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THE FISH-BENTHOS CONNECTION: A DEFINITION OF PREY GROUPS IN THE GULF OF MAINE

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ABSTRACT Dietary data are described for the six dominant species of fish from the Sheepscot Bay, Gulf of Maine, and are compared with collections from offshore and the adjacent Johns Bay. For this comparison, the prey species were assigned to functional groups based on their life habits and relation to the sediment. Geographic as well as temporal comparisons are described for each of the six predators. In both coastal and offshore areas the functional groups are similar with the most important being polychaetes, fish, epibenthic and infaunal crustaceans as well as echinoderms. Within species comparisons show a good degree of stability in the functional prey groups over the entire Gulf with the exception of echinoderms which are much more important in the diet of offshore species. Temporal comparisons between Johns and Sheepscot Bays also demonstrate stability in the fishes' predatory habits along mid-coast Maine over a ten-year period. The implications of this spatial and temporal stability are discussed with regard to the development of ecological models that describe the trophic linkages between the macrobenthos and their fish predators.

INTRODUCTION

The Gulf of Maine is a unique body of water along the eastern seaboard of the United States of America and Canada. Geologically, it is a relatively recent structure, originating during the last glacial period approximately 11 000 years ago. It has been described as an epicontinental sea functioning as a macro-estuary (Uchupi, 1966; Emery & Uchupi, 1972; Campbell, 1986) with a broader range of sediment types than the remainder of the US eastern continental shelf (Emery *et al.*, 1965). The Gulf of Maine has always been important as a region of rich fishing grounds with areas such as Cape Cod Bay being named, in 1602, as a direct result of the abundance of Atlantic cod.

Commercial fisheries have been monitored over the years in the Gulf of Maine and there is an abundant literature on the changes in the various fish stocks (Conservation and Utilization Division, 1988). There are also a number of faunistic surveys of both fish and invertebrates so that most of the faunal constituents of the Gulf are known (Bigelow & Schroeder, 1953; Rowe *et al.*, 1975; Watling *et al.*, 1988; Langton & Uzmann, 1989). Several extensive studies of the food habits of fishes in the offshore Gulf have also been

completed in the recent past (Grosslein *et al.*, 1980; Langton & Bowman, 1980, 1981; Bowman & Michaels, 1984; Bowman *et al.*, 1987). In contrast, little effort has been expended on constructing food webs and quantitatively, or even qualitatively, evaluating the linkages that exist between the fish community and their prey (MacDonald & Green, 1986) except by inference from daily ration calculations for specific species of fish (e.g. Durbin *et al.*, 1983; MacDonald & Waiwood, 1987) or through theoretical energy budget calculations (e.g. Schlitz & Cohen, 1984).

In the last several years work has been initiated to study the relationship between fish and the associated benthic community at two specific locations, the Portland Fishing Grounds and Sheepscot Bay, in the Gulf of Maine (Fig 1). Some of the results have been described in reports by Packer (1988) and Ward (1988). The present paper extends this work by establishing functional prey groupings for the dominant fish species at the Sheepscot Bay site as well as comparing and discussing the trophic relationships that exist between the fish and benthos on a broader scale throughout the Gulf of Maine.

MATERIAL AND METHODS

In the Sheepscot Bay otter trawling was conducted on 25 days from June 1987 to November 1988, using the University of Maine's research vessel the R.V. LEE. The R.V. LEE is a 10.4-m vessel and was able to tow a 9.14-m head rope net with a 2.54-cm mesh codend which retained fish down to 10 cm in total length. Three stations in the Sheepscot Bay were visited during daylight hours (Fig 1). A 30-min tow started from a reference Loran C position and proceeded in a direction that was dependent on weather conditions.

The catch from each tow was sorted by species and the total length (to nearest cm) of all fish was individually measured. A subsample of the catch was preserved in 10% formalin for stomach content analysis. Fish were selected at random from the catch, without regard to size, and the sample size for each species was usually no more than ten fish.

In the laboratory the stomachs were cut open over a fine mesh screen and rinsed to remove the formalin. The contents were sorted to the lowest taxonomically discrete group and the wet weight determined.

The dietary data are presented here as either the percentage of the total weight of the stomach contents for the six dominant fish and/or as a percentage of the frequency of occurrence for each of the prey categories for the different predators. Dependence on a particular functional group was categorised on a % weight basis of the total stomach contents for each predator with above 30% representing a high degree of dependence, 10 to 30% being intermediate, and 5 to 10% being the lowest level recognised.

Prey species were divided into a series of functional groups using as criteria aspects of their life habits but particularly their relation to the benthos. For example, where the animal lives, such as in tubes in the sediment, at the sediment-water interface, on the sediment surface, or immediately above the sediment in the water column, summarises the relationship of the prey to the benthos. Other factors, such as mobility and morphological relationships, as well as how the prey might be perceived by the fish, were also considered. Using these general criteria, contents of fish stomachs from the Gulf of Maine

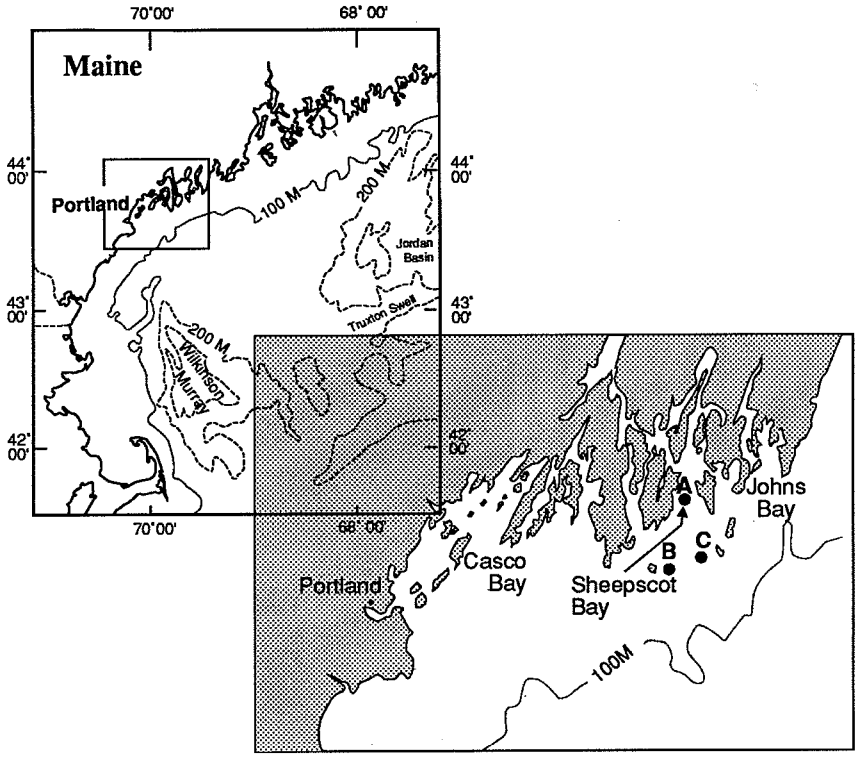

Fig 1.—Location of sampling sites for the study of fish diets in the mid-coast region of the Gulf of Maine. The Sheepscot Bay site included three distinct sampling stations, A, B and C.

have been assigned to the following functional groups: fish and squid (usually indicating predation on small or juvenile fish or squid), nektonic crustaceans (primarily euphausiids), epibenthic crustaceans (mysids, shrimp, juvenile crabs, and lobsters), infaunal crustaceans (amphipods, isopods, cumaceans), polychaetes (this group may well include several functional groupings but has been pooled because of the difficulty in identifying polychaete prey), bivalves, echinoderms (sand dollars, brittle stars), nemerteans, and cnidarians. These groups parallel, to a certain extent, the feeding classification of fish as browsers on infauna, predators on epifauna, and predators on mobile swimmers developed for the small inshore fishes of Scotland (Gibson & Ezzi, 1987).

In developing the data set for comparison with another site in the mid-coast area of Maine as well as the offshore region, information on stomach contents, as % weight, was taken from reports by Mauer & Bowman (1975), Langton & Bowman (1980, 1981), Hacunda (1981), and Bowman & Michaels (1984) and expressed in terms of functional prey groups. The methodology utilised in originally generating the dietary data in these reports is comparable with the analytical methods described above except for the geographic area sampled.

RESULTS AND DISCUSSION

SHEEPSCOT BAY FISH POPULATIONS

Thirty-two species of fish made up the catch of 2866 at the three trawl stations in Sheepscot Bay but relatively few of them were numerically important. Twelve species accounted for 98% of the catch and six species, alone, accounted for 87%. Dietary data on the populations of these six dominant species are presented in this paper. These species include *Myoxocephalus octodecemspinosus*, the longhorn sculpin; *Raja erinacea*, the little skate; *Pseudopleuronectes americanus*, the winter flounder; *Limanda ferruginea*, the yellowtail flounder; *Hippoglossoides platessoides*, the American plaice; and *Macrozoarces americanus*, the ocean pout.

FUNCTIONAL GROUPS OF PREY SPECIES

In an attempt to delimit patterns in the dietary habits of the six dominant fish from the Sheepscot Bay, as well as from the other data available on Gulf of Maine fishes, the stomach contents were combined into functional prey groups (Table I). The subdivision of the benthos into functional groups results from the observation that most of the bottom-feeding fishes in the Gulf of Maine have food preferences that are constrained either phyletically or ecologically. These preferred prey groups differ among the fish species (Tyler, 1972), and within the constraints of a particular prey group, a broad range of species is invariably found in the fish stomachs, especially in the Gulf of Maine where the species richness of potential prey is high. Furthermore, each of the fish-benthos studies in the Gulf have used different analytical techniques to deal with the array of species found both in the benthos and in fish stomachs (Tyler, 1972; Hacunda, 1981; MacDonald & Green, 1986). Because of the variability in such factors as sampling intensity and identification of prey species that exists between all fish dietary studies, an analysis that does not rely strictly on species identities would be most reliable in elucidating the dominant fish-benthos connections for the region.

SHEEPSCOT BAY FISH DIETARY HABITS

Longhorn sculpin preyed primarily on epibenthic and infaunal crustacean prey groups (Table I). Crustaceans were most important with the epibenthic *Mysis stenolepis* being the largest single contributor on a weight basis (13.56%) although infaunal aorid amphipods (*Unciola inermis*) were the most frequent dietary component (29.70% occurrence). These prey items were followed in importance by Atlantic herring, *Clupea harengus*, and wrymouth, *Cryptacanthodes maculatus*, although they occurred in relatively few stomachs, 3.21% and 0.43%, respectively.

Little skate consumed a variety of prey including fish, epibenthic crustaceans, and polychaetes (Table I). Atlantic herring contributed most to the weight of identifiable fish prey, which overall, made up 25% of the diet. Crustacean prey included epifaunal pandalid shrimp, brachyurans (*Cancer* spp.), sand shrimp (*Crangon septemspinosa*), lobsters (*Homarus americanus*), and the infaunal mud shrimp (*Axius serratus*). Infaunal amphipods, although

TABLE I

Food of fish from Sheepscot Bay. Presented as a percentage of the total weight of stomach contents and summarised for the different functional groups. + indicates presence of a prey category with a weight <0.01 g while — or — — indicates total absence of the particular prey or a functional group.

	Longhorn sculpin	Little skate	Winter flounder	Yellowtail flounder	American plaice	Ocean pout
Fish	**33.65**	**25.72**	**0.70**	**7.34**	**33.16**	——
Clupea harengus	12.75	14.49	—	7.34	12.06	—
Cryptacanthodes maculatus	12.87	—	—	—	—	—
Other Osteichthyes	8.03	11.23	0.70	—	21.10	+
Epibenthic Crustaceans	**33.26**	**26.05**	**2.66**	**0.63**	**18.74**	**0.47**
Mysis spp.	17.60	0.37	0.06	0.35	5.85	0.37
Other Mysidacea	1.64	0.03	+	+	0.35	0.01
Pandalus montagui	3.28	6.64	—	—	—	—
Other Pandalidae	0.97	1.98	—	—	+	—
Crangon septemspinosa	3.98	3.00	0.19	—	12.54	0.04
Homarus americanus	—	5.61	—	—	—	—
Cancer spp.	5.79	8.42	2.41	0.28	—	0.05
Infaunal Crustaceans	**14.88**	**7.20**	**19.49**	**30.48**	**0.88**	**2.96**
Diastylis quadrispinosa	0.20	0.12	1.52	2.22	+	0.01
Other Cumacea	0.03	+	1.77	0.21	+	0.04
Unciola inermis	4.05	0.92	12.32	25.07	0.31	0.15
Leptocheirus pinguis	1.00	2.24	1.34	0.14	0.35	0.06
Erichthonius fasciata	0.12	0.04	0.17	0.07	+	—
Ampelisca macrocephala	0.28	0.27	0.12	0.28	—	—
Other Amphipoda	4.06	1.37	2.25	2.49	0.22	0.07
Axius serratus	5.14	2.24	—	—	—	2.63

Polychaetes	**7.81**	**17.27**	**33.12**	**41.55**	**37.89**	**9.24**
Ampharete arctica	0.03	+	3.03	2.98	0.93	—
Melinna cristata	—	0.88	2.40	1.73	6.69	0.32
Ophelina acuminata	0.06	1.62	0.39	4.50	0.93	—
Maldane sp.	+	0.06	1.11	0.21	+	—
Nephtys spp.	4.24	4.45	0.91	1.87	0.35	4.05
Lumbrineris fragilis	—	0.81	1.49	4.22	1.33	—
Ninoe nigripes	0.07	—	4.31	0.21	—	0.02
Other Annelida	3.41	9.45	19.48	25.83	27.66	4.85
Bivalves	**0.72**	**0.02**	**3.40**	**2.77**	**2.17**	**69.14**
Nucula spp.	0.60	—	0.38	1.04	0.75	24.64
Sphenia sp.	0.01	—	0.01	—	0.09	16.59
Other Bivalvia	0.11	0.02	3.01	1.73	1.33	27.91
Echinodermata	**0.11**	**0.57**	**0.10**	——	**0.27**	**2.67**
Nemertina	——	**3.60**	**1.50**	**6.58**	——	——
Cnidarians	——	**0.45**	**14.49**	——	**0.18**	——
Cerianthus spp.	—	—	9.62	—	—	—
Other Cnidaria	—	0.45	4.87	—	0.18	—
Other Arthropoda	4.04	2.39	0.30	+	+	3.51
Other Mollusca	0.02	0.03	0.03	0.07	—	+
Other Invertebrates	0.01	0.15	2.98	1.59	1.06	0.70
Organic Matter	5.21	16.49	20.77	8.59	5.63	11.33
Sand and Rocks	0.29	0.06	0.43	0.42	—	—
Number of stomachs	468	149	306	52	173	61
Mean contents wt (g)	0.76	2.05	0.44	0.28	0.13	1.38
Mean population length (cm)	18	37	18	23	18	34

weighing very little, occurred frequently (more than 30% of the stomachs) in the diet.

Winter flounder preyed primarily on polychaete and infaunal crustacean prey groups (Table I). Overall, polychaetes contributed 33% by weight of the stomach contents but unfortunately much of this group could not be identified. Members of the Ampharetidae, *Ampharete arctica* and *Melinna cristata*, and Lumbrinereidae, *Ninoe nigripes* and *Lumbrineris fragilis*, contributed over 5% of the diet. *Unciola inermis* was the most frequent infaunal crustacean prey. Cnidarians were also an important, but infrequent, prey group with the tube-dwelling anemone, *Cerianthus*, being the one genus identified. Polychaetes were the most frequent prey (35.29%).

Yellowtail flounder were found to prey primarily on polychaete and infaunal crustaceans (Table I), which together accounted for over 70% by weight of the stomach contents. Many of the polychaetes could not be identified although three species alone accounted for above 10% of the weight: *Ophelina acuminata*, *Lumbrineris fragilis*, and *Ampharete arctica*. Yellowtail also preyed on nemerteans, which constituted part of the "worm-like" prey. Among the infaunal crustaceans only *Unciola inermis* was of any importance in terms of weight of stomach content. Also of interest was the predation on Atlantic herring. When the data are examined on the basis of frequency of occurrence *U. inermis* is the single most important prey (48.08%) although almost all of the amphipods identified in the diet were frequent prey items. Similarly, many of the identified polychaete prey were more important in their occurrence in the diet than as a percentage of the weight of stomach contents.

The diet of American plaice was dominated by fish, polychaetes, and epibenthic crustacean prey groups (Table I). Unidentified fish and Atlantic herring together accounted for 33% by weight of the stomach contents. This was followed by unidentified polychaetes, although one species, *Melinna cristata*, contributed an additional 7% of the diet and was the single most important polychaete. Epibenthic crustaceans also added significantly to the weight of stomach contents, primarily in the form of the sand shrimp and *Mysis* spp. In terms of frequency of occurrence the fish prey were less significant while polychaetes (26.59%), sand shrimp (13.87%), and the mysid, *Mysis mixta* (10.4%), continued to be important food items.

Ocean pout were almost exclusively predators on the bivalve prey group (Table I). Over 69% by weight of the stomach contents consisted of bivalves with two genera, *Nucula* and *Sphenia*, accounting for 50% of the total. Bivalves also dominated the diet when considered on the basis of frequency of occurrence with values ranging from 18 to 62%. Crustaceans assumed greater importance on the basis of occurrence with some of the smaller infaunal forms, such as isopods and amphipods, being preyed on more frequently than weights of stomach contents would indicate.

COMPARISON WITH OTHER DATA

When constructing food webs, what is perhaps more useful than a consideration of the various functional groups for a single fish community is to evaluate the fidelity of a single species' dietary habits over space as well as time. For such a spatial comparison we have summarised (Fig 2), our Sheep-

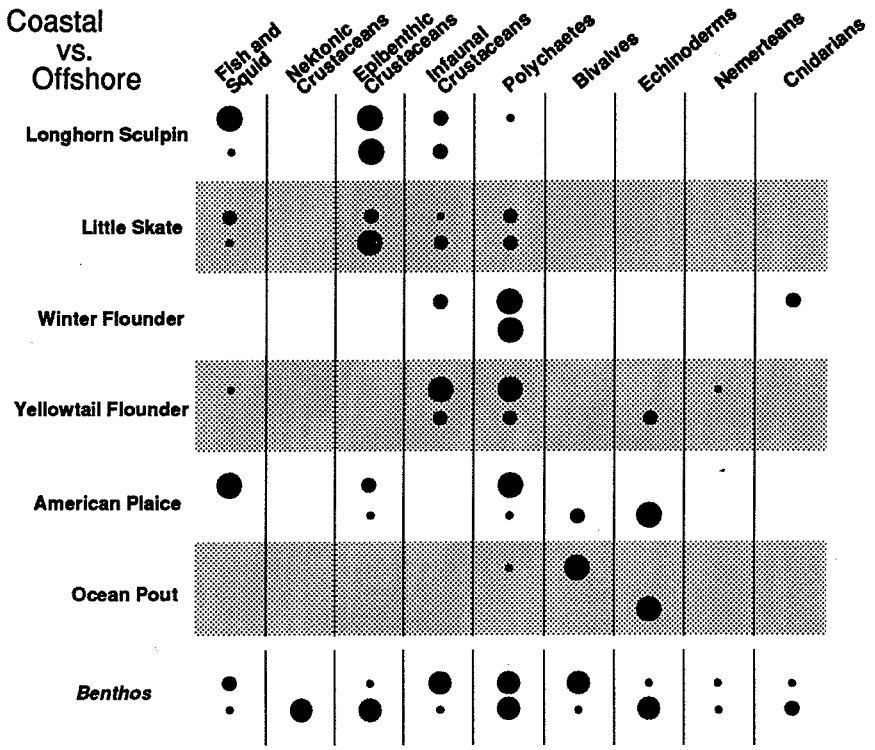

Fig 2.—Dietary data for six species of fish and relative composition of the benthos for the coastal region of the Gulf of Maine (upper rows of dots) and the offshore waters (lower rows of dots). Prey species (benthos) are combined into functional groups indicated along the y-axis and their levels of importance are indicated by the three different size dots. These represent $\geqslant 5$ to $<10\%$ (smallest), $\geqslant 10$ to $\leqslant 30$ (intermediate), and $>30\%$ (largest) of the total weight of stomach contents for each predator.

scot data and the more offshore data provided by the surveys of the National Marine Fisheries Service (Langton & Bowman, 1980, 1981; Bowman & Michaels, 1984). These data also include a temporal component within the geographic comparison but a more direct temporal comparison is found in Figure 3 where the Sheepscot Bay data for 1987–1988 are shown together with Hacunda's (1981) data from the neighbouring Johns Bay for 1978–1979.

Longhorn sculpin, for example, are strongly dependent on most of the same functional groups in both the coastal and offshore regions of the Gulf of Maine (Fig 2). The functional prey groups of the longhorn sculpins are again remarkably constant over time with epibenthic crustaceans, fish and infaunal crustaceans being the primary prey categories (Fig 3). A similar level of agreement is found for little skate with the exception that fish are more important in their diet, at the present time, inshore than in either of the other studies. This may reflect the current high abundance of Atlantic herring in

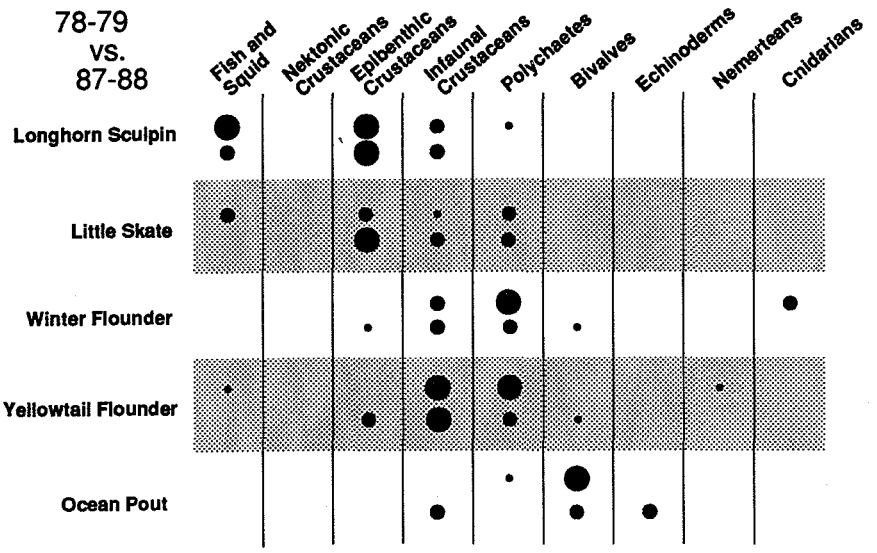

Fig 3.—Dietary data for fish collected along mid-coast Maine separated in time by eight years. Data from Sheepscot Bay are shown as the upper row of dots for each species while the data from Johns Bay are included as the lower row. Values of the dots are as in Figure 2. Johns Bay data are from Hacunda (1981).

the Gulf of Maine (Conservation and Utilization Division, 1988). Winter flounder have a slightly more diverse diet inshore than offshore but many studies have shown this species to be extremely cosmopolitan in its dietary preferences (Langton & Bowman, 1981). Yellowtail flounder shows a strong dependence on polychaetes and infaunal crustaceans both coastally and offshore although one distinction, that is also reflected in the temporal comparison, is predation on Atlantic herring occurring in the Sheepscot Bay.

In contrast to the other flatfish, the longhorn sculpin and little skate, the diet of American plaice varies substantially geographically. The major functional groups include fish and polychaetes in the Sheepscot Bay while offshore the single most important prey group is echinoderms (chiefly brittle stars). This may, however, reflect a size-related shift in dietary habits for this species (see Langton & Bowman, 1981) as well as availability of prey at the Sheepscot Bay site. The fish at the coastal site averaged 18 cm total length while the mean size offshore was 28 cm.

A complete geographic shift in diet was noted for ocean pout where the coastal population in the Sheepscot Bay was found to prey almost exclusively on bivalves, while offshore the single important functional group was echinoderms. The temporal comparison between Johns and Sheepscot Bays demonstrates a wider diversity of prey being eaten in the earlier time period. In this case, however, the three populations have similar mean lengths (34, 34, and 37 cm for offshore) so that the differences cannot be attributed to a size-related change in diet but rather simply a more catholic approach to feeding. From a functional perspective, it may also be true that bivalves and echino-

derms are indistinguishable by the ocean pout. Both the bivalve and ophiuroid prey live in the top few centimetres of soft muddy sediment and are similar-sized calcareous animals.

DISTRIBUTION OF PREY GROUPS IN THE BENTHOS

The benthic communities of the Gulf of Maine have only recently been characterised in a quantitative manner (Watling, unpubl. data; Watling *et al.*, 1988). In general, the coastal muddy bottom areas are dominated by the infaunal crustacean, polychaete, and bivalve prey functional groups. In these areas there may be a large number of species (more that 150) that could be consumed by the demersal fishes. In contrast, the offshore soft sediment areas are dominated by the epibenthic crustacean, polychaete, and echinoderm prey functional groups. The last, represented almost entirely by the brittle star *Ophiura sarsi*, is the most important both in terms of abundance and biomass (Watling, unpubl. data; Langton & Uzmann, 1989). The offshore area is also characterised by large numbers of nektonic crustaceans, chiefly euphausiids. While the offshore area exhibits a wider diversity of prey functional groups, the coastal zone often has at least an order of magnitude more individuals and total benthic biomass. These differences are reflected in the diets of some of the demersal fish from the two areas, especially with respect to the availability of infaunal crustacean, bivalve, and echinoderm prey functional groups (Fig 2).

STABILITY OF FUNCTIONAL GROUPS

Evaluating the stability of the functional groups identified in this paper is difficult because of the limited information on composition and production of the benthic communities of the Gulf of Maine (Wildish *et al.*, 1986; Ward, 1988; Watling *et al.*, 1988; Langton & Uzmann, 1989). The fish community has, however, been monitored over many years by the National Marine Fisheries Service so that it is, at least, possible to discuss the potential stability of the fish and squid prey functional group for some of the more piscivorous species in the Gulf. Three gadiform species have been monitored from 1969–1972 and 1973–1976 as part of a study of fish diets of the northwest Atlantic; the Atlantic cod, *Gadus morhua*; the pollock, *Pollachius virens*; and the white hake, *Urophycis tenuis*. During 1969–1972 these three populations relied heavily on fish as part of their diet and on clupeids, the Atlantic herring, in particular (Fig 4). During this same period and continuing until 1982 the herring stocks in the Gulf were declining. Consequently, during 1973–1976 these three piscivores shifted their predatory habits to other species of fish, including cannibalism for the pollock and hake, such that the proportion of fish in their diet remained relatively constant. Atlantic cod and pollock did, however, compensate for the decline in their preferred prey, herring, by broadening their diet to include squid which were undergoing a population increase during this period (Conservation and Utilization Division, 1988). Similar compensatory predation has been discussed by Waiwood & Majkowski (1984) for Atlantic cod in the Gulf of Saint Lawrence suggesting that, indeed, there is stability within appropriately defined functional groups for similar-sized fish. Also interesting is the importance of juvenile herring in the

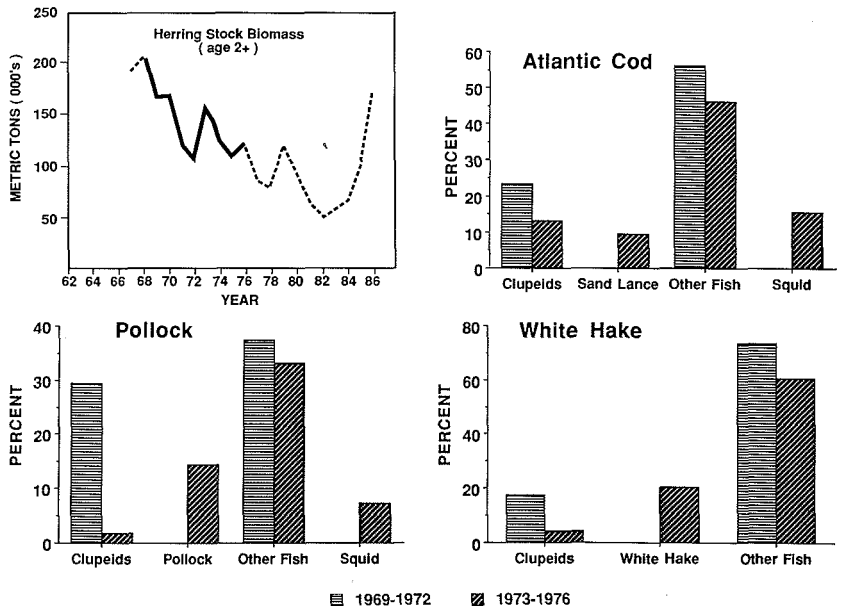

Fig 4.—Piscivorous components of the diet of three gadiform fishes from the Gulf of Maine for 1969–1972 and 1973–1976. The data show a shift in predation from Atlantic herring to other species of fish and squid with a decline in the herring stocks in the Gulf of Maine. Data are from Bowman & Michaels (1984) and Conservation and Utilization Division (1988).

diet of the fish most recently sampled in the Sheepscot Bay suggesting a return to a herring-based food web in the Gulf of Maine coincident with the documented increase in the herring stock to near the levels of the late 1960s (Fig 4).

It is equally important to consider the size composition of the predator populations when evaluating the stability of functional groups and establishing trophic linkages between demersal fish and their prey. Although this paper has treated each predator species sampled as a single group for comparative purposes with other published data, ontogenetic changes in the diet of some fish species are very well documented. It has, on many occasions, been suggested that in ecological models these dietary differences should override taxonomic groupings (Langton, 1982; Gibson & Ezzi, 1987; among others). In this paper such a size-related dietary shift has been reconfirmed for American plaice (Fig 2).

In addition to considering the size structure of the predator populations and its potential influence on the stability of functional groups, it is also important to account for the behaviour of the various fish species when establishing functional prey groups. Stability of these functional groups is likely to be more dependent on predator foraging behaviour and/or size-related shifts in this behaviour than on the taxonomic groups to which the prey belong. In this paper we have used some taxonomic constraints in

creating the various functional groups but it has also been suggested, for example, that bivalves and echinoderms may be functionally indistinguishable as far as ocean pout are concerned (MacDonald, 1983). Similarly, nemerteans have been described as "worm-like" prey for yellowtail flounder suggesting that polychaetes and nemerteans, although taxonomically distinct, may be functionally identical as prey items. Predation on the siphons of bivalves by various species of flatfish (Ansell & Gibson, 1990) as well as predation on cnidarians by winter flounder reported here and elsewhere (Langton & Bowman, 1981) suggests another taxonomically independent functional grouping. We view the proper definition of prey functional groups as a dynamic process that will probably have to be done anew for each geographic region depending on the dietary habits of the component fish species.

IMPLICATIONS FOR ECOLOGICAL MODELLING

Most of the models published to date that deal with energy flow between the macrobenthos and their demersal fish predators use a single equation containing some average value to describe the exchange between these groups. This is often not the case for studies of pelagic ecosystems where the zoological components of the water column are distinguished as size dependent (i.e., functional) groups (Longhurst, 1983; Pace *et al.*, 1984). For example, the model by Pace *et al.* (1984) for continental shelf food webs has four subdivisions of zooplankton which lead to pelagic fish, but only a single macrobenthic category that leads to demersal fish. The model simulation, not surprisingly, predicts with reasonable accuracy the production of pelagic fish under several different scenarios but does not do well at predicting macrobenthic or demersal fish production.

The inclusion of all macrobenthos in a single group and all benthic feeding fishes into a single demersal fish box obscures important relationships and, therefore, is not likely to result in the accuracy necessary to model and manage the demersal fish resource. Cohen *et al.* (1982), for example, noted that when combining all macrobenthos into a single box for their model of energy cycling on Georges Bank, they were forced to choose some intermediate, average, value of production which did not typify many of the taxa found. Values of production per unit biomass vary widely yet overlap for polychaetes, amphipods, bivalves, and a brittle star (Warwick *et al.*, 1978; Collie, 1985), as do caloric values on an ash-free dry weight basis (Brey *et al.*, 1988; Steimle & Terranova, 1988). Brey *et al.* (1988) also note that caloric values for echinoderms, polychaetes, bivalves, and crustaceans are quite different when considered on a dry weight basis. On the other hand, even though several of the functional groups may have a similar level of production, they could differ substantially in their digestibility by different species of fish (MacDonald *et al.*, 1982; MacDonald & Waiwood, 1987; Macpherson *et al.*, 1989). When a bivalve is ingested by a fish, the high inorganic content is likely to result in a longer gut residence time and consequently a lower ranking in terms of digestibility. As demonstrated above, many demersal fish species feed on only one or a few of the several functional groups that comprise the benthic community and there is stability in these feeding relationships (see also, Grosslein *et al.*, 1980). Consequently, we suggest that one way to reduce the complexity found in these systems, without

eliminating it altogether (as has been done in the past), is to subdivide the macrobenthos into functional prey groups for modelling purposes.

Reducing the complexity of a system by aggregation, even according to common function, is not without its risks (Sugihara, 1984). While functional groups can be defined in many different ways depending on the purposes of the study at hand, the aggregations need to be based on sound understanding of the natural history of both prey and predator species. Some objective measure of internal group homogeneity needs to be developed to ensure that aggregations are not determined solely on the basis of investigator preconceptions. In addition, aggregations may be so inclusive that subtle, but ecologically important, patterns are obscured. Consequently, we view the definition of functional prey groups as an iterative process, open to change as the relationships between predator and prey are better defined.

In order to make benthic food web and energy transfer models more predictive, investigations on the production and, from the fishes' perspective, digestibility of functional prey groups are urgently needed. It is clear from our review of the available data on contents of fish stomachs from the Gulf of Maine, that the demersal fishes subdivide the available resource, that they perceive prey in a manner that differs substantially from the view of most benthic ecologists, and this behaviour of these predators needs to be reflected in our ecological models.

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DEPTH-RELATED TRENDS IN DIET OF A DEEP-SEA BOTTOM-LIVING FISH ASSEMBLAGE OF THE ROCKALL TROUGH

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ABSTRACT The diets of the deep-sea bottom-living fishes of the continental slope and rise of the Rockall Trough between 500 and 3000 m have been described. The majority of species fed on benthopelagic organisms and little use was made of the benthos. Until recently it has been difficult to relate the consumption of prey to the fish population as a whole because of the difficulty of obtaining estimates of the abundance and biomass of large, fast-moving organisms in the deep sea. The use of large trawls towed at faster speeds than those commonly used in the deep-sea has resulted in better estimates of fish biomass. These estimates have been used to compare the consumption of different categories of prey organisms in relation to the total fish biomass and depth. On the upper slopes fish make up a major component of the diet of the sharks and scabbard fish, which make a significant contribution to the biomass at these zones. Beginning on the mid-slopes macrourid and other benthopelagic feeders account for the overall diversity of prey organisms eaten. The high proportion of unidentified material of a gelatinous nature associated with the alepocephalid species at mid-slope depths suggests that salps, ctenophores, and other gelatinous organisms may contribute to the increase in fish biomass at these depths.

INTRODUCTION

It is only by comparing the catches of a wide range of gears that the fisheries scientist can obtain a realistic estimate of abundance and biomass. Sampling in the deep-sea has not been extensive despite the first use of an otter trawl to sample depths down to 5160 m as long ago as 1910 (Murray & Hjort, 1912) and the number of different trawl types used has been relatively small and consequently estimates of abundance and biomass are poor.

One of the aims of the Scottish Marine Biological Association's deep-sea fish programme was to use as many different sampling methods as possible. The first samples were caught by an epibenthic sledge or an Agassiz trawl (both forms of beam trawl). A few years later a commercial type Granton trawl of 20.6 m headline fished on paired warps was used. This was restricted by the length of the paired warps on R.R.S. CHALLENGER to fishing at depths of 1250 m or less. To sample at greater depths a small otter trawl (headline 11.4 m) was fished on a single warp over the same depth range as the Granton