DIET OVERLAP BETWEEN ATLANTIC COD, *GADUS MORHUA*, SILVER HAKE, *MERLUCCIUS BILINEARIS*, AND FIFTEEN OTHER NORTHWEST ATLANTIC FINFISH

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ABSTRACT

Diet overlap calculated as the percentage similarity between the diets of Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and 15 other finfish species was computed from stomach contents data collected in the northwest Atlantic between Cape Hatteras, North Carolina, U.S.A., and western Nova Scotia, Canada, from 1973 through 1976. Since crustaceans are preyed on by both Atlantic cod and silver hake and most of the 15 other groundfish species representing members of the Rajiformes, Perciformes, Gadiformes, and Pleuronectiformes, completely dissimilar diets occur very rarely. Although the overlap values are quite variable, the greatest overlap, with few exceptions, occurs among the gadiform fishes themselves rather than between the gadids and species from the three other ordinal taxonomic levels. Furthermore, Atlantic cod and silver hake show a size dependent shift in diet (at 60-70 cm for Atlantic cod and 20-25 cm for silver hake) from crustaceans to fish so that, generally, the major overlap levels are for the smaller size classes of fish. Overlap levels are discussed in relation to the prey species the predators share and also in terms of their usefulness in identifying potential trophic linkages between northwest Atlantic finfish.

The traditional way of identifying fish is by recognizing individual species as discrete taxonomic units. Although the species concept is fundamental to any biological work, fishery biologists have been considering other means of grouping species. These are usually attempts to lump species in an ecological sense and they often depend on the fishes' diet. These feeding niche groupings may then be related to the morphology and size of the fish or the prey. Food related size classes for fish have, for example, been identified by Parker and Larkin (1959), Paloheimo and Dickie (1965), and Tyler (1972). These classes are referred to as threshold lengths or feeding stanzas. Grouping of fish based on gut morphology alone has been explored extensively for flatfish by deGroot (1971), while prey size grouping was developed by Ursin (1973) and applied to northwest Atlantic fish by Hahm and Langton (1980[2]). More recently, scientists on the west coast of the United States have been looking at Pacific fish assemblages (Gabriel and Tyler 1980) and have proposed the idea of an Assemblage Production Unit (Tyler et al. in press). The Assemblage Production Unit is defined as a geographically limited natural production system of interacting organisms, in which all production is trophically linked.

The key to all these schemes of species independent linkages is a complete understanding of whatever criteria are used to group like animals. In the present paper, fish predators have been grouped by species in 5 cm size classes and the diet of each 5 cm length group described quantitatively as a percentage weight of the total stomach contents for each group. Diet overlap has then been calculated for each species-size class combination and the overlap levels related to actual diet composition. Although diet overlap calculations have their limits (discussed in Langton and Bowman 1980), as do any other methods of data reduction, this paper offers one way of evaluating real and/or potential trophic linkages between northwest Atlantic finfish.

METHODS

Stomachs were collected from both demersal and pelagic fish by personnel at the Northeast Fisheries Center Woods Hole Laboratory, as part of a multispecies food-habit study conducted from 1973 through 1976. The sampling area covered the continental shelf waters from Cape Hatteras, N.C., to the Canadian coast of Nova

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[2]Hahm, W., and R. Langton. 1980. Prey selection based on predator/prey weight ratios for some northwest Atlantic fish. Int. Counc. Explor. Sea, C.M. 1980/L:62, 9 p.

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Scotia. Details of this food-habit survey were described in an International Council for the Exploration of the Sea document and will not be repeated here (Langton et al. 1980[3]).

Diet overlap, expressed as the percentage similarity between diets, was calculated according to the formula of Shorygin (Ivlev 1961) and has been described in several other papers as a means of evaluating the diet of northwest Atlantic finfish (Langton and Bowman 1980; Grosslein et al. 1980) although there are other methods of indexing like diets (Lipovsky and Simenstad 1978). The calculation is quite simple and is done by summing the smaller value, as a percentage weight in the present case, for all prey shared by the two predators. The computed value ranges from 0 to 100%, with 0% representing no diet overlap and 100% representing identical diets. The final overlap value is sensitive to the taxonomic level at which the prey was identified and for this paper the finest taxonomic breakdown available was used, i.e., prey identified to species whenever possible. Because of the sensitivity of this overlap measure to the taxonomic breakdown of prey, statistical methods of evaluating absolute overlap values are not practical. Instead, the values have been classified as low, 0-29%; medium, 30-60%; or high, >60% for the purpose of discussion.

The computation of diet overlap was automated and the actual computer program checked by running diet overlap for any one predator against itself. In this case the computer generates a value of 100% overlap for fish in the same size class and then a mirror image of values on each side of the 100% line. This is shown graphically in Figure 1 where Atlantic cod is plotted three dimensionally versus Atlantic cod. The plotting program only considered size classes up through class 25 (125 cm maximum fork length), but by truncating the output at this level little data was eliminated (a total of 5 cod out of 1,714 examined, for example). In fact, since the fish were taken randomly from the catch, the majority of the samples came from the most frequently occurring size classes which, even for Atlantic cod, did not approach this maximum size. Furthermore, size classes that did not include a sample size of at least 10 fish were eliminated before the data were plotted since very small samples would not necessarily be representative of the size class.

This study concentrates on two of the major fish predators in the northwest Atlantic, silver hake and Atlantic cod, and on the questions of their diet overlaps with 15 other finfish species. The food habits information presented is limited to an explanation of the prey shared by the predators which results in the observed overlap values. Detailed descriptions of the diet of the fish collected by the Northeast Fisheries Center are in preparation or have been given elsewhere. Dietary information on the northwest Atlantic Gadiformes and Pleuronectiformes can, for example, be found in Langton and Bowman (1980, 1981), Bowman and Bowman (1980), and Durbin et al. (1980)[4] while data on fish from other taxa are described in Edwards and Bowman (1979) and Grosslein et al. (1980).

RESULTS

Atlantic Cod — Little Skate

Atlantic cod, *Gadus morhua* Linnaeus, and little skate, *Raja erinacea* Mitchell, show relatively little similarity in diet (Fig. 2A). The maximum value of 48% was found for the overlap between size class 3 (11-15 cm) Atlantic cod and size class 3 little skate. The prey shared by these predators are primarily small crustaceans, in particular amphipods such as *Unciola*. Unfortunately, slightly more than 10% of the diet of each of these fish was unidentifiable with a resulting increase in the overlap values. As can be seen from Figure 2A, apart from the peak of 48%, medium levels of dietary overlap exist between Atlantic cod 11-20 cm (size classes 3 and 4) and little skate up to 45 cm total length (size class 9). Medium overlap values again occur between little skate 36-55 cm (size classes 8-11) and Atlantic cod 31-65 cm (size classes 7-13). This overlap can generally be attributed to the preponderance of a variety of crustaceans in the diet of both predators. For larger Atlantic cod the overlap values with little skate are extremely low, primarily because of a

[3]Langton, R., B. North, B. Hayden, and R. Bowman. 1980. Fish food habit studies-sampling procedures and data processing methods utilized by the Northeast Fisheries Center, Woods Hole Laboratory, U.S.A. Int. Counc. Explor. Sea, C.M. 1980/L:61, 16 p.

[4]Durbin, E., A. Durbin, R. Langton, R. Bowman, and M. Grosslein. 1980. Analysis of stomach contents of Atlantic cod (*Gadus morhua*) and silver hake (*Merluccius bilinearis*) for the estimation of daily rations. Int. Counc. Explor. Sea, C.M. 1980/L:60 (revised), 21 p.

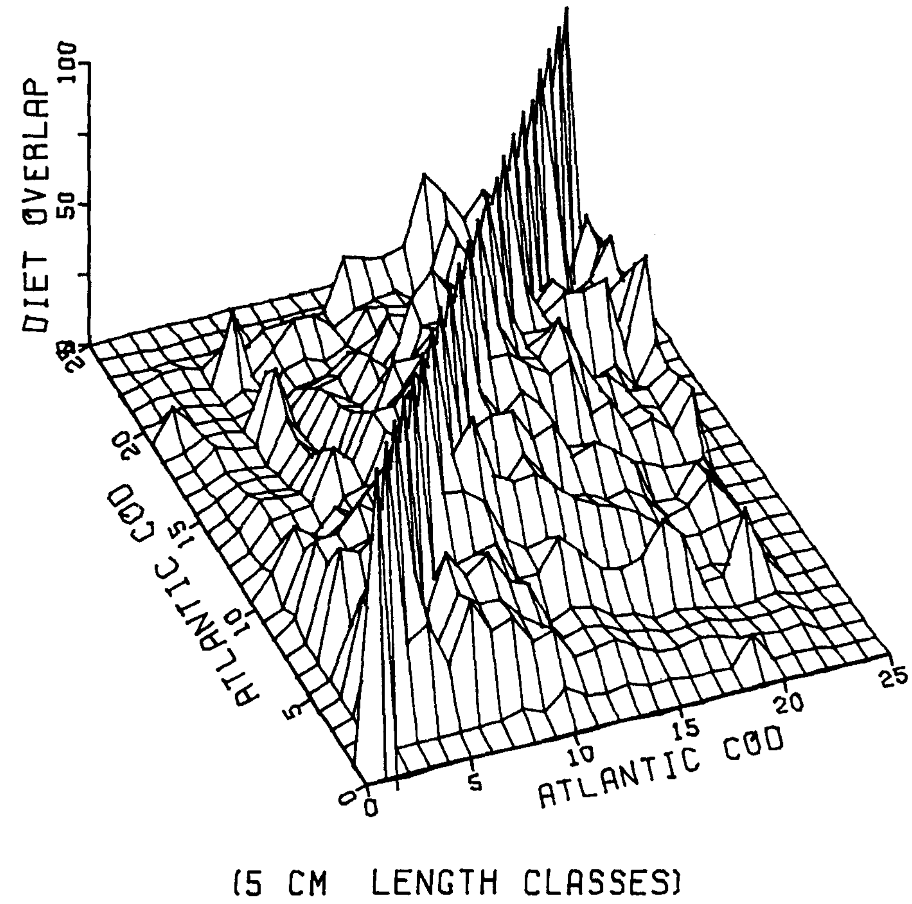

FIGURE 1.—Three dimensional plot of the diet overlap of Atlantic cod versus Atlantic cod; the same data set. Presented here is an example of the graphics output from diet similarity calculations. The peak represents 100% overlap for the same 5 cm length class of fish with a mirror image of values on either side of the peak.

shift in the diet of Atlantic cod from crustaceans to fish.

Atlantic Cod — Redfish

Atlantic cod and redfish, *Sebastes marinus* (Linnaeus), generally show low levels of diet overlap (Fig. 2B). There were, however, some medium overlap values occurring between the smaller Atlantic cod and redfish. The peak value of 49% occurred between redfish 16-20 cm (size class 4) and Atlantic cod 6-10 cm (size class 2) which was primarily the result of predation on pandalid shrimp *Dichelopandalus leptocerus*. Unfortunately, few of the redfish stomachs examined in this size class contained prey (2 out of 21 examined) so this peak may be artificially high, although in the other cases where medium overlap levels were found, pandalid shrimp were generally consumed by both predator species.

Atlantic Cod — Longhorn Sculpin

The pattern of diet overlap between Atlantic cod and longhorn sculpin, *Myoxocephalus octodecemspinosus* (Mitchill), shows low to medium overlap values over much of the size range of both species. The values do decrease, however, between the larger Atlantic cod (>61 cm, size class 13) and smaller longhorn sculpin (<16 cm, size class 3) (Fig. 2C). The peak value of 38% occurred between two different predator size classes, and in both instances the single most important prey contributing to this overlap was the

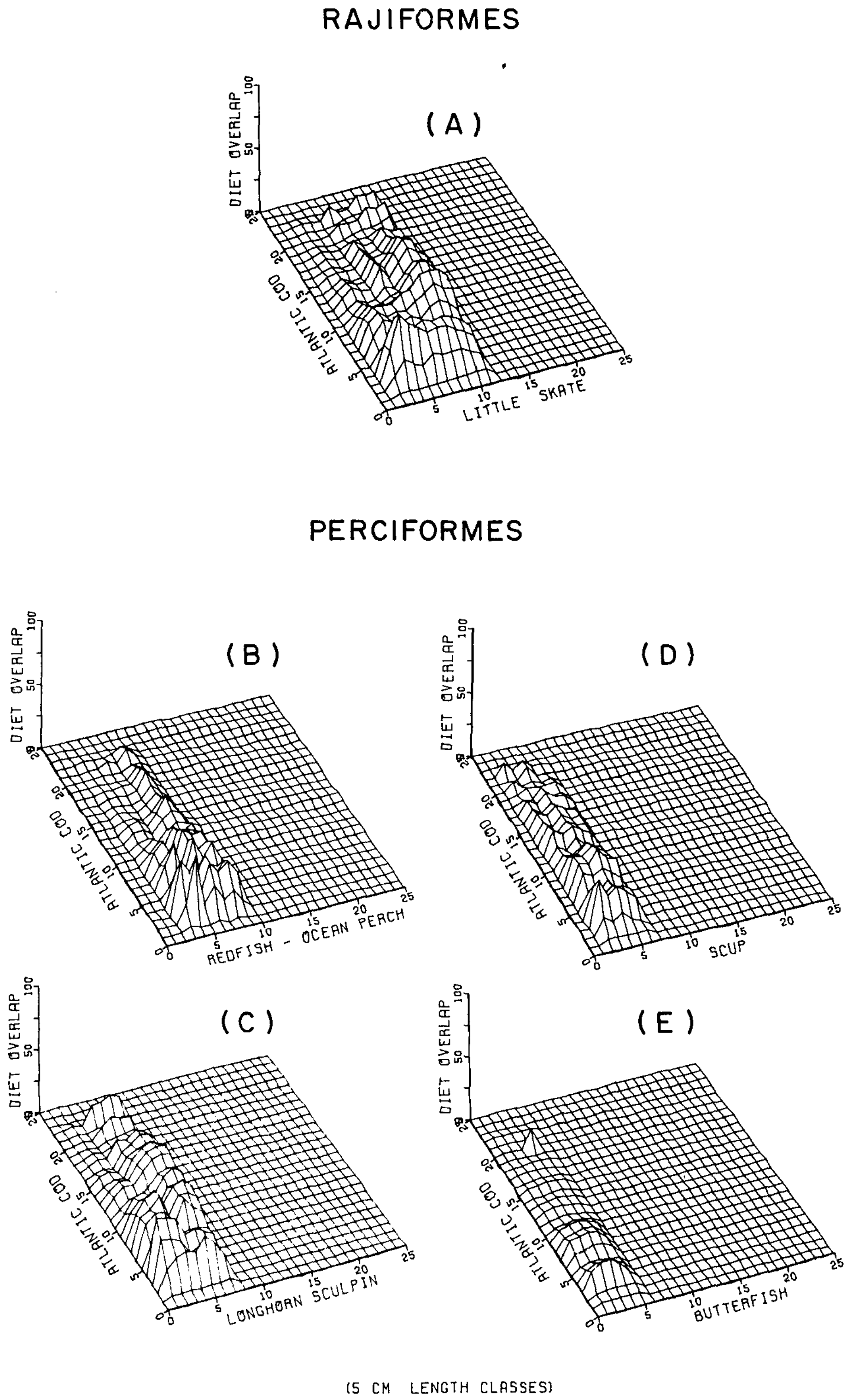

FIGURE 2.—Three dimensional plot of the diet overlap of Atlantic cod with selected rajiform and perciform fishes.

pandalid shrimp *Dichelopandalus leptocerus*, although a large variety of other crustaceans contributed to both of the predator's diets.

Atlantic Cod — Scup

Overlap between the diet of Atlantic cod and scup, *Stenotomus chrysops* (Linnaeus), is at a low level (Fig. 2D), and the low values represent a broad array of prey, principally crustaceans, that constitutes the forage base of these two predators. The only trend in these values is that they are at their lowest for large Atlantic cod (>80 cm) and all size classes of scup. This is the result of the larger Atlantic cod's piscivorous habits.

Atlantic Cod — Butterfish

The Atlantic cod and butterfish, *Peprilus triacanthus* (Peck), show very low diet overlap levels, the maximum being 19% for 11-15 cm (size class 3) fish of both species. There was, however, relatively more overlap between the smaller Atlantic cod (<45 cm) and all sizes of butterfish sampled (Fig. 2E).

Atlantic Cod — White Hake

The diet of white hake, *Urophycis tenuis* (Mitchill), shifts from crustaceans such as euphausiids, shrimp, and mysids when they are small (<≅50 cm) to primarily fish for the larger white hake. This parallels the change in the Atlantic cod's diet with size. The result is a varying degree of dietary overlap across all size classes of fish examined (Fig. 3A). Low levels occurred between the smaller white hake and the larger size classes of Atlantic cod and vice versa. Intermediate levels, values in the 30-50% range, are found in clusters which are the result of a variety of shared prey types. Some of these values in the 40 and 50% range depend upon the fish components in the diet. In particular, silver hake and herring, *Clupea harengus*, together with unidentified fish are the most commonly occurring prey that these predators share. The greatest overlaps observed were between 21-25 cm (size class 5) Atlantic cod and several larger size classes of white hake (36-85 cm, size classes 8-17) (Fig. 3A). This high overlap is somewhat artificial since it is the result of unidentified fish prey in both predators' diets. It does, however, amplify the importance of fish prey to these predators.

Atlantic Cod — Red Hake

Atlantic cod and red hake, *Urophycis chuss* (Walbaum), have low to intermediate levels of diet overlap. The lowest values occur between small red hake and large Atlantic cod (Fig. 3B). These small red hake prey quite heavily on crustaceans while the larger Atlantic cod have shifted their habits from crustacean prey to fish. The diet of red hake does, however, include more fish prey as the predators themselves grow, so that the overlap values between the larger size classes of red hake and Atlantic cod remain at an intermediate level.

Atlantic Cod — Spotted Hake

Atlantic cod and spotted hake, *Urophycis regia* (Walbaum), have diets which overlap at low to intermediate levels (Fig. 3C). The prey that they have in common is primarily crustaceans but may also include some fish. The cluster of intermediate values occurring between 11-25 cm (size classes 3-5) Atlantic cod and 11-30 cm (size classes 3-6) spotted hake is, for example, the result of predation on crustaceans such as *Meganyctiphanes*, *Dichelopandalus*, *Crangon*, *Unciola*, and other less significant taxa, while the intermediate overlap peaks between 31-35 cm spotted hake and Atlantic cod are due to fish predation.

Atlantic Cod — Pollock

Atlantic cod and pollock, *Pollachius virens* (Linnaeus), show low to intermediate levels of diet overlap over all size classes of both predators examined. Both of these species are crustacean/fish predators, relying more heavily on fish as they increase in size. For the smaller pollock, the euphausiid *Meganyctiphanes norvegica* and the shrimp *Pasiphaea multidentata* were the major components of the diet while the Atlantic cod relied on a much broader variety of prey. For the larger fish of both species a variety of pisces were included in the diet, some of which was not readily identifiable at any lower level than simply fish flesh. The problem in identifying fish remains generated two artificial peaks in overlap

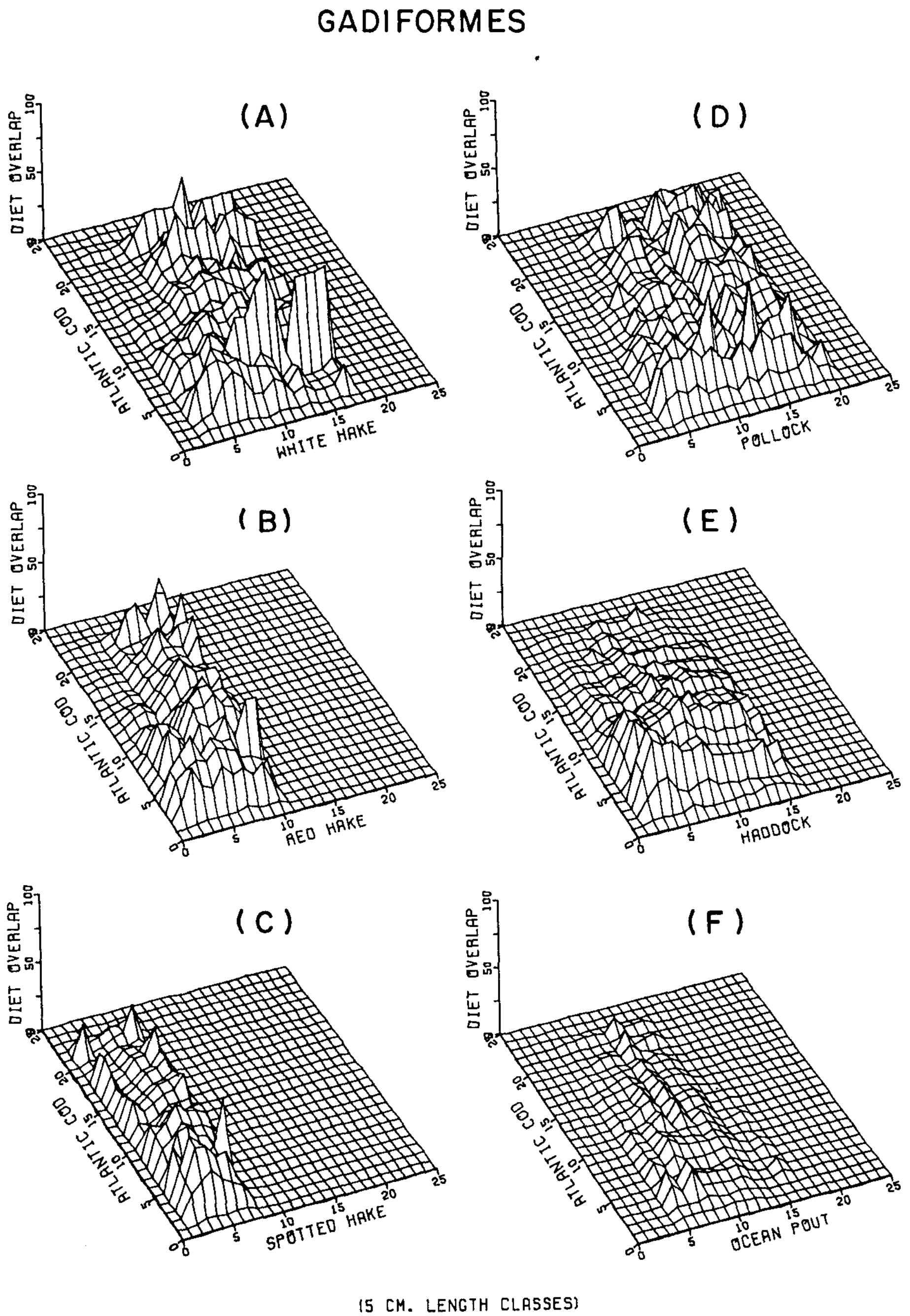

FIGURE 3.—Three dimensional plot of the diet overlap of Atlantic cod with selected gadiform fishes.

between Atlantic cod of size class 5 and pollock of size classes 10 and 14 as seen in Figure 3D.

Atlantic Cod — Haddock

Haddock, *Melanogrammus aeglefinus* (Linnaeus), is primarily benthic in its feeding habits with the result that its diet is similar to Atlantic cod's only when the Atlantic cod are also feeding on the benthos. Consequently, the degree of diet overlap between these two predators is highest for the smaller animals, as can be seen in Figure 3E. The diversity of prey that both these predators consume reduces the computed overlap values. The relatively low maximum values, 47% being the highest for 16-20 cm (size class 4) Atlantic cod and 11-15 cm (size class 3) haddock, make it difficult to identify any particular species of prey that gives rise to the observed intermediate levels of overlap.

Atlantic Cod — Ocean Pout

Ocean pout, *Macrozoarces americanus* (Schneider), are fairly specific in their predatory habits, and these habits do not overlap with those of Atlantic cod to any extent (Fig. 3F). A single prey species, the sand dollar, *Echinarachnius parma*, accounts for most of the diet of ocean pout although amphipods were also present in many of the fish stomachs examined.

Atlantic Cod — American Plaice

The diets of Atlantic cod and American plaice, *Hippoglossoides platessoides* (Fabricius), overlap at quite low levels, the highest value being 33% for 26-30 cm (size class 6) Atlantic cod and 21-25 cm (size class 5) American plaice. American plaice prey on a variety of benthic animals but, as they grow larger, they rely more on echinoderms than crustaceans and polychaetes. This is reflected in the diet overlap plot (Fig. 4A); the larger size classes of American plaice (>45 cm) have extremely small overlap with Atlantic cod because of predation on the sand dollar.

Atlantic Cod — Witch Flounder

Little diet overlap occurs between Atlantic cod and witch flounder, *Glyptocephalus cynoglossus* (Linnaeus), with all of the calculated values being 30% or less (Fig. 4B). Witch flounder are benthic predators with polychaete worms being of major importance as prey although they do consume crustaceans and other invertebrates. It is the crustacean component of the diet which accounts for these low levels of overlap with the Atlantic cod.

Atlantic Cod — Yellowtail Flounder

The diets of Atlantic cod and yellowtail flounder, *Limanda ferruginea* (Storer), overlap at generally low levels (Fig. 4C). There is only one cluster of intermediate levels involving yellowtail flounder from a single size class (class 3, 11-15 cm) which reflects the occurrence of pandalid shrimp *Dichelopandalus leptocerus* in both predators' diets. As with many other species, a reduction in the level of overlap occurs as the disparity in fish size increases. For yellowtail flounder this is quite apparent when compared with the larger Atlantic cod because the large Atlantic cod are primarily piscivorous. However, this reduction is not as noticeable for large yellowtail flounder and small Atlantic cod since the benthic habits of yellowtail flounder change little as the fish increase in size.

Atlantic Cod — Fourspot Flounder

Atlantic cod and fourspot flounder, *Paralichthys oblongus* (Mitchill), show low and intermediate levels of diet overlap (Fig. 4D) which is primarily a result of predation on crustaceans. The single most important crustacean prey was the pandalid shrimp *Dichelopandalus leptocerus* which makes up from 17% to 30% of the diet of 21-30 cm fourspot flounder and 3% to 40% of the diet of 6-45 cm Atlantic cod.

Silver Hake — Little Skate

The pattern of diet overlap between silver hake, *Merluccius bilinearis* (Mitchill), and little skate is shown in Figure 5A. Generally, overlap levels are low but medium levels range up to a high of 44% between small silver hake 1-15 cm (size classes 1-3) and little skate 11-45 cm total length (size classes 3-9). This degree of overlap can be attributed to the crustaceans in each of these predators' diets with the sand shrimp, *Crangon septemspinosa*, being of particular importance. For larger silver hake the diet overlap with little skate is insignificant since these larger hake prey on fish while little skate of all sizes prey primarily on benthic crustaceans.

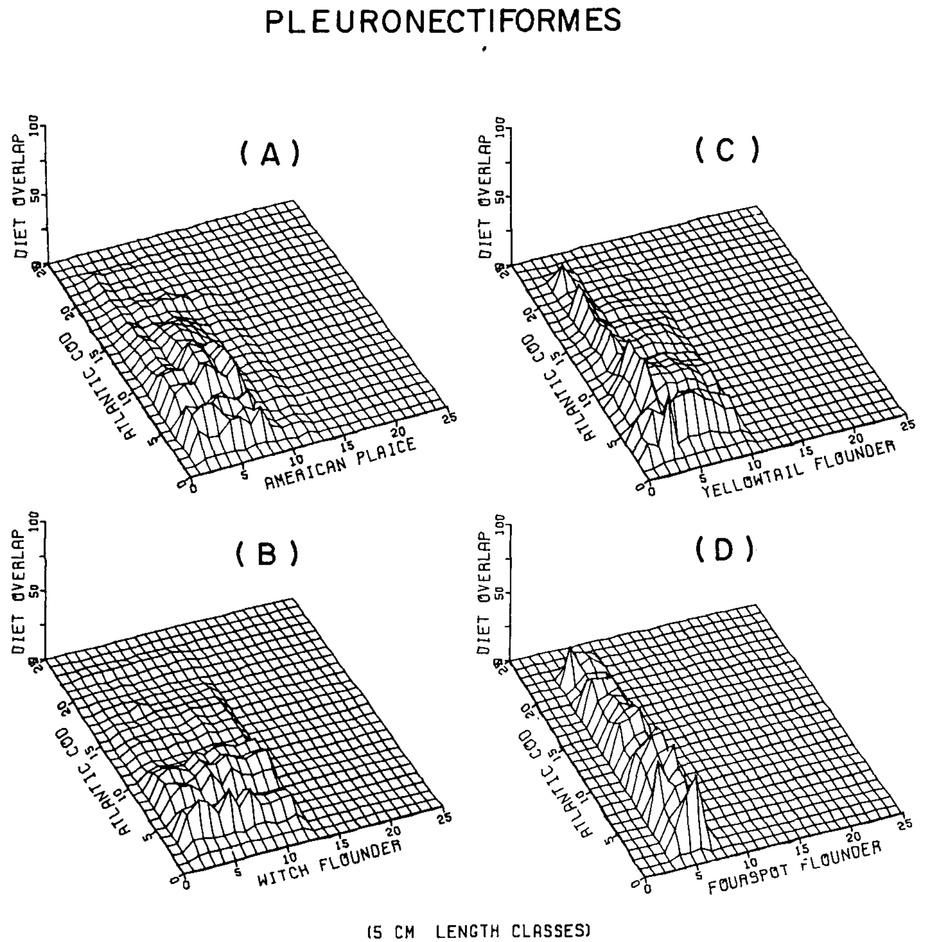

FIGURE 4.—Three dimensional plot of the diet overlap of Atlantic cod with selected pleuronectiform fishes.

Silver Hake — Redfish

High levels of overlap occur between 16-20 cm (size class 4) silver hake and 11-45 cm (size classes 3-9) redfish (Fig. 5B). The peak value is 75% for 31-35 cm (size class 7) redfish and these smaller silver hake. Most of this overlap is due to predation on the euphausiid *Meganyctiphanes norvegica*, which accounted for 60% and 63% of the diet of these 16-20 cm silver hake and 31-35 cm redfish, respectively. The other high overlap values between these two predators can also be attributed to euphausiids making up more than 50% of the diets. Medium levels of overlap, 30-42%, were found for other size silver hake and redfish. Once again *Meganyctiphanes norvegica* was a major dietary item but in some cases *Dichelopandalus leptocerus* also contributed significantly. For the larger silver hake (>35 cm, greater than size class 7) there was little, if any, diet overlap. These large silver hake prey heavily on fish while redfish are predominantly crustacean predators.

Silver Hake — Longhorn Sculpin

Intermediate diet overlap values occur between silver hake ranging from 6 to 15 cm in length (size classes 2-3) and most of the size classes of longhorn sculpins examined (Fig. 5C). This overlap is due to both predators' reliance on crustaceans such as *Crangon septemspinosa*, *Dichelopandalus leptocerus*, and *Neomysis americana*. For the larger silver hake, those that are primarily piscivorous, there is virtually no over-

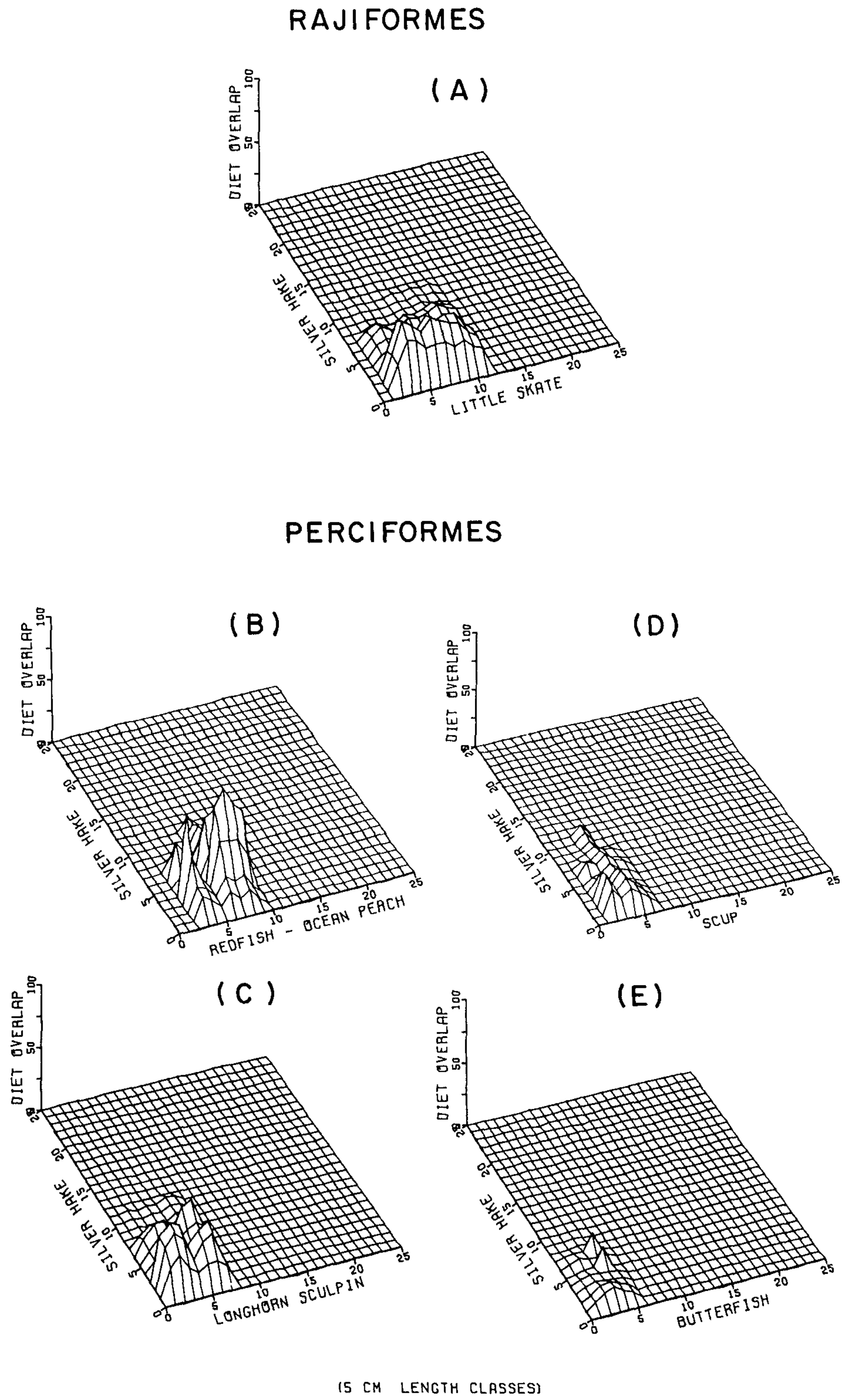

FIGURE 5.—Three dimensional plot of the diet overlap of silver hake with selected rajiform and perciform fishes.

lap or, at least, extremely low levels of overlap with longhorn sculpin.

Silver Hake — Scup

Silver hake and scup both prey on crustaceans, but they share few prey species in common so that diet overlap values are quite low (Fig. 5D). There is a trend for the overlap values to decrease when comparing larger silver hake and scup which mirrors the shift towards fish predation by these larger silver hake.

Silver Hake — Butterfish

The diets of silver hake and butterfish overlap at very low levels, the highest value being 17% which was the result of predation on the squid *Loligo* (Fig. 5E). Generally, the butterfish is more planktonic in its predatory habits than the silver hake which is reflected in the low overlap values.

Silver Hake — Atlantic Cod

Silver hake and Atlantic cod are generally found to have low to intermediate levels of diet overlap and very few values that are >60% (Fig. 6A). All of the high values are the result of unidentified fish remains forcing up the computed overlap values. Both of these predators become more piscivorous as they grow larger, but this size-specific dietary shift is not reflected in an obvious change in the level of diet overlap. In other words, the smaller fish share crustacean prey species such as euphausiids while the larger predators both prey on a number of different species of fish.

Silver Hake — White Hake

There is a clear pattern of overlap when comparing the diets of silver and white hake (Fig. 6B). The diets of the larger fish of both species do not overlap with the smaller fish of the opposite species. In other words, the diet of small silver hake has little in common with the larger white hake and vice versa. The explanation for this is a size dependent change in diet for both predators. When small, they both rely on crustaceans, such as euphausiids, and then gradually shift to fish as the predator grows. For example, the high value, 74% between 16-20 cm (size class 4) silver hake and 31-35 cm (size class 7) white hake results from over 50% of either of these predators feeding on *Meganyctiphanes norvegica*. For comparison, the other high value, 75%, for 41-45 cm (size class 9) silver hake and 66-70 cm (size class 14) white hake, is the result of fish predation on such fish as silver hake, clupeids, and other unidentifiable fish remains.

Silver Hake — Red Hake

The diet overlap between silver and red hake ranges from 0% to intermediate levels as high as 56%. The general pattern is increasing overlap with increasing predator size up to 26-30 cm (size class 6) and then leveling off or decreasing slightly between the larger fish (Fig. 6C). The peak value, occurring between 26-30 cm silver hake and 41-45 cm (size class 9) red hake, can be explained by predation on fish, *Dichelopandalus leptocerus*, and other invertebrates.

Silver Hake — Spotted Hake

Silver and spotted hake show, for the most part, intermediate to high levels of diet overlap between similar size fish (Fig. 6D). Peak values of 60% and 70% occur, for example, between 11-20 cm (size classes 3-4) and 16-25 cm (size classes 4-5) silver and spotted hake, respectively. These peaks are the result of a reliance by both predators on *Meganyctiphanes norvegica*, *Dichelopandalus leptocerus*, and *Crangon septemspinosa*. The intermediate overlap values are also, however, a reflection of predation on fish, especially for the larger silver and spotted hake.

Silver Hake — Pollock

High diet overlap values exist between silver hake 16-20 cm (size class 4) and pollock 16-65 cm (size classes 4-13). Two prey categories are responsible for these high levels, *Meganyctiphanes norvegica* and unidentified fish remains. Medium levels of overlap between these two predators are common for most size classes except for silver hake below 10 cm. Overlap between these smaller silver hake and all sizes of pollock falls into the lower overlap category. There are also extremely low values between small pollock and large silver hake (Fig. 6E).

Silver Hake — Haddock

Silver hake and haddock show little similarity in their diets and the resulting diet overlap val-

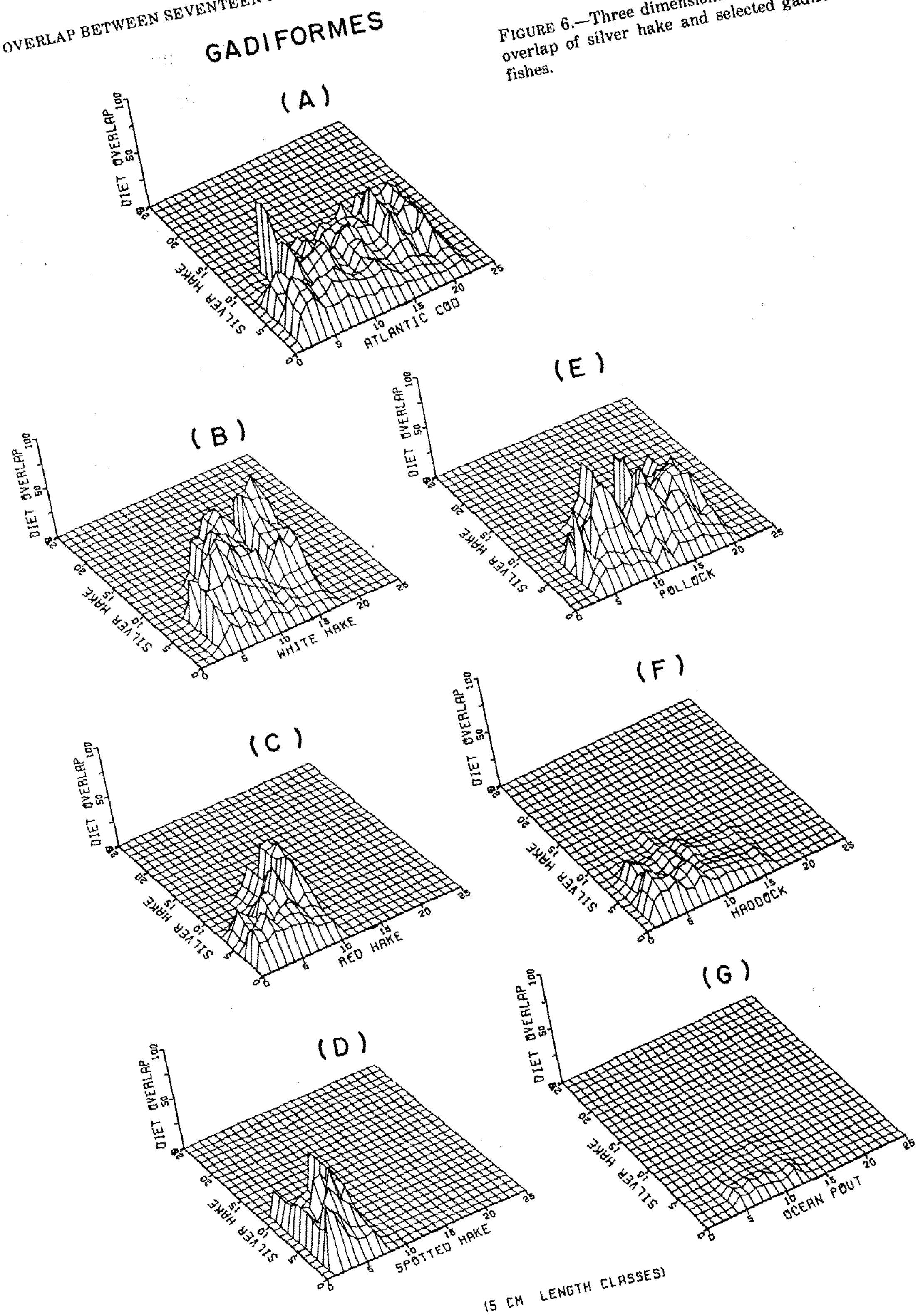

FIGURE 6.—Three dimensional plot of the diet overlap of silver hake and selected gadiform fishes.

ues are all quite low (Fig. 6F). Even with these low values, there is an obvious trend; the higher values occur between the smaller individuals of these two predators which reflects the dependance of small silver hake and haddock on crustacean prey.

Silver Hake — Ocean Pout

The diets of silver hake and ocean pout are mutually exclusive so that there is an extremely small degree of diet overlap (Fig. 6G). The only prey that they share in common are amphipods, but again, this is at a very low level.

Silver Hake — American Plaice

Silver hake and American plaice show very low levels of dietary overlap (Fig. 7A). Despite the lack of diet similarity, a pattern does emerge when comparing these two predators. The larger size classes of both species show virtually no overlap, while what similarity does exist occurs between silver hake and American plaice <40 cm. The diet of these larger individuals is quite specific, fish for silver hake and echinoderms for American plaice, so little overlap is to be expected, while the smaller individuals of both species prey on invertebrates.

Silver Hake — Witch Flounder

Silver hake and witch flounder share little prey in common with resulting low levels of diet overlap. The only exception to these low levels is a high peak (66% and 67%) between 16-20 cm (size class 4) silver hake and 11-20 cm (size classes 3-4) witch flounder (Fig. 7B). A single prey species,

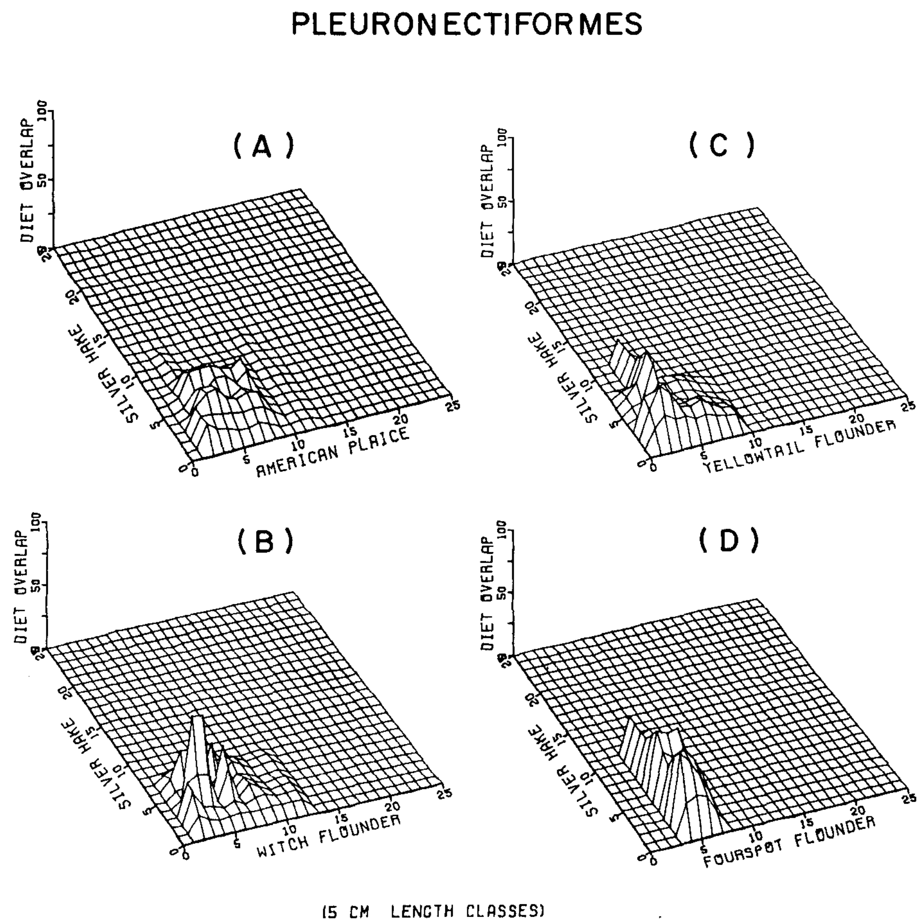

FIGURE 7.—Three dimensional plot of silver hake and selected pleuronectiform fishes.

Meganyctiphanes norvegica, is responsible for this since it alone accounts for >63% of each predator's diet. Similarly, the smaller peaks in the figure are also the result of having euphausiids as a common prey item.

Silver Hake — Yellowtail Flounder

Silver hake and yellowtail flounder have, for the most part, low levels of diet overlap (Fig. 7C). The few intermediate levels that do occur are, in all but one instance, related to yellowtail flounder that are 11-15 cm in length (size class 3) which have preyed on *Crangon septemspinosa*, *Dichelopandalus leptocerus*, or small unidentified fish. The one exception is for 6-10 cm (size class 2) yellowtail flounder and silver hake. These fish preyed primarily on *Crangon septemspinosa*, *Neomysis americana*, and amphipods with a resulting diet overlap of 39%. Even with these low overlap levels an overall pattern is apparent; the greatest overlap occurs between the smaller size classes of both species.

Silver Hake — Fourspot Flounder

The diets of silver hake and fourspot flounder overlap at low to intermediate levels (Fig. 7D). The highest value, 54%, occurs between 6-10 cm (size class 2) silver hake and 16-20 cm (size class 4) fourspot flounder. The peak, as with most of the other intermediate values, is the result of predation on crustaceans such as *Crangon septemspinosa*, *Neomysis americana*, and *Dichelopandalus leptocerus*.

DISCUSSION

The diet overlap comparisons presented here are one way to simplify fish food habits data and to identify real or, at least, potential pathways of energy exchange. As with any method of data reduction, however, certain compromises have to be accepted which must be kept in mind when discussing the results. The limitations of percentage similarity calculations have been described by several authors (Day and Pearcy 1968; Moyle 1977; Keast 1977; Langton and Bowman 1980; MacPherson 1981) and these limits include both biotic and abiotic factors. Such factors as the taxonomic level of prey identification, the actual quantity of prey consumed (especially since percentage similarity is a relative measure of dietary constituents), predator/prey distribution and abundance, and temporal factors that influence both predator and prey behavior all have to be considered in evaluating the meaning of diet overlap data.

The present data consider the entire northwest Atlantic as a single homogeneous ecological system since all the available data were grouped by species for the diet overlap calculations. This is a first attempt to examine size-specific finfish predation in the northwest Atlantic and, without more extensive basic biological information on finfish and invertebrate community structure, there was no reason to subdivide the data set. The research survey cruises on which the fish stomachs were collected were, however, planned for discrete geographic regions (e.g., Gulf of Maine, Georges Bank) and employed stratified random sampling based primarily on depth dependent strata (Grosslein 1969; Clark and Brown 1977). If the research survey catch data were analyzed statistically, using techniques such as cluster analysis, to identify fish species associations or assemblages, then there may be justification for subdividing the data set. Such methods have been utilized recently to identify northwest Pacific finfish assemblages (Gabriel and Tyler 1980; Tyler et al. in press) and have been used, to a limited degree, for northwest Atlantic fishes (Tyler 1972, 1974; Knight and Tyler 1973). Whatever techniques are employed the basic problem is the same: defining what constitutes an ecologically homogeneous system.

From the figures presented, it is clear that completely dissimilar diets occur very rarely. This raises the question of the significance of diet overlap and whether such measures are indicative of resource competition. The limits of diet overlap calculations have been dealt with briefly above and the significance of any given numerical value for diet overlap has also been mentioned. Diet overlap has some value as an indicator of potential energy flow pathways but it is not an absolute measure of trophic linkages. The overlap values are obviously indicators of coexistence rather than competition, especially since overlap values have been observed to decrease rather than increase when resources are limited (Zaret and Rand 1971; Keast 1978; MacPherson 1981). The ideas of competition versus coexistence have been considered for gadoid fishes by Jones (1978). Jones pointed out some of the more subtle distinctions between the diets of three gadoid species which, on cursory examination, appear to overlap. For example, although both haddock and Atlantic cod from the same trawl haul preyed on juvenile *Sebastes*, they were preying on different-sized juveniles and, in general, Jones observed that Atlantic cod tended to consume larger prey than haddock of the same size. This type of detailed stomach contents analysis, together with observations on fish feeding behavior in the laboratory and in situ, is the type of biological information necessary for accurately defining what constitutes an ecologically homogeneous system, or, more importantly, an energetically coupled unit within the system.

There are some general patterns to the overlap values which may indicate real, or at least potential, trophic linkages. In comparing Atlantic cod with six other gadids, for example, the overlap levels generally are at their lowest between the larger cod (greater than size class 10, >50 cm) and the smaller size classes of the other predators (Fig. 3). This reflects the shift in the Atlantic cod's feeding habits from being primarily a crustacean predator to a piscivore with an increase in body size. In effect, Atlantic cod occupy different, size-specific, feeding niches which correspond to these other predators only when both species are small and more dependent on crustacean prey. For silver hake (Fig. 6) the pattern is similar but silver hake are a smaller fish than Atlantic cod and switch to a piscivorous habit at a smaller size. In addition to this pattern, there is also a noticeable shift in overlap between silver hake, the three other hake species, and pollock. The overlap with the smaller size classes of silver hake is low or even decreases slightly as the four other gadid species increase in size. Conversely, overlap is highest for the larger silver hake and these four gadids. This is a result of predation on many different species of crustaceans by all these predators and a shift towards fish predation as they grow.

In comparing both Atlantic cod and silver hake with the one rajiform and the four perciform fish species, the overall pattern of diet overlap is the same. The larger Atlantic cod and silver hake show a decreasing level of overlap with the smaller size classes of these other finfish predators (Figs. 2, 5). Atlantic cod and silver hake do not show a similar pattern of diet overlap when compared with the four pleuronectiform species of finfish (Figs. 4, 7). With the three pleuronectid species (Fig. 4A-C) the highest levels of overlap with Atlantic cod occur between the smaller size classes of all three species while the lowest levels occur between the larger size classes. This is similar to changes in overlap observed for the perciform species. For the one bothid (Fig. 4D) a size-dependent shift in overlap is not readily apparent. The overlap values for silver hake and flatfishes are at a maximum, albeit low overall, for the smaller individuals of the three pleuronectids (Fig. 7A-C) but, like the Atlantic cod, are fairly constant over all size classes of the one bothid species examined (Fig. 7D). This pattern of diet overlap with the pleuronectids may be attributed to the crustacean/fish shift in diet for the Atlantic cod and silver hake, and either little change in the flatfish diet or, as with American plaice, a change in diet to one that does not include much, if any, fish prey.

Atlantic cod and silver hake are crustacean/fish predators with a size-dependent shift in predation from crustaceans to fish as these predators grow. In the present data the shift to fish predation for Atlantic cod occurs at about 60-70 cm and for silver hake at about 20-25 cm. These sizes are not absolute and depend very much on the availability of prey. Daan (1973), for example, observed a difference in North Sea cod feeding habits when comparing samples from the northern and southern North Sea. Crustaceans predominated in the stomachs of the larger specimens from the southern region while their northern counterparts had already shifted over to a piscivorous habit. In the northwest Atlantic a similar, but less obvious, shift was observed in the diet of cod when compared over a 10-yr period (Grosslein et al. 1980). When the finfish biomass was low (1973-76 vs. 1963-66), crustaceans were slightly more important as prey although the general impression resulting from studying the two data sets was a fairly constant pattern of predation over time. The diets of Atlantic cod, and presumably most of these other predators, are fairly stable although there is an apparent degree of fine tuning that depends upon the availability of prey and other controlling factors in the environment.

In summary, assuming that the diets of Atlantic cod and silver hake are reasonably stable over time, and that the same is true for the 15 other predators examined, then the pattern of overlap described above suggests that the greatest overall potential for interaction exists between the smaller stages of the two gadids and the other predators. Furthermore, the greatest overlap, with few exceptions, occurs among the gadiform fishes themselves rather than between the gadids and the other ordinal taxonomic levels.

This observation may not only be reassuring to the taxonomist but is also of significance to fishery biologists in their attempts to identify ecological units. It suggests that future food habit studies should be directed towards the juvenile, or at least smaller, stages of closely related species if the goal is to understand how finfish coexist by partitioning food resources in the marine environment.

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