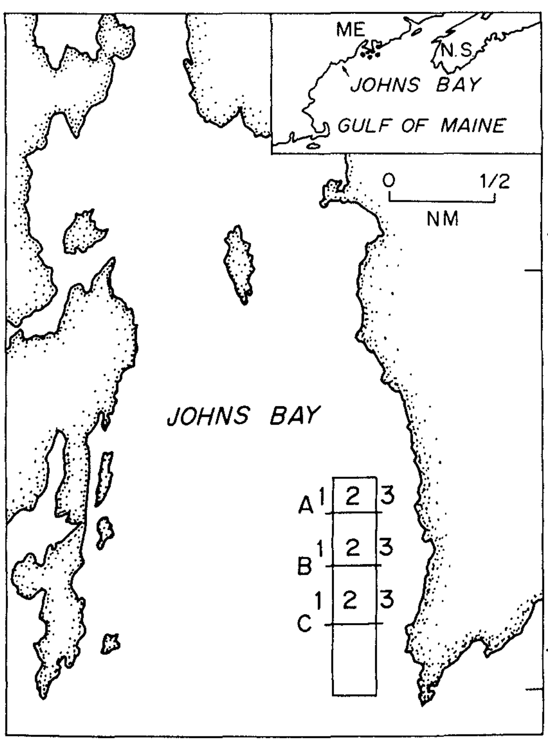

FIGURE 1.—Location of trawling area (closed box) and benthic sampling sites (transects A-C, stations 1-3) in Johns Bay, Maine.

I determined the contribution of different prey categories to the diet of a fish species by three methods: 1) the percentage weight of a prey category (pooled) to the weight of the total stomach contents, 2) the percentage abundance of individuals of a prey category to the total number of individual prey in the stomachs, and 3) the percentage frequency of occurrence of the number of stomachs in which a prey category occurred to the total number of stomachs examined. Berg (1979) discussed the limitations of using any single measure to evaluate the importance of a food taxon. Therefore, an index of relative importance, modified from Pinkas et al. (1971), has been calculated since it incorporates all three measures and gives a better assessment of the dietary importance of a prey group. The formula used is as follows: $IRI = (N + W)F$, where N = numerical percentage, W = weight percentage, F = percentage frequency of occurrence, and IRI = index of relative importance. The original formulation proposed by Pinkas et al. (1971) used volumetric percentage instead of percentage weight.

I calculated niche overlap using the formula proposed by Pianka (1973):

$$A_{ij} = \frac{[\Sigma p_{ih} p_{jh}]}{[\Sigma p^2_{ih}\ \Sigma p^2_{jh}]}$$

where A_{ij} is the overlap of species j on species i; p_{ih} is the proportion (percentage weight) of a particular food h ($h = 1\ldots,s$) in the diet of species i; and p_{jh} is the proportion of the same food h in the diet of species j. Values for the overlap index may vary between 0, if no overlap occurs, and 1 for complete overlap. A value >0.3 is significant and ones >0.7 are considered high (Keast 1978).

The division of principal prey among the predators was examined by means of a partition plot. I defined principal prey as those with an IRI >100 because this emphasized the major food sources of each predator. Principal prey accounted for 73.3-94.7% by number of the food items in predator diets. The partition plot facilitates the calculation of the percentage reoccurrence of prey in more than one predator, which is empirically defined as the number of reoccurrences observed divided by the total number of reoccurrences possible in the plot, multiplied by 100 (Tyler 1972). One reoccurrence is defined as the presence of a prey in two predators. The total number of reoccurrences possible is obtained by the number of predators minus one, multiplied by the number of prey. The percentage reoccurrence of principal prey was calculated a second way by modifying the above procedure and ranking the principal prey in each predator's diet in terms of relative importance (e.g., first = 4 points, second = 3 points, third = 2 points, fourth = 1 point, each additional principal prey = ½ point). In this case, points are totaled for principal prey that are shared by two or more predators, and this value is divided by the total points possible if complete overlap occurred for all principal prey in all predators, the result being multiplied by 100 to give a percentage.

I made length measurements of crustacean prey species for several predators according to the procedure used by Ross (1977). A sample ($N \leq 25$) of each principal prey species was measured for several specimens of each predator. Measurements were made to the nearest millimeter along the axis of greatest dimension. Mouth measurements of fish species were also taken to compare prey size with mouth morphology. Upper jaw length was the distance from the posterior end of the maxillary to the tip of the snout. Mouth width was the distance between the posterior edges of the maxillaries with the mouth fully closed.

I collected benthic samples in September using a ponar grab. A series of three transects was established along the trawl tract (Figure 1). Three stations at different depths were sampled along each transect. Each ponar grab sampled a 0.05 m^2 area. Samples were washed through a 0.5 mm sieve and then fixed in 10% Formalin. I analyzed grab samples in the same manner as the stomach contents.

RESULTS

Abundance of Fishes

Twenty species of fish were collected during the 13-mo sampling period. The most abundant species were the longhorn sculpin, *Myoxocephalus octodecemspinosus*, and the winter flounder, *Pseudopleuronectes americanus*. The fish community showed the greatest diversity and abundance during summer. From January to March the fish fauna was limited and no fish at all were taken in the February sample.

The fish community can be broken down into different temporal components (Tyler 1971). "Regulars" were those species present on nearly every sampling date and included the longhorn sculpin; winter flounder; yellowtail flounder, *Limanda ferruginea*; and the Atlantic cod, *Gadus morhua*. "Summer periodics" were those species found in samples taken during the warmer months: the windowpane, *Scopthalmus aquosus*; ocean pout, *Macrozoarces americanus*; red hake, *Urophycis chuss*; and little skate, *Raja erinacea*. There was no corresponding "winter periodics" group. "Occasionals" were fish that occurred in low numbers at infrequent intervals: the sea raven, *Hemitripterus americanus*; the winter skate, *R. ocellata*; thorny skate, *R. radiata*; American plaice, *Hippoglossoides platessoides*; fourspotted flounder, *Paralichthys oblongus*; witch flounder, *Glyptocephalus cynoglossus*; cunner, *Tautogolabrus adspersus*; silver hake, *Merluccius bilinearis*; white hake, *Urophycis tenuis*; alligatorfish, *Aspidophoroides monopterygius*; moustache sculpin, *Triglops murrayi*; and sand lance, *Ammodytes* sp.

Foods

I examined the foods of the eight most abundant species (longhorn sculpin, winter flounder, windowpane, yellowtail flounder, ocean pout, little skate, Atlantic cod, and red hake). The diet for each species for the entire sampling period is summarized in Tables 1-8.

Longhorn Sculpin

Sixty-three prey taxa were identified in the 299 longhorn sculpin stomachs. Crustaceans were the most important prey group, making up 58.4% of the diet by weight and 95.8% of the diet by number (Table 1). Amphipods were most heavily preyed upon, especially *Unciola* sp. and *Leptocheirus pinguis*, which had the two highest indices of relative importance. Decapods were next in importance, with the sand shrimp, *Crangon septemspinosa*, and rock crab, *Cancer irroratus*, constituting 18.2% of the diet by weight. Mysids, principally *Mysis mixta*, were also significant food items. Pisces were the second major prey group and made up 25.2% of the diet by weight. Larval Atlantic herring, *Clupea harengus harengus*, were important fish prey. Other phyla (Porifera, Polychaeta, Mollusca) formed a minor portion of the diet.

TABLE 1.—Stomach contents of 299 longhorn sculpins ranging from 15.8 to 32.2 cm TL (mean 21.1±3.4 cm) and 21 to 380 g (mean 101±52 g). Twenty-four stomachs were empty. *IRI* = index of relative importance (see text).

	Percentage			
Taxon	Weight	Number	Frequency[1]	*IRI*
Porifera total	0.00	0.02	0.33	0
Polychaeta total	2.92	1.08	19.40	78
Mollusca total	.34	.61	7.69	7
Crustacea total	58.42	95.84	88.63	13,672
Mysidacea total	3.55	10.26	29.10	402
Neomysis americana	1.23	4.11	7.69	41
Mysis mixta	1.79	4.80	14.72	97
Other Mysidacea	.53	1.35		
Cumacea total	.04	.32	4.01	1
Isopoda total	1.50	2.55	13.38	54
Edotea montosa	.17	1.96	8.70	19
Cirolana sp.	1.33	.59	5.35	10
Amphipoda total	25.66	78.94	82.61	8,641
Unciola sp.	10.58	46.64	64.55	3,694
Leptocheirus pinguis	10.21	16.94	40.47	1,099
Aeginella longicornis	1.12	6.22	25.08	184
Erichthonius rubricornis	.20	3.09	14.72	48
Hippomedon serratus	.30	1.32	8.36	14
Monoculodes sp.	.13	.95	10.70	12
Other Amphipoda	3.12	3.78		
Decapoda total	27.67	3.77	30.77	967
Crangon septemspinosa	10.05	2.06	14.72	178
Cancer irroratus	8.15	.71	6.69	59
Other Decapoda	9.47	1.00		
Pisces total	25.19	2.45	18.39	508
Clupea h. harengus	11.04	2.01	10.03	131
Other Pisces	14.15	.44		
Remains	11.16			
Detritus	1.97			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

TABLE 2.—Stomach contents of 201 winter flounder ranging from 15.2 to 42.6 cm (mean 24.0±6.0 cm) and 29 to 1,120 g (mean 209±187 g). Fifty-seven stomachs were empty. *IRI* = index of relative importance (see text).

	Percentage			
Taxon	Weight	Number	Frequency[1]	*IRI*
Nemertea total	0.16	0.05	0.50	0
Algae total	12.67	0	2.49	32
Polychaeta total	18.26	8.11	53.73	1,417
Phyllodoce sp.	.28	2.19	20.90	52
Melinna cristata	2.16	2.19	4.48	19
Maldanidae	.69	.80	9.95	15
Lumbrineris fragilis	2.79	.53	6.97	23
Pherusa affinis	5.03	.42	5.47	30
Other Polychaeta	7.31	1.98		
Mollusca total	6.09	3.13	24.88	229
Bivalvia total	5.13	2.60	22.89	177
Cerastoderma pinnulatum	4.21	1.87	17.91	109
Other Bivalvia	.92	.73		
Gastropoda total	.96	.53	3.98	6
Crustacea total	32.50	86.72	70.65	8,422
Cumacea total	1.02	3.99	27.36	137
Diastylis quadrispinosa	.50	1.87	14.43	34
Other Cumacea	.52	2.12		
Isopoda total	.20	.58	6.97	5
Edotea montosa	.15	.47	5.97	4
Other Isopoda	.05	.11		
Amphipoda total	25.74	81.96	69.65	7,502
Ampelisca agassizi	.49	7.09	9.45	72
Leptocheirus pinguis	9.18	16.24	32.34	822
Corophium sp.	.11	1.77	10.95	21
Erichthonius rubricornis	.01	1.37	13.44	17
Unciola sp.	10.17	44.30	56.22	3,062
Pontogeneia inermis	.29	.76	4.98	5
Aeginella longicornis	2.86	6.94	16.92	166
Other Amphipoda	2.63	3.49		
Decapoda total	5.53	.18	3.98	23
Echinodermata total	.50	1.98	24.38	62
Ophiuroidea total	.39	1.87		52
Amphipholis squamata	.16	.92	11.94	13
Other Ophiuroidea	.23	.95		
Asteroidea total	0	.03	.50	0
Echinoidea total	.11	.08	1.49	0
Remains	15.03			
Detritus	14.81			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Winter Flounder

Sixty-six prey taxa were identified from the 201 winter flounder stomachs. Crustaceans were the major prey group for the winter flounder (Table 2). Amphipods accounted for the largest percentage of the diet by weight (25.7%). *Unciola* sp., *Leptocheirus pinguis*, and *Aeginella longicornis* were the principal amphipods consumed. Cumaceans, isopods, and decapods were of minor importance. After crustaceans, polychaetes were the next major prey group, making up 18.3% of the diet by weight. Polychaete identification was often difficult due to partial digestion or incomplete animals and this obscured the importance of some species. *Melinna cristata, Lumbrineris fragilis, Pherusa affinis*, and *Phyllodoce* sp. were the principal polychaetes consumed. Mollusks were of little importance, but one species, the bivalve *Cerastoderma pinnulatum*, was preyed on significantly and constituted 4.2% of the diet by weight. Algae made up 12.7% of the diet. Echinoderms accounted for only a small fraction of the stomach contents.

Windowpane

The windowpane had a specialized diet and only seven prey taxa were found in the 37 stomachs. Crustaceans were by far the most important prey group, constituting 79.3% of the diet by weight and 99.0% of the diet by number (Table 3). Mysids, principally *Mysis mixta*, were the main component of the crustacean prey. *Mysis mixta* accounted for 72.4% of the diet by weight. Pisces, namely *Clupea h. harengus*, were secondary in importance and made up 20.3% of the diet by weight. Polychaetes composed a negligible portion of the diet.

Yellowtail Flounder

The 60 yellowtail flounder stomachs analyzed contained 39 prey taxa. Crustacea accounted for

TABLE 3.—Stomach contents of 37 windowpane ranging from 21.0 to 33.6 cm (mean 27.3±3.3 cm) and 90 to 482 g (mean 244±90 g). Eight stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage Weight	Number	Frequency[1]	*IRI*
Polychaeta total	0.13	0.06	2.70	1
Crustacea total	79.27	98.99	75.68	13,490
Mysidacea total	78.78	98.74	75.68	13,434
Neomysis americana	1.16	2.46	8.11	29
Mysis mixta	72.41	94.65	59.46	9,933
Other Mysidacea	5.21	1.63		
Amphipoda total	.26	.19	8.11	4
Decapod total	.23	.06	2.70	1
Pisces *Clupea h. harengus*	20.25	0.94	2.70	57
Remains	0.36			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

almost half the diet by weight (48.5%) and almost the entire diet by number (95.1%) (Table 4). Amphipods were the most important crustaceans consumed, followed by mysids, cumaceans, and decapods. *Unciola* sp. was the principal amphipod prey, making up 28.7% of the diet by weight and 82.0% of the diet by number. The amphipod *Leptocheirus pinguis* and mysid *Mysis mixta* were also important. After crustacea, polychaetes (10.2% of the diet by weight) and mollusks (5.2% of the diet by weight) were the next largest dietary components. The bivalve *Cerastoderma pinnulatum* was a significant prey item. Other prey groups (Nemertea, Echinodermata, Pisces) were of minor importance.

TABLE 4.—Stomach contents of 60 yellowtail flounder ranging from 19.0 to 42.0 cm (mean 30.9±7.2 cm) and 42-670 g (mean 280±174 g). Fourteen stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage Weight	Number	Frequency[1]	*IRI*
Nemertea total	3.50	0.00	1.67	6
Polychaeta total	10.15	2.38	35.00	438
Phyllodoce sp.	.32	.40	10.00	7
Nephtys sp.	2.64	.04	3.33	9
Glycera sp.	.23	.18	5.00	2
Maldanidae	.87	.44	11.67	15
Other Polychaeta	6.09	1.32		
Mollusca total	5.19	2.33	36.67	276
Bivalvia total	5.19	2.29	36.67	274
Nucula proxima	1.46	.63	5.00	10
Cerastoderma pinnulatum	3.41	1.44	26.67	129
Other Bivalvia	.32	0.22		
Gastropoda total	0	.04	1.67	0
Crustacea total	48.50	95.07	68.33	9,810
Cumacea total	.45	1.57	21.67	44
Diastylis quadrispinosa	.23	.36	8.33	5
Other Cumacea	.22	1.21		
Amphipoda total	33.58	85.78	63.33	7,559
Leptocheirus pinguis	1.73	.99	25.00	68
Unciola sp.	28.66	82.01	53.33	5,903
Hippomedon serratus	.27	.49	11.67	9
Monoculodes sp.	.41	.72	13.33	15
Other Amphipoda	2.51	1.57		
Mysidacea total	12.51	7.27	3.33	66
Mysis mixta	12.19	7.18	3.33	65
Other Mysidacea	.32	.09		
Decapoda *Crangon septemspinosa*	1.59	.13	5.00	9
Isopoda total	.37	.32	8.33	6
Echinodermata total	.05	.13	6.67	1
Pisces total	.05	.04	1.67	0
Remains	16.38			
Detritus	16.20			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Ocean Pout

Twenty-seven prey taxa were found in the 46 ocean pout stomachs. A comparison of the relative contributions of echinoderms and crustaceans to the diet showed that echinoderms were the most important prey group in terms of percent weight (20.6% vs. 13.7%), while crustaceans had a greater *IRI* (7,382 vs. 974) (Table 5). Amphipods and, to a lesser extent, cumaceans were the principal crustacean orders present in the ocean pout diet. The amphipods *Unciola* sp. and *Leptocheirus pinguis* and the cumacean *Diastylis quadrispinosa* were significant prey. Principal echinoderm prey were the sea urchin, *Strongylocentrotus droebachiensis*; the sand dollar, *Echinarachnius parma*; and

TABLE 5.—Stomach contents of 46 ocean pout ranging from 18.2 to 49.0 cm (mean 34.3±5.9 cm) and 24 to 660 g (mean 214±11.8 g). Five stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage Weight	Number	Frequency[1]	*IRI*
Polychaeta total	1.41	0.27	19.57	33
Mollusca total	9.78	12.11	45.65	999
Gastropoda total	.21	.45	13.04	9
Bivalvia total	9.57	11.66	39.13	831
Placopecten magellanicus	4.57	.81	4.35	23
Cerastoderma pinnulatum	3.85	4.88	21.74	190
Mya arenaria	.91	5.33	8.70	54
Other Bivalvia	.24	.64		
Crustacea total	13.65	83.37	76.09	7,382
Mysidacea total	.14	.27	4.35	2
Cumacea total	2.12	18.78	41.30	863
Diastylis quadrispinosa	1.86	15.90	26.09	463
Other Cumacea	.26	2.88		
Isopoda *Edotea montosa*	.02	.36	6.52	2
Amphipoda total	10.29	63.32	71.74	5,281
Leptocheirus pinguis	1.15	2.71	17.39	67
Unciola sp,	8.00	57.99	58.70	3,874
Pontogenia inermis	.09	.91	6.52	7
Aeginella longicornis	.07	.54	6.52	4
Other Amphipoda	.98	1.17		
Decapoda total	1.08	.64	10.87	19
Echinodermata total	20.63	4.25	39.13	974
Echinoidea total	19.81	1.35	23.91	506
Strongylocentrotus drobachiensus	1.78	.99	15.22	42
Echinarachnius parma	18.03	.36	10.87	200
Ophiuroidea total	.82	2.90	26.09	97
Amphipholis squamata	.40	2.18	15.22	39
Other Ophiuroidea	.42	.72		
Detritus	47.55			
Remains	6.99			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

the brittle star, *Amphipholis squamata*. Mollusca constituted 9.8% of the diet by weight. The sea scallop, *Placopecten magellanicus*; the soft-shell clam, *Mya arenaria*; and the cockle, *Cerastoderma pinnulatum*, were noteworthy. Polychaetes formed a small portion of the diet. A large amount of bottom sediment and organic material was found in the stomachs examined.

Little Skate

Thirty-one prey taxa were found in the 33 little skate stomachs. The little skate fed primarily on crustaceans (Table 6). The decapods were the most important group, making up 50.7% of the diet by weight. *Crangon septemspinosa* and *Cancer irroratus* were principal prey species. Amphipods were next in importance with *L. pinguis*, *Unciola* sp., and *Monoculodes* sp. as significant prey items. The remaining crustacean groups did not constitute a substantial part of the diet. Polychaetes were the next major prey group, accounting for 10.1% of the diet by weight. Porifera, Nematoda, and Pisces were of minor importance.

TABLE 6.—Stomach contents of 33 little skates ranging from 25.6 to 55.2 cm (mean 39.6±10.1 cm) and 71 to 1,194 g (mean 496±346 g). There were no empty stomachs. *IRI* = index of relative importance (see text).

Taxon	Percentage Weight	Number	Frequency[1]	*IRI*
Porifera total	0.15	0.00	3.03	0
Nematoda total	.08	4.17	15.15	64
Polychaeta total	10.14	.17	36.36	375
Crustacea total	66.89	94.78	96.97	15,677
Mysidacea total	.19	1.22		
Mysis mixta	.13	.70	6.06	5
Other Mysidacea	.06	.52		
Cumacea total	.08	1.22	15.15	20
Amphipoda total	15.80	70.78	84.85	7,347
Ampelisca agassizi	.06	1.04	9.09	10
Leptocheirus pinguis	5.01	24.17	66.67	1,946
Unciola sp.	1.37	12.52	51.52	716
Pontogenia inermis	.08	1.57	12.12	20
Anonyx sarsi	2.38	3.13	9.09	50
Monoculodes sp.	2.42	24.52	57.58	1,551
Other Amphipoda	4.48	3.83		
Decapoda total	50.71	21.39	78.79	5,680
Crangon septemspinosa	18.51	9.22	57.58	1,596
Cancer irroratus	22.68	9.39	36.36	1,166
Other Decapoda	9.52	2.78		
Isopoda total	.11	.17	3.03	1
Pisces total	.67	.87	15.15	23
Detritus	1.60			
Remains	20.47			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Atlantic Cod

The 75 Atlantic cod stomachs contained a total of 30 prey taxa. Crustaceans were the major prey group, accounting for 40.3% of the diet by weight and 98.5% of the diet by number (Table 7). Amphipods, especially *Unciola* sp. and *L. pinguis*, were most heavily preyed upon. The decapods made up 18.2% of the diet by weight, with *Crangon septemspinosa* and *Cancer irroratus* as principal prey. The mysids, notably *Mysis mixta*, were next in importance. Cumaceans and isopods made up a negligible portion of the diet. Pisces were the next major group and constituted 14.6% of the diet by weight. Other phyla (Nematoda, Polychaeta, Mollusca, and Echinodermata) were of little importance. A large amount of unidentifiable remains (40.9% of the diet by weight) was found in the stomachs examined.

TABLE 7.—Stomach contents of 75 Atlantic cod ranging from 15.0 to 53.6 cm (mean 22.5±5.5 cm) and 27 to 1,555 g (mean 128±195 g). Ten stomachs were empty. *IRI* = index of relative importance (see text).

Taxon	Percentage Weight	Number	Frequency[1]	*IRI*
Nematoda total	0.00	0.35	4.00	1
Polychaeta total	1.06	.35	12.00	17
Mollusca total	.02	.43	1.33	1
Crustacea total	40.27	98.45	84.00	11,652
Mysidacea total	4.00	8.46	38.67	481
Mysis mixta	2.45	7.42	25.33	250
Other Mysidacea	1.55	1.04		
Cumacea total	.07	1.04	5.33	6
Isopoda total	1.01	.43	5.33	8
Cirolana polita	1.01	.35	4.00	5
Other Isopoda	.00	.08		
Amphipoda total	16.98	85.85	72.00	7,404
Ampelisca agassizi	.51	10.01	2.67	28
Leptocheirus pinguis	2.44	3.80	21.33	133
Unciola sp.	11.16	66.01	58.67	4,528
Pontogenia inermis	.12	1.21	10.67	14
Hippomedon serratus	.45	1.55	12.00	24
Aeginella longicornis	.05	.69	6.67	5
Other Amphipoda	2.25	2.58		
Decapoda total	18.21	2.67	24.00	501
Crangon septemspinosa	9.06	1.55	13.33	141
Cancer irroratus	6.07	.26	4.00	25
Other Decapoda	3.08	.86		
Echinodermata total	1.94	.17	1.33	3
Pisces total	14.61	.26	5.33	79
Detritus	1.17			
Remains	40.94			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Red Hake

Twenty-four prey taxa were found in the 30 red hake stomachs. The red hake fed principally upon crustaceans, and this group accounted for 72.4% of the diet by weight (Table 8). Amphipods were the most important order with *L. pinguis*, *Unciola* sp., and *Ampelisca agassizi* as significant prey items. Decapods were also heavily preyed upon and

Crangon septemspinosa was a principal prey species. Mysids, cumaceans, and isopods were of minor importance. Other groups (Algae, Porifera, Polychaeta, Mollusca) constituted a small portion of the diet.

TABLE 8.—Stomach contents of 30 red hake ranging from 15.0 to 40.1 cm (mean 25.6±6.1 cm) and 22 to 392 g (mean 121±86 g). Three stomachs were empty. *IRI* = index of relative importance (see text).

	Percentage			
Taxon	Weight	Number	Frequency[1]	*IRI*
Algae total	1.60	0.00	3.33	5
Porifera total	.16	0.00	3.33	1
Polychaeta total	3.35	.63	20.00	80
Crustacea total	72.36	99.36	86.67	14,884
Mysidacea total	.24	.31	3.33	2
Cumacea total	.16	2.19	13.33	31
Isopoda total	3.19	.94	10.00	41
Cirolana polita	2.96	.63	6.67	24
Other Isopoda	.23	.31		
Amphipoda total	31.87	87.46	80.00	9,546
Ampelisca agassizi	2.48	28.53	10.00	310
Leptocheirus pinguis	13.98	26.65	50.00	2,031
Unciola sp.	6.71	21.94	60.00	1,719
Hippomedon serratus	1.44	4.08	13.33	74
Aeginella longicornis	.32	2.19	16.67	42
Other Amphipoda	6.94	4.07		
Decapoda total	36.90	8.46	40.00	1,815
Crangon septemspinosa	28.67	7.21	26.67	957
Other Decapoda	8.23	1.25		
Mollusca total	.16	0.00	3.33	1
Detritus	.88			
Remains	21.49			
Grand total	100.00	100.00		

[1]Frequency of occurrence of food item.

Dietary Overlap

The fish community in Johns Bay showed a considerable degree of food overlap (Table 9). Eight species-pairs had overlap values >0.50. This is a reflection of the dominance of crustaceans in the diets of the predators examined. The greatest dietary overlap occurred between the Atlantic cod and longhorn sculpin. In addition, high dietary overlaps occurred among the Atlantic cod, red hake, longhorn sculpin, little skate, winter flounder, and yellowtail flounder, a consequence of the dependence of these predators on amphipod and decapod prey.

Although over 100 prey taxa were found during the study, only 13 were classified as principal prey. In the partition plot predators that share principal prey are generally arranged adjacent to one another (Table 10). Difficulty in identifying digested organisms necessitated using the broad classification of Polychaeta in this partition plot. Generally, predators consumed 4 or 5 principal prey, and the percentage reoccurrence of principal

TABLE 9.—A summary of the predator feeding habits and food overlap in fishes from Johns Bay, Maine. Species pairs with overlaps 0.50 or greater are in italics.

			Predator species						
Predator number	Predator species	Feeding habits	2	3	4	5	6	7	8
1	Longhorn sculpin	Crustaceans and fish	*0.74*	*0.59*	*0.63*	0.43	0.43	0.19	0.18
2	Atlantic cod	Crustaceans and fish		*.57*	*.62*	*.60*	.34	.05	.13
3	Little skate	Crustaceans, particularly decapods			*.68*	.13	.19	.05	.01
4	Red hake	Crustaceans				.27	.36	.11	.01
5	Yellowtail flounder	Crustaceans and polychaetes					*.51*	.38	.36
6	Winter flounder	Crustaceans and polychaetes						.27	.01
7	Ocean pout	Mollusks, echinoderms, and crustaceans							.01
8	Windowpane	Specialist on mysids							

TABLE 10.—Partition plot of principal prey for demersal fishes in Johns Bay, Maine. Numbers listed are index of relative importance values for principal prey. Prey classifiction: (I) Infaunal, (E) Epifaunal, (N) Nektonic.

Prey	Longhorn sculpin	Atlantic cod	Red hake	Little skate	Winter flounder	Yellowtail flounder	Ocean pout	Windowpane
Unciola (I)	[1]3,694	[1]4,528	1,719	716	[1]3,062	[1]5,903	[1]3,874	—
Leptocheirus (I)	1,099	133	[1]2,031	[1]1,946	822	—	—	—
Crangon (E)	178	141	957	1,596	—	—	—	—
Polychaeta (I)	—	—	—	375	1,417	438	—	—
Cerastoderma (I)	—	—	—	—	109	129	190	—
Aeginella (E)	184	—	—	—	166	—	—	—
Mysis (N)	—	250	—	—	—	—	—	[1]9,933
Monoculodes (I)	—	—	—	1,551	—	—	—	—
Ampelisca (I)	—	—	310	—	—	—	—	—
Diastylis (I)	—	—	—	—	—	—	463	—
Cancer (E)	—	—	—	1,166	—	—	—	—
Echinarachnius (E)	—	—	—	—	—	—	200	—
Clupea (N)	131	—	—	—	—	—	—	—

[1]Indicates most important principal prey of prey of predator.

prey in more than one predator was 20% (19/96) by Tyler's (1972) method and 57% (65.5/116) by the ranked principal prey method.

Prey Size and Predator Mouth Morphology

Resource partitioning by prey size was examined for several predators by means of length-frequency distributions of crustacean prey. Crustaceans were analyzed because of their importance as a food group and because their hard external skeletons permitted reliable measurements.

A comparison of three flounder species showed that the winter flounder consumed the smallest prey (Figure 2). The majority of the winter flounder prey ranged between 4 and 10 mm long ($\overline{X} \pm 95\%$ CL = 6.8±0.6). The yellowtail flounder prey lengths were bimodally distributed. In one group most prey ranged between 5 and 10 mm, while in the second they were between 14 and 17 mm ($\overline{X} \pm 95\%$ CL = 10.8±1.3). The windowpane utilized the largest prey, with most ranging between 13 and 17 mm ($\overline{X} \pm 95\%$ CL = 14.4±0.7).

The longhorn sculpin and Atlantic cod, were two other important crustacean predators examined. Longhorn sculpin prey showed a wide range in size (1-30 mm) (Figure 3). The largest proportion of longhorn sculpin prey was between 5 and 15 mm long ($\overline{X} \pm 95\%$ CL = 11.1±0.7). The distribution of cod prey sizes was similar to that of the longhorn sculpin. Most of the cod prey were between 4 and 13 mm long ($\overline{X} \pm 95\%$ CL = 9.0±0.7).

Data on mouth measurements are presented in Table 11. The basic mouth shape is given as the ratio of the mean mouth width to mean upper jaw

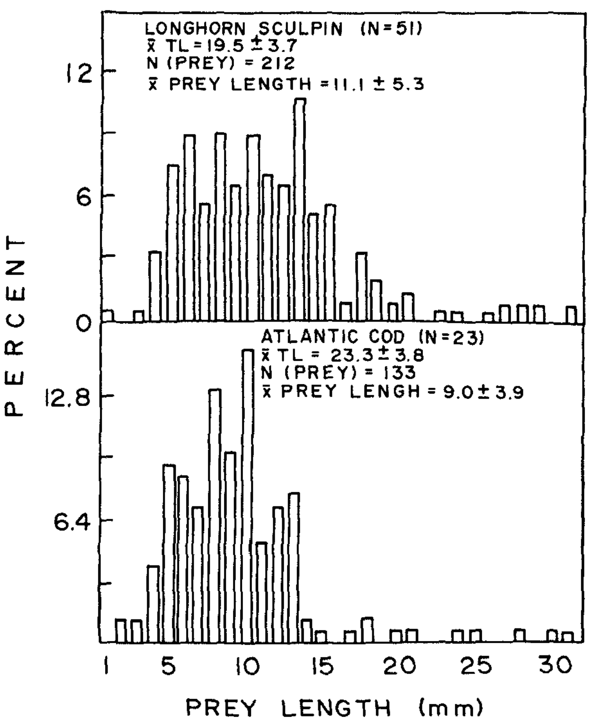

FIGURE 2.—Prey size distributions for winter flounder, yellowtail flounder, and windowpane.

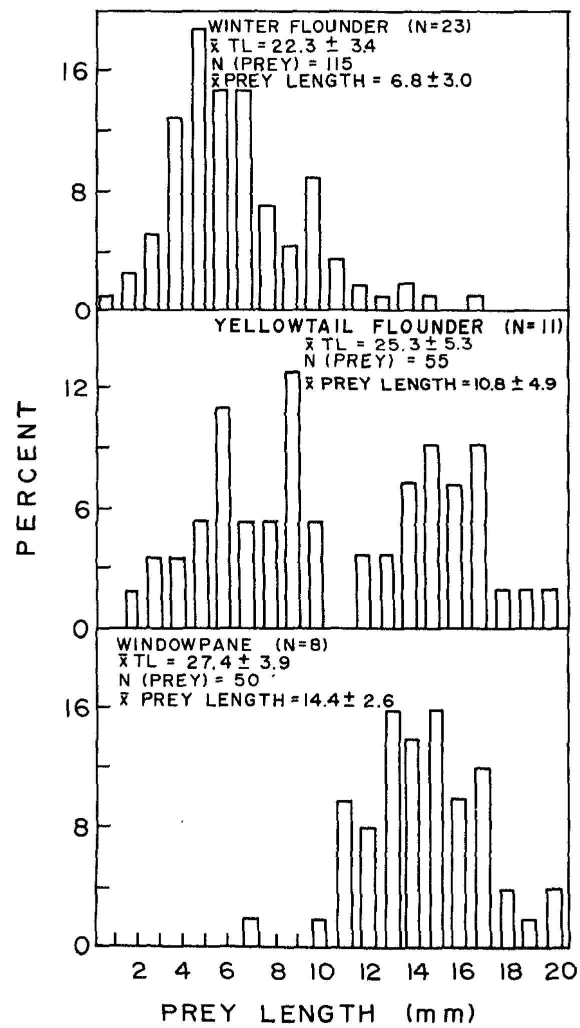

FIGURE 3.—Prey size distributions for longhorn sculpin and Atlantic cod.

TABLE 11.—Mouth dimensions of fish species.

Species	N	TL (cm) $\bar{X}\pm$SD	Upper jaw length (% TL) $\bar{X}\pm$SD	Mouth width (% TL) $\bar{X}\pm$SD	$\bar{X}$ mouth width ÷ $\bar{X}$ upper jaw length
Winter flounder	30	25.5±5.3	4.9±0.32	4.3±0.38	0.87
Yellowtail flounder	6	30.7±8.2	5.0± .39	3.8± .47	.76
Windowpane	17	24.7±4.5	9.2± .44	4.0± .80	.43
Longhorn sculpin	19	22.1±3.3	15.1± .69	16.9±1.67	1.12
Atlantic cod	3	24.5±3.1	11.7± .75	10.5± .62	1.11

length. The flounders had different ratios (windowpane 0.43, yellowtail flounder 0.76, winter flounder 0.87). The longhorn sculpin (1.12) and the Atlantic cod (1.11) had similar mouth shapes.

Benthos Analysis

A summary of the species composition by numbers and weights for the benthic samples is given in Tables 12 and 13. The sediment at stations A-1, A-2, B-1, and C-1 was silty sand, and remaining stations were sand. A total of 55 species were identified. The polychaetes were the dominant group and constituted 51.4% (by number) of the organisms present. Crustaceans (34.1%) and mollusks (12.8%) were next in abundance. The remaining groups (sipunculids(?), nematodes, echinoderms) accounted for only 1.7% of the total number of individuals. The most abundant species were the polychaetes *Prionospio steenstrupi*, *Exogone hebes*, *Tharyx acutus*, *Lumbrineris fragilis*; the crustaceans *Unciola* sp. and *Ampelisca agassizi*; and the mollusk *Nucula proxima*. In terms of biomass (percentage wet weight) mollusks (41.2%) were the most important group followed by polychaetes (41.0%) and crustaceans (8.8%). The biomass was dominated by the mollusk *N. proxima* (34.6%) and to a lesser extent by the polychaetes *L. fragilis*, *Sternaspis scutata*, and *P. steenstrupi*, and the crustaceans *A. agassizi* and *Unciola* sp.

DISCUSSION

Recent studies of temperate, coastal marine fish communities have suggested that there is considerable division of food resources among predators (Tyler 1972; Kislalioglu and Gibson 1977). Tyler (1972) examined the food utilization among demersal fishes in Passamaquoddy Bay, New Brunswick, and found relatively little overlap among diets based on the percentage reoccurrence of principal prey among predators (16% summer community; 24% winter community). In Johns Bay the percentage reoccurrence of principal prey among demersal fishes was 20% which is within the range (10-24%) that Tyler calculated for other marine communities. However, assessing dietary overlap by means of the method proposed by Tyler may be misleading because all principal prey are weighted equally in the calculation (see Methods). For example, although the percentage reoccurrence of principal prey of the fishes in Johns Bay suggests considerable resource division, a closer examination of the data reveals that seven of the eight predators rely primarily on two prey types, *Unciola* and *Leptocheirus* (Table 10). If the principal prey items in each predator's diet are weighted in terms of relative importance a more accurate evaluation of dietary overlap may be determined from the partition plot. For the demersal fishes in Johns Bay the percentage reoccurrence of ranked principal prey is 57%, which indicates that predators rely on many of the same major food sources. This conclusion is supported by the food overlap values that were obtained using Pianka's (1973) formula (Table 9).

There is insufficient information provided in Tyler's (1972) paper to evaluate the relative importance of his principal prey; however, a study by Kislalioglu and Gibson (1977) provided another source of data. These authors calculated a 14.7% reoccurrence of principal prey for shallow-water fishes from three habitats in Loch Etive, western Scotland. Food resource partitioning, however, is not as dramatic as this value would indicate because of the inclusion of five pelagic fishes in the calculation. Moreover, almost all the demersal species (13 out of 15) in Loch Etive were primarily dependent on amphipods as their most important food source (based on a points method of stomach content analysis), and among these fishes 25.7% had significant dietary overlap in terms of the proportion of different amphipod species utilized. If the percentage reoccurrence of principal prey is recalculated using weighted principal prey, the result is 56%.[5] Trophic similarity is especially evident for the fishes from the open sand-shell mud habitat (which corresponds to the habitat examined in Johns Bay) where there was significant overlap in amphipod species consumed between four of the five species examined. In Loch

[5]Resource division is not strictly comparable to Johns Bay because of the differing degrees of principal prey subdivision which may affect the result of the calculation.

TABLE 12.—Summary of the numbers of live invertebrates identified in nine benthic samples (0.05 m^2) taken from Johns Bay, Maine, in September 1978 (N = number; % = percent number). See Figure 1 for locations of transects.

	Station			Station			Station			Total	
Taxon	A-1	A-2	A-3	B-1	B-2	B-3	C-1	C-2	C-3	*N*	%
Mollusca:											
Nucula proxima	16	7	36	9	72	—	68	—	—	208	9.85
Mya arenaria	3	9	2	1	7	1	—	—	—	23	1.09
Cerastoderma pinnulatum	—	—	—	—	3	1	—	2	3	9	.43
Thyasira gouldi	—	—	5	1	2	—	—	—	—	8	.38
Crenella grandula	—	—	4	—	4	—	—	—	—	8	.38
Astarte undata	—	—	1	—	4	—	—	—	—	5	.24
Margarites sp.	—	—	—	—	—	—	—	—	2	2	.09
Nuculana tenuisculcata	—	1	—	—	—	—	—	—	—	1	.04
Yoldia sp.	—	—	—	1	—	—	—	—	—	1	.04
Unidentified bivalves	1	3	—	1	1	—	—	—	—	6	.28
									Total	271	12.82
Crustacea:											
Unciola sp.	—	—	—	—	—	114	2	72	190	378	17.90
Ampelisca agassizi	—	3	259	—	37	—	—	—	—	299	14.16
Aeginella longicornis	—	—	1	1	2	1	—	—	—	5	.24
Hippomedon propinquus	—	—	3	—	—	—	1	—	1	5	.24
Monoculodes sp.	—	—	—	1	1	1	—	—	—	3	.14
Petalosarsia declivis	—	—	—	—	—	—	—	1	2	3	.14
Edotea montosa	—	—	—	1	—	1	—	—	—	2	.09
Hippomedon sp.	—	1	—	—	1	—	—	—	—	2	.09
Harpinia propinqua	—	—	2	—	—	—	—	—	—	2	.09
Anonyx liljeborgi	—	—	2	—	—	—	—	—	—	2	.09
Eudorella sp.	—	—	—	1	—	—	—	—	1	2	.09
Corophium sp.	—	—	—	—	—	1	—	—	1	2	.09
Protomedeia fasciata	—	—	—	—	—	1	—	—	1	2	.09
Ampelisca macrocephala	—	—	—	—	—	—	1	1	—	2	.09
Erichthonius rubricornis	—	—	—	—	—	—	—	1	—	1	.05
Diastylis sp.	—	1	—	—	—	—	—	—	—	1	.05
D. sculpta	—	—	—	—	—	—	—	1	—	1	.05
D. quadrispinosa	—	—	1	—	—	—	—	—	—	1	.05
Leptocheirus pinguis	—	—	—	—	—	1	—	—	—	1	.05
Cyathura polita	—	—	—	—	—	—	—	—	1	1	.05
Unidentified amphipods	—	—	—	—	—	4	2	—	—	6	.28
									Total	721	34.12
Polychaeta:											
Prionospio steenstrupi	1	—	19	5	458	—	30	—	—	513	24.29
Exogone hebes	—	—	—	—	1	64	—	8	78	151	7.15
Tharyx acutus	—	14	6	7	9	12	5	2	12	67	3.17
Lumbrineris fragilis	12	16	8	3	18	—	7	—	—	64	3.03
Aricidea catherinae	14	11	—	7	—	4	2	1	16	55	2.60
Clymenella torquata	—	—	1	—	4	19	1	—	23	48	2.27
Phyllodoce mucosa	3	5	—	4	9	2	—	—	4	27	1.[illegible]
Scoloplos sp.	7	1	2	11	—	—	3	—	—	24	1.14
Ammotrypane aulogaster	—	1	5	—	15	—	—	—	—	21	.99
Scolecolepides viridis	18	—	—	—	—	—	—	—	—	18	.85
Nephtys sp.	—	3	—	—	3	—	3	4	—	13	.62
N. incisa	1	1	2	4	2	—	1	—	1	12	.57
Scalibregma inflatum	—	1	1	1	3	—	3	—	—	9	.43
Flabelligeridae	2	—	—	1	—	1	2	1	—	7	.33
Amphitrite affinis	—	—	—	—	—	3	—	—	3	6	.28
Nereis virens	—	—	—	1	4	—	—	—	—	5	.24
Phyllodoce sp.	—	—	4	—	—	—	—	—	—	4	.19
Melinna cristata	—	—	2	—	—	—	2	—	—	4	.19
Polynoidae	—	2	—	—	2	—	—	—	—	4	.19
Maldanidae	—	—	—	—	4	—	—	—	—	4	.19
Terebellides stroemi	—	—	1	—	—	—	—	—	—	1	.05
Phyllodoce maculata	—	—	—	—	1	—	—	—	—	1	.05
Sabellidae	—	—	—	—	—	1	—	—	—	1	.05
Pherusa affinis	—	—	—	—	—	—	—	—	1	1	.05
Nereis sp.	—	—	—	—	—	—	—	—	1	1	.05
Paraonis sp.	—	—	—	—	—	—	—	—	1	1	.05
Spiophanes bombyx	—	—	—	—	—	—	—	—	1	1	.05
Ampharete acutifrons	—	—	—	—	—	—	1	—	—	1	.05
Sternaspis scutata	1	5	2	2	5	—	3	2	—	20	.95
									Total	1,084	51.35
Sipuncula(?)	11	—	3	—	—	—	—	—	2	16	.76
Nematoda	—	—	—	—	—	6	—	—	11	17	.80
Echinodermata											
Amphipholis squamata	—	—	—	—	—	1	—	—	—	1	.05
Echinarachnius parma	—	—	—	—	—	—	—	—	1	1	.05
									Total	2	.10
									Grand total	2,111	99.95

TABLE 13.—Summary of the weights of live invertebrates identified in nine benthic samples (0.05m²) taken from Johns Bay, Maine in September 1978 (Wt = weight in grams; % = percent weight; tr = <0.01 gram) See Figure 1 for location of transects.

	Station			Station			Station			Total	
Taxon	A-1	A-2	A-3	B-1	B-2	B-3	C-1	C-2	C-3	Wt	%
Mollusca:											
Nucula proxima	0.30	0.12	0.54	0.19	1.49	—	1.92	—	—	4.56	34.60
Mya arenaria	.03	.08	.02	.01	.14	tr	—	—	—	.28	2.12
Margarites sp.	—	—	—	—	—	—	—	—	0.14	.14	1.06
Thyasira gouldi	—	—	.03	.01	.02	—	—	—	—	.06	.46
Astarte undata	—	—	.01	—	.05	—	—	—	—	.06	.46
Crenella glandula	—	—	.02	—	.03	—	—	—	—	.05	.38
Yoldia sp.	—	—	—	.05	—	—	—	—	—	.05	.38
Nuculana tenuisculcata	—	.02	—	—	—	—	—	—	—	.02	.15
Cerastoderma pinnulatum	—	—	—	—	.03	tr	—	0.04	.04	.11	.83
Unidentified bivalves	.01	.07	—	tr	.02	—	—	—	—	.10	.76
									Total	5.43	41.20
Crustacea:											
Ampelisca agassizi	—	.01	.48	—	.05	—	—	—	—	.54	4.10
Unciola sp.	—	—	—	—	—	0.13	tr	.07	.26	.46	3.49
Monoculodes sp.	—	—	—	.01	.01	.01	—	—	—	.03	.23
Hippomedon sp.	—	.01	—	—	.02	—	—	—	tr	.03	.23
Ampelisca macrocephala	—	—	—	—	—	—	tr	.02	—	.02	.15
Hippomedon propinquus	—	—	.02	—	—	—	—	—	—	.02	.15
Leptocheirus pinguis	—	—	—	—	—	.01	—	—	—	.01	.08
Edotea montosa	—	—	—	.01	—	tr	—	—	—	.01	.08
Aeginella longicornis	—	—	tr	tr	tr	tr	—	—	—	tr	—
Erichthonius rubricornis	—	—	—	—	—	—	—	tr	—	tr	—
Harpinia propinqua	—	—	tr	—	—	—	—	—	—	tr	—
Corophium sp.	—	—	—	—	—	tr	—	—	tr	tr	—
Anonyx liljeborgi	—	—	tr	—	—	—	—	—	—	tr	—
Protomedeia fasciata	—	—	—	—	—	tr	—	—	tr	tr	—
Diastylis sp.	—	tr	—	—	—	—	—	—	—	tr	—
D. sculpta	—	—	tr	—	—	—	—	tr	—	tr	—
D. quadrispinosa	—	—	tr	—	—	—	—	—	—	tr	—
Eudorella sp.	—	—	—	tr	—	—	—	—	tr	tr	—
Petalosarsia declivis	—	—	—	—	—	—	—	tr	tr	tr	—
Cyathura polita	—	—	—	—	—	—	—	—	tr	tr	—
Unidentified amphipods	—	—	—	—	—	.03	.01	—	—	.04	.30
									Total	1.16	8.81
Polychaeta:											
Lumbrineris fragilis	.02	.12	.40	.02	.49	—	.11	—	—	1.16	8.80
Sternaspis scutata	.01	.11	.05	—	.22	—	.25	—	—	.64	4.86
Prionospio steenstrupi	tr	—	.01	tr	.48	—	.03	—	—	.52	3.95
Nephtys sp.	—	.01	—	.02	.04	—	.01	.24	.03	.35	2.66
Clymenella torquata	—	—	.03	—	.01	.11	tr	—	.15	.30	2.28
Maldanidae	—	.10	.07	—	.03	—	—	.08	—	.28	2.12
Tharyx acutus	.03	.04	.01	.03	.03	.03	.03	tr	.01	.21	1.59
N. incisa	tr	.01	.10	.03	.01	—	.03	—	.02	.20	1.52
Scoloplos sp.	.02	.02	.02	.05	.01	—	.02	—	—	.14	1.06
Scolecolepides viridis	.03	—	—	—	.11	—	—	—	—	.14	1.06
Aricidea catherinae	.02	.02	—	—	—	.01	.01	tr	.01	.07	.53
Scalibregma inflatum	—	tr	.02	—	.03	—	—	—	tr	.05	.38
Exogone hebes	—	—	—	—	tr	.02	—	.01	.03	.06	.46
Pherusa affinis	—	—	—	—	—	—	—	—	.06	.06	.46
Melinna cristata	—	—	.02	—	—	—	.03	—	—	.05	.38
Amphitrite affinis	—	—	—	—	—	.01	—	—	.03	.04	.30
Paraonis sp.	—	—	—	—	—	—	—	—	.04	.04	.30
Ammotrypane aulogaster	—	tr	tr	—	.04	—	—	—	—	.04	.30
Flabelligeridae	.01	—	—	tr	—	tr	tr	.01	—	.02	.15
Terebellides stroemi	—	—	.02	—	—	—	—	—	—	.02	.15
Sabellidae	—	—	—	—	—	.02	—	—	—	.02	.15
Ampharetes acutifrons	—	—	—	—	—	—	.02	—	—	.02	.15
Phyllodoce mucosa	tr	.01	—	tr	tr	tr	—	tr	tr	.01	.08
Phyllodoce sp.	—	—	.01	—	—	—	—	—	—	.01	.08
Polynoidae	—	.01	—	—	—	—	—	—	—	.01	.08
Phyllodoce maculata	—	—	—	—	tr	—	—	—	—	tr	—
Nereis virens	—	—	—	tr	tr	—	—	—	—	tr	—
Nereis sp.	—	—	—	—	—	—	—	—	tr	tr	—
Spiophanes bombyx	—	—	—	—	—	—	—	—	tr	tr	—
Unident. polychaetes	—	.24	.08	—	.15	.07	.18	.09	.13	.94	7.13
									Total	5.40	40.98
Nemertea:	—	.05	—	—	.25	—	.70	—	—	1.00	7.59
Sipuncula(?):	.12	—	—	—	.04	—	.03	—	—	.19	1.44
Nematoda:	—	—	—	—	—	tr	—	tr	—	tr	—
Echinodermata:											
Amphipholis squamata	—	—	—	—	—	tr	—	—	tr	tr	—
									Grand total	13.18	100.00

Etive as in Johns Bay, use of an unweighted percentage reoccurrence of principal prey to evaluate dietary overlap gives an exaggerated picture of partitioning of prey types.

Trophic partitioning by prey size was apparent for the three flounder species examined from Johns Bay (Figure 2). Keast and Webb (1966) have stressed the importance of mouth morphology and body form in channeling predators towards distinct prey. The small-mouthed winter flounder selected small crustaceans, mainly amphipods, and the larger mouthed windowpane concentrated on larger prey, primarily mysids. The yellowtail flounder had a mouth size intermediate between the other two flounder species and it fed on prey from both size ranges. Ross (1977) noticed a similar segregation of prey sizes by searobins as spatial overlap increased. Resource partitioning by prey size was at a minimum between the Atlantic cod and longhorn sculpin (Figure 3). Both of these species had a similar mouth shape and ingested prey of the same size range. The similarity of prey size utilization is reflected in the high food overlap value (0.74) for these two species. Hespenheide (1975) observed a strong correlation between prey size overlap and prey type overlap for cohabiting birds.

An analysis of the benthic infauna was made to determine potentially available food and selectivity of prey by the demersal fishes (Tables 12, 13). Availability depends not only on prey abundance, but also on the interactions of other factors, including prey size, microdistribution, capture success, and speed of movement (Griffiths 1975). Although polychaetes and mollusks dominated in the bottom sediments, crustaceans were the preferred food of the demersal fishes. Generally, predators consumed prey that were active either at the sediment surface or in the upper few centimeters of the bottom sediments. Some abundant food items, such as *Nucula proxima, Prionospio steenstrupi*, and *Exogone hebes* were not important dietary constituents. The small size of *P. steenstrupi* and *E. hebes* probably limits their selection by predators. Predation on *N. proxima* may be low because the feeding structures of some predators prevent extensive burrowing in the sediment or because of this bivalve's low caloric value. Optimal feeding strategy predicts that animals should feed on prey that give the maximum energy yield per unit time and this will govern the degree of palatability of a prey item (Schoener 1971; Emlen 1973).

Recent work by Virnstein (1977) in Chesapeake Bay concluded that infaunal densities in soft-bottom communities are predator controlled. The cropping pressure of the demersal predators checks the population growth of many prolific benthic invertebrates. The benthos in Johns Bay is subject to varying amounts of predation pressure throughout the year. During the winter, the fish community in Johns Bay was very depauperate and it is likely that many fishes moved into warmer water offshore (Edwards 1964). Many of these demersal fishes show a decrease in feeding rate as temperature drops (Tyler[6]) and the winter flounder ceased feeding during the cold months. Because of the reduced abundance and lowered metabolism of the fishes, predation on the benthos was probably at a minimum during the winter. During the warmer months there was an influx of fish species into the bay and an increase in fish diversity and abundance. Environmental conditions are favorable at this time and the food supply may be abundant enough to support the expanded fish community without competitive interactions.

The demersal fishes in Johns Bay occupy the same habitat and there is considerable spatial overlap in their foraging zones. Active predators (e.g., Atlantic cod, red hake) forage over a wider area than sedentary predators (e.g., longhorn sculpin, ocean pout). These wide-ranging species may feed in the foraging zones of several sedentary individuals. My data suggest that the benthic fishes partition food resources by selecting prey from different depth strata (microhabitats) in the environment. Predators may choose either infaunal, epifaunal, or nektonic organisms and the proportion of these prey types in the diet is a reflection of preferred foraging strata (Table 14). At one extreme are predators that feed largely on nektonic prey (e.g., windowpane), while other fishes are strongly dependent on bottom-dwelling organisms (e.g., yellowtail flounder).

The trophic similarity of the demersal fishes in this coastal community suggests that in a food-limited environment many of these predators would experience intense competition. However, establishing food limitation is a difficult task because information is lacking both on benthic production rates and the food rations required by the

[6]Tyler, A. V. 1971. Monthly changes in stomach contents of demersal fishes in Passamaquoddy Bay, N.B. Fish. Res. Board Can., Tech. Rep. 288, 114 p.

TABLE 14.—Numerical percentage of prey types in predator diets.

Predator	Nekton	Epifauna	Infauna
Windowpane	100.0	0.0	0.0
Little skate	2.1	21.4	76.5
Longhorn sculpin	12.7	10.0	77.3
Atlantic cod	8.7	3.5	87.8
Red hake	.3	10.7	89.0
Winter flounder	0	9.1	90.9
Yellowtail flounder	7.3	.3	92.4
Ocean pout	0.3	5.0	94.7

fishes. Another factor to consider is the multidimensional aspect of resource partitioning. Previous studies of fish assemblages have suggested that subtle differences of resource use along complimentary dimensions offer a possible means of reducing interspecific competition (Werner 1977; Ross 1977; Keast 1978). There is evidence that time (e.g., daily and seasonal activity patterns) and space (e.g., foraging pattern) are additional dimensions of importance influencing food utilization by the demersal fish community in Johns Bay. However, unraveling the confounding effects of resource use along several dimensions depends upon more detailed study of these cohabiting fishes as well as increased sophistication of techniques for community analysis (Pianka 1980).

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