Food and feeding ecology of the swordfish *Xiphias gladius* in the western North Atlantic Ocean with estimates of daily ration *

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ABSTRACT: Analysis of stomach contents and predator-prey relations of 168 swordfish from the western North Atlantic Ocean is presented. The predominant food of swordfish is squid (82 % by frequency of occurrence) followed by fish (53 %) consisting primarily of gadids, scombrids, butterfish, bluefish, and sand lance. Average food volume in stomachs is 1 % of average body weight. Estimates of daily ration range from 0.94 % to 1.6 % of average body weight, with yearly consumption ranging from 3.4 to 5.8 times average body weight per year. The prey biomass consumed by the swordfish population in the Georges Bank area is estimated to range from 2,100 to 11,000 mt over a residency time of 5 mo.

INTRODUCTION

The swordfish *Xiphias gladius* is a large predatory marine fish distributed worldwide between Latitudes 45 °N to 45 °S (Sakagawa & Bell 1980). In the western Atlantic Ocean, swordfish range from the coast of Newfoundland to Argentina (Tibbo et al. 1961, de Sylva 1962, Wise & Davis 1973). The food of swordfish throughout their range has been described by numerous authors (Bigelow & Schroeder 1953, Tibbo et al. 1961, Scott & Tibbo 1968, 1974, Beckett 1974, Palko et al. 1981). Scott & Tibbo (1968) were the first to provide quantitative measurements of the food items found in swordfish stomachs. Despite the many observations by the above authors on the food of swordfish, no attempts have been made to estimate the daily ration or biomass of prey consumed by this species. The purpose of this research was to expand the understanding of the feeding ecology of the swordfish in the western North Atlantic with respect to diet, feeding behavior, and food consumption. This paper is a contribution to the MARMAP program of the National Marine Fisheries Service.

METHODS

Stomach samples were collected from swordfish captured by commercial and research vessels using long-

lines from 1975–81 and from a sport fishing tournament held in Ocean City, New Jersey during August 1979 and 1980. All stomachs were from fish caught along the slope and margin of the continental shelf between Cape Hatteras, N. C. (USA) and the Tail of the Grand Banks (Fig. 1). Stomachs were examined from fish collected during all months except January, with the majority (116) being taken from May through October.
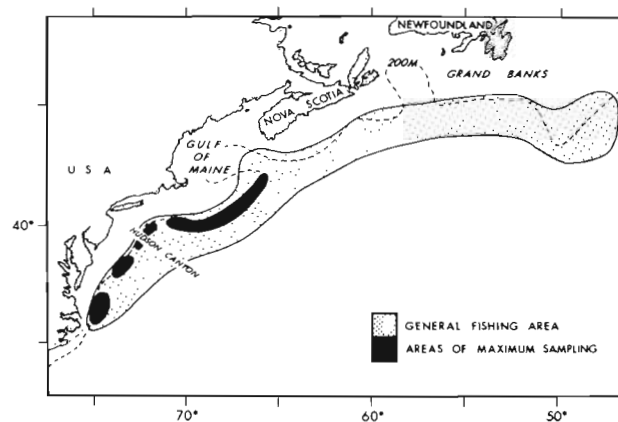
The contents of most stomachs were examined at sea

Fig. 1. Fishing area where 168 swordfish were sampled for food-habit studies. Stomachs were collected during longline fishing operations conducted from research and commercial vessels (1975–81) and at a swordfishing tournament held at Ocean City, N. J., USA (1979–80)

(research cruises) or when brought to the dock (sport catches). Stomachs collected by commercial fishermen were iced or frozen and examined upon arrival at the laboratory.

Examination of stomach contents included identification, enumeration, and volumetric measurement of each food item or type. A conversion of 1 ml = 1 g was used to convert volume to weight. Prey items were identified to species or to the lowest taxonomic level whenever possible. Fish and squid remains in advanced stages of digestion were classed as unidentified teleosts or Cephalopoda, respectively. Measure-

ments of the maximum stomach capacity were made for a wide range of swordfish sizes. The technique, described in Stillwell & Kohler (1982) provides a useful measure of the theoretical maximum capacity of a stomach and was used in this study to describe the degree of stomach fullness when the volume of the stomach contents is expressed as a proportion of stomach capacity.

The major forage categories were evaluated by number, volume and occurrence and compared by area, sex and size. Statistical analyses consisted of t-⁀sts of differences between means (P < 0.05).

Table 1. List of prey species or family groups occurring in 168 swordfish stomachs from the western North Atlantic Ocean (1975–81) by number, volume, and frequency of occurrence

	Num- ber	% No	Vol (ml)	% Vol	Fre- quency	% Frequency
Cephalopoda						
Ommastrephidae	626	27.95	24,422	20.70	52	28.57
Illex illecebrosus (short-finned squid)	665	29.69	30,036	25.46	48	26.37
Gonatidae	13	0.58	12	0.01	5	2.75
Octopoteuthidae	19	0.85	301	0.26	4	2.20
Histioteuthidae	3	0.13	7	0.01	3	1.65
Onychoteuthidae	30	1.34	163	0.14	2	1.10
Sepiolidae	9	0.40	2	0.00	2	1.10
Octopoda	3	0.13	2	0.00	2	1.10
Loligo pealei (long-finned squid)	3	0.13	60	0.05	1	0.55
Thysanoteuthidae	4	0.18	1	0.00	1	0.55
Chiroteuthidae	2	0.09	1	0.00	1	0.55
Architeuthidae	1	0.04	1	0.00	1	0.55
Unidentified Cephalopoda	467	20.85	24,423	20.70	56	30.77
Teleosts						
Merluccius bilinearis (silver hake)	72	3.21	11,126	9.43	11	6.04
Scomber scombrus (Atlantic mackerel)	25	1.12	6,385	5.41	9	4.94
Gadidae (codfishes)	16	0.71	3,090	2.62	6	3.30
Pomatomus saltatrix (bluefish)	10	0.45	4,735	4.01	5	2.75
Ammodytes americanus (sand lance)	18	0.80	195	0.16	5	2.75
Peprilus triacanthus (butterfish)	55	2.46	1,800	1.53	3	1.65
Cubiceps athenae (bigeye cigarfish)	6	0.27	750	0.64	3	1.65
Gempylidae (snake mackerels)	10	0.45	234	0.20	3	1.65
Stromateidae (butterfishes)	5	0.22	65	0.06	3	1.65
Myctophidae (lanternfishes)	4	0.18	18	0.02	3	1.65
Alepisauridae (lancetfishes)	2	0.09	615	0.52	2	1.10
Brevoortia tyrannus (Atlantic menhaden)	2	0.09	574	0.49	2	1.10
Paralepis atlantica (duckbill barracudina)	4	0.18	310	0.26	2	1.10
Scopelosauridae	4	0.18	51	0.04	2	1.10
Nemichthys scolopaceus (snipe eel)	4	0.18	20	0.02	2	1.10
Sebastes marinus (redfish)	8	0.36	2,775	2.35	1	0.55
Scorpaenidae (scorpionfishes)	1	0.04	400	0.34	1	0.55
Clupea harengus (Atlantic herring)	1	0.04	200	0.17	1	0.55
Hyperoglyphe perciformis (barrelfish)	1	0.04	95	0.08	1	0.55
Cottidae (sculpins)	1	0.04	15	0.01	1	0.55
Unidentified teleosts	123	5.49	4,914	4.16	41	22.53
Miscellaneous						
Animal remains	2	0.09	190	0.16	2	1.10
Salpidae	4	0.18	1	0.00	1	0.55
Nematoda	17	0.76	1	0.00	1	0.55
Total	2,240		117,990			

RESULTS

Food analysis

Stomachs from 168 swordfish of which 151 (90 %) contained food were examined. The total sample was comprised of 59 females, 44 males and 65 sex unknown.

The families and species of prey represented in all the stomach samples are presented in Table 1 and listed by decreasing frequency of occurrence in 2 food categories: Cephalopoda and teleosts. The table shows there is considerable diversity in the swordfish diet including near surface, demersal, and mesopelagic species.

The prey list from Table 1 is combined into 9 major forage categories (Fig. 2) in order to illustrate the importance of each in the swordfish diet.
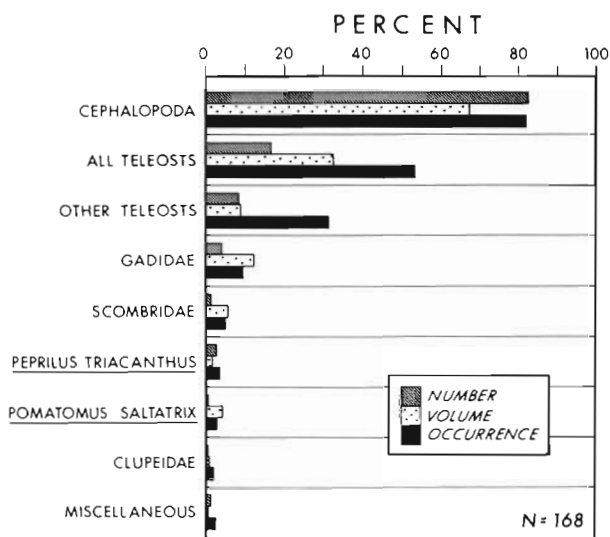

Fig. 2. *Xiphias gladius*. Nine major forage categories observed in 168 stomachs collected from fish caught over the slope and edge of the continental shelf in the area from Cape Hatteras, N. C. (USA) to the Tail of the Grand Banks (1975–81). Data expressed in terms of percentages by number, volume, and frequency of occurrence

Cephalopoda

Cephalopods comprised the most important food in the swordfish diet, having the highest percentages by number (82 %), volume (67 %), and frequency of occurrence (82 %) (Fig. 2). This food group was represented by 11 taxa (9 families, 2 species) of squids and 1 octopod (Table 1). When key characteristics necessary for identification to species were digested away, the upper and lower beaks (after Clarke 1962) and the mantle locking cartilage were the primary means of

identification to family. The family Ommastrephidae occurred most frequently with *Illex illecebrosus* the predominant identifiable species. Members of the families Gonatidae, Octopoteuthidae, Histioteuthidae, and Onychoteuthidae occurred with decreasing frequency and were most often identified from beaks and mantle locking cartilages. Sepiolidae, Octopoda, Architeuthidae, Chiroteuthidae and Thysanoteuthidae were identified exclusively from beaks. *Loligo pealei* was observed in only 1 stomach from a swordfish caught at the shelf break northeast of Cape Hatteras, N. C.

Unidentified cephalopod remains accounted for a large portion of the squid component in the overall diet (Table 1). A good part of these samples were collected in the early stages of the study when no attempt was made to identify squids beyond the class level. Because the ommastrephid squids contributed significantly to the swordfish's diet, it is probable that much of the unidentified cephalopod remains were from this family group.

Teleosts

Teleosts occurred in 53 % of the stomachs (Fig. 2) and were represented by 20 species or family groups (Table 1). Fish are of secondary importance in this study as seen in Fig. 2 and consist of 'Other teleosts' (a catch-all group composed of mesopelagic and miscellaneous species represented by a few individuals) followed by gadids, scombrids, butterfish, bluefish and clupeids (by percent frequency of occurrence). The first 4 fish taxa in Table 1 are the most important by volume and occurrence. The sand lance ranked fifth in occurrence but only contributed 195 ml of food. Because of this low volume and their small size, the sand lance is probably of less significance in the diet than their frequency of occurrence implies. Silver hake was the most important fish prey by number, volume, and frequency of occurrence. One stomach contained 43 specimens averaging 28 cm in length. Other stomachs with silver hake held remains of 1 or 2 fish. Atlantic mackerel ranked second in importance in the diet. The possibility of confusing natural mackerel prey and bait was minimized by examining remains for hook damage. We were able to identify mackerel baits in stomachs for up to 12 h after ingestion. Remains in advanced stages of digestion (head, tail and abdominal cavity disintegrated) were considered to be natural prey.

The Gadidae included hakes *Urophycis* sp. and fish remains identified as cod or haddock. Although this family group is ranked third in Table 1 by occurrence, it actually contributed less in volume than bluefish which were larger in size than the hakes that com-

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prised most of the gadid species. Bluefish are ranked fourth based on number and occurrence but were third volumetrically (Table 1). Their occurrence, however, was restricted to stomachs collected from swordfish caught off North Carolina in spring. Gadids on the other hand, and hakes in particular, were observed in stomachs from a much larger geographic area making them a more important prey.

The remaining 15 species or families decreased rapidly in number, volume, and occurrence except for the butterfish and redfish which were important volumetrically (Table 1). All of these taxa can probably be considered occasional prey, eaten incidently as individual items or in quantity depending on their abundance or availability in a given locality. The dense schooling behavior demonstrated by butterfish and the aggregating behavior of some of the vertically migrating prey, including *Nemichthyes scolopaceus*, *Paralepis atlantica*, Myctophidae, Gempylidae, Alepisauridae, and Scopelosauridae, enhance their attraction as prey.

Feeding ecology

Feeding variability by area, sex and size

Examination of the data for areal differences in diet showed that squid was the predominant food by number, volume and occurrence south of Hudson Canyon but was about equal in importance to fish north of this area. Shifts in importance of forage groups is influenced by their availability and abundance in an area, i.e. gadids, mackerel and butterfish are more abundant to the north, whereas bluefish do not appear to be available off the continental shelf in the north, but occur in the offings of Cape Hatteras, N.C. in the spring (Wilk 1977). Silver hake occurred only in stomachs from swordfish caught between southern New England and Emerald Bank south of Nova Scotia. Mackerel occurred in stomachs throughout the study area but were most prevalent in those from north of Hudson Canyon.

We saw no indication of food preference with respect to sex or size throughout the sampling area. A scatter diagram (26 points) of swordfish fork lengths *versus* mantle lengths of ommastrephid squids suggested small, medium and large (> 200 cm) fish usually fed on approximately the same size-range of squids (7 to 25 cm). A similar trend was noted where all sizes of swordfish fed on various sized schooling and vertically migrating species, including sand lance, butterfish, lanternfish, snake mackerel, and barracudinas.

Relation of body size to food volume and maximum stomach capacity

The average round weight of 122 weighed fish was 58 kg (range 5.0 to 204.0 kg). Females were heavier than males throughout the sampling area. Average weights for 56 females and 41 males were 57.3 and 53.0 kg with weight ranges of 6.0 to 204.0 and 5.0 to 131.0 kg, respectively. There was a trend of increasing body weight from south to north with average weights of 52.0 and 45.0 kg for females and males south of Hudson Canyon increasing to 61.0 and 55.4 kg in the area north of the canyon.

The average food volume for all fish examined was 604 ml (range 0 to 6,380 ml) equivalent to 1.0 % of the average body weight (BW). Percentages ranked as high as 8.3 % BW. Average food volumes from stomachs collected north and south of Hudson Canyon were 849 ml (1.4 % BW; avg. BW 60.3 kg; n = 93) and 301 ml (0.6 % BW; avg. BW 52.0 kg; n = 75), respectively. These average volumes were significantly different (t-test, p < 0.01). To discern differences in average food volumes by size, fish were separated into juveniles and adults based on the findings of Irby* (pers. comm.) who estimated weights at maturity to be 21 and 67 kg for males and females, respectively. Our analysis showed there was no significant difference in average food volume by weight class (immature, mature) between the sexes within each area. Food volumes increased with increasing body length, but decreased per unit body weight (ml kg^{-1}) as fish weight increased.

To determine degree of stomach fullness, a ratio (in terms of volume) of the food content to the maximum water capacity of the stomach was calculated. The average of 92 ratios was 23.5 % with a range of 0.05 to 72.4 %. The stomach with the highest ratio (72.4 %) was from a 304 kg fish that contained 9.0 l (approximately 9.0 kg) of flesh from the mantle of a large squid. The mean fluid capacity of 98 stomachs was 2.3 l and amounted to 4.0 % of the average body weight. The highest percentage determined was 11.2 %. This was from a 30 kg fish whose stomach held 3,350 ml of water.

Role of the sword in feeding

Indications from this study show that the swordfish's bill is an important adaptation for obtaining food. Examinations of stomach contents revealed that swordfish engulfed whole food items as well as slashed and maimed a variety of prey types before ingesting them. Approximately 25 to 30 % of the squid with mantle lengths of 7 to 25 cm found in the stomachs were decapitated or showed slash marks across the

mantle. In 1 stomach, mantle remains 1.5 to 3.0 cm thick from a large squid showed evidence of having been cleanly slashed into edible sized portions. A second stomach contained the posterior end of a squid mantle that had a fin width of 31 cm. One of the lancetfish was severed in two, 3 of the redfish had deep gashes behind the head and many of the mesopelagics were partly or completely cut in half. In general, small prey items often showed signs of having been struck with the sword in a random fashion, whereas larger items (redfish, lancetfish, large squid) appeared to have been singled out and incapacitated or reduced in size with a slash or more from the sword.

Estimates of daily ration and annual food consumption

An estimate of daily ration for swordfish was calculated using the average stomach content volume and a stomach evacuation rate derived by Equation 1 from Elliot & Persson (1978):

$$S_t = S_o e^{-Rt} \qquad (1)$$

where S_o and S_t = amounts of food in the stomach at beginning and end of t h; R = exponential rate of gastric evacuation. In the model, R is unaffected by fish size, food size, meal size, and feeding frequency. Temperature and rate of food consumption are assumed to be constant with gastric evacuation occurring without an appreciable time lag after food is ingested.

There is virtually no information on stomach evacuation rates for swordfish, but because they cohabit the same trophic levels with the blue and shortfin mako shark and display similarities in prey (Kohler & Stillwell 1981, Stillwell & Kohler 1982) and daily activities (Carey & Robison 1981), we assumed it was reasonable to apply R values derived from Equation 1 for the blue (0.0376 h⁻¹) (Kohler & Stillwell 1981) and shortfin mako shark (0.0479 and 0.0639 h⁻¹) (Stillwell & Kohler 1982) to calculate minimum and maximum daily ration estimates for the swordfish. The 2 R values for the mako shark were derived using digestion time intervals of 48 and 36 h, respectively. Assuming the R values are applicable, daily ration (C) for the swordfish was calculated by the equation:

$$C = 24 \, \overline{S}R \qquad (2)$$

where $\overline{S}$ = mean weight (.604 kg) of stomach contents. Equation (2) is the reduced version of the Elliot & Persson (1978) model given that the above assumptions are true. The minimum daily ration estimate using the blue shark R value was 0.545 kg (0.94 % BW). At this feeding rate the average swordfish would consume 199 kg or 3.4 times its weight per year. Daily rations based on the shortfin mako data resulted in estimates of 0.694 and 0.926 kg (1.2 and 1.6 % BW) with annual consumption weights of 253 and 338 kg which amount to 4.4 and 5.8 times the average body weight. The daily ration estimates thus derived appear reasonable and compare favorably with values determined for other predatory species (Table 2).

Table 2. Comparison of daily ration and annual food consumption values for swordfish and other predatory fish species

Species	Average length (cm)	Average weight (kg)	kg d⁻¹	kg yr⁻¹	% BW[a] d⁻¹	× BW yr⁻¹	Source
Teleosts							
Swordfish	153	58.0	0.545–0.926	199.0–338.0	0.94–1.6	3.4–5.8	This study
Skipjack tuna	44	1.6	0.136	50.0	8.6	31.0	Magnuson (1969)
Giant bluefin tuna		364.0[b]	26.0–42.0[c]		8.0–10.0		Butler & Mason (1977)
Giant bluefin tuna		250.0[d]			3.0		Tiews (1978)
Sharks							
Mako	175	63.0	2.0	730.0	3.2	11.6	Stillwell & Kohler (1982)
Lemon	70				3.0		Gruber (1982)
Lemon	Immature				1.4		Clark (1963)
Lemon	274				0.5		Clark (1963)
Scalloped hammerhead		49.9	0.680	248.2	1.4	5.0	Clark (1963)
Sand tiger	137		0.680	248.2			Clark (1963)
Nurse		152.4	0.450	164.3	0.3	1.1	Clark (1963)
Blue	172	38.5	0.144	52.6	0.4	1.4	Kohler & Stillwell (in prep.)
Sandbar		32.8	0.143	52.2	0.3–0.5	1.6	New England Aquarium[e]
Sandbar	56	1.8	0.018	6.6	1.0	3.6	Medved, Stillwell & Casey (in press)

[a] BW = Body weight
[b] Average estimated round weight
[c] Depending on feeding frequency
[d] Average weight at end of ~ 100 feeding days
[e] G. Early, Biologist, New England Aquarium, Central Wharf, Boston, MA 02110, USA 1979

Estimates of minimum and maximum prey biomass consumed by swordfish were determined for the region of Georges Bank where the biomass of swordfish is estimated to vary from a minimum of 1091.2 mt (metric tons) to possibly 3 times that amount (Casey et al. in press). Using the average stomach content weight of .849 kg from swordfish north of Hudson Canyon which is representative of those fish from Georges Bank and R values from the blue (0.0376 h^{-1}) and mako (0.0639 h^{-1}) sharks, we calculated daily rations ranging from 0.766 to 1.302 kg. These are equal to 1.27 and 2.15 % of the average body weight for the area. In terms of prey biomass consumed, these percentages are equivalent to 13.8 and 23.5 mt d^{-1}. Assuming an average swordfish residency time of 153 d (Casey et al. in press), the amount of prey consumed may vary from 2,100 to 3,600 mt. If the swordfish biomass is indeed 3 times greater than the minimum value suggested, the food consumed could be as high as 6,000 to 11,000 mt.

DISCUSSION

Results from this study indicate that cephalopods (squids) are the primary dietary component of the swordfish in the western North Atlantic Ocean. Yabe et al. (1959), Ovchinnikov (1970), and Toll & Hess (1981) also showed this to be the case after examining swordfish from the Pacific, tropical Atlantic and south Florida coast, respectively. Earlier reports (Goode 1883, Rich 1947, Bigelow & Schroeder 1953, Tibbo et al. 1961, Beckett 1974) for the western North Atlantic emphasized the importance of fish in the swordfish diet with squid being relatively unimportant. These reports were based on qualitative observations only, but results of volumetric measurements by Scott & Tibbo (1968) of the food from 135 swordfish stomachs examined in 1964–65 from fish collected on the eastern part of Georges Bank also reflected low (16 % by volume) utilization of squid as food. Our data show that a different situation exists at the present time, which is a result of a steadily increasing abundance of squid along the continental margin from Cape Hatteras to the Gulf of Maine (Lange & Sissenwine 1980, Lange 1982). Lange (1982) has shown that from 1968 to 1981 the estimated biomass of *Illex* sp. in this area increased from 1,845 to 68,611 mt. The biomass of *Loligo pealei* fluctuated yearly during this period from as low as 18,800 to over 51,000 mt, but since this species only occurs out to 200 m depth on the upper continental shelf (Lange & Sissenwine 1980) it is not available to swordfish captured by pelagic longlines further offshore.

The importance of silver hake in the swordfish diet was noted by us (Table 1) and was also reported as a major forage item by Bigelow & Schroeder (1953), Tibbo et al. (1961), and Scott & Tibbo (1968, 1974). The last authors were the first to provide a numerical ranking of importance and showed that predation on this species occurred on Georges Bank and to the east. Woodhead (1964) reported that the silver hake is primarily a benthic species that rises off the bottom at night where according to Scott & Tibbo (1968) it becomes available as prey for swordfish.

The occurrence of hake (*Urophycis* sp.) and cod-like remains (see Gadidae, Table 1) in 6 stomachs was not unexpected in view of the diversity of species observed. Scott & Tibbo (1968) however considered hake a rare food item since they saw only 3 specimens in 1 stomach of over 500 examined. In contrast, they reported the barracudina *Paralepis atlantica* to be the second most important prey by volume and occurrence in their examination of over 650 stomachs. We identified only 4 specimens in 2 stomachs, but cannot discount the possibility that a portion of the unidentified fish remains occurring in some of the stomachs was comprised of this species, making it more important than our data indicate.

The occurrence of 8 redfish in 1 stomach (Table 1) was similar to situations described by Tibbo et al. (1961) and Scott & Tibbo (1968) where multiple numbers of a particular prey species (e.g. redfish, herring) were eaten by a single swordfish. This condition was also observed on a few occasions by commercial longliner Captains Phillip and James Ruhle (pers. comm.) while cleaning swordfish caught on the banks south of Nova Scotia and Newfoundland.

The differences observed in body weight and food volume north and south of the Hudson Canyon region cannot be discounted as artifacts in the data nor the results of too few samples. The increase in size (length and weight) of swordfish along the east coast of the US and southern Canada from south to north has been observed and reported by Beckett & Tibbo (1968) and Beckett & Freeman (1974). Most recently, Hoey & Casey[*] (pers. comm.) confirmed earlier observations that average size increases with increasing latitude after analysing dressed weight data from several thousand swordfish. The region separating our 2 areas approximates those used by Beckett & Freeman (1974) and Hoey & Casey (pers. comm.) to divide their data into bio-geographic zones. We are cognizant of the fact that our area south of Hudson Canyon is proportionately smaller than the nothern area but suggest the fish

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Fig. 3. Mean depth zones occupied diurnally by *Xiphias gladius* occurring over deep-water and showing the overlap of the daily vertical migrations (DVM) of swordfish, mesopelagic fish, and pelagic squids. Number values following squid family names indicate approximate maximum depths attained by species within each family (adapted from Marshall 1971)
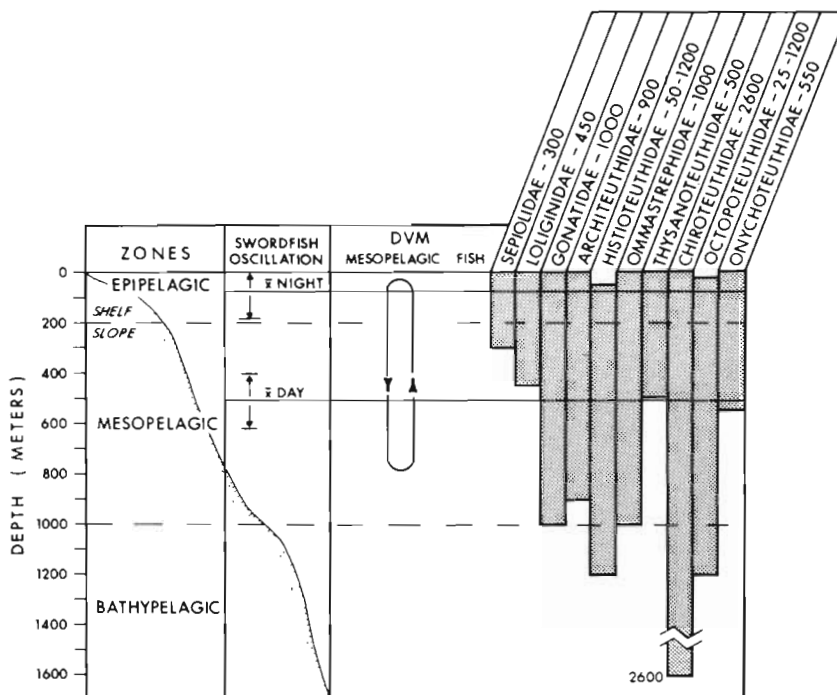
here are probably representative of those occurring at least as far south as 33° 00′ N latitude, which is the one used by Hoey & Casey to define the southern boundary of their 'Hatteras' zone.

The increasing food volumes in swordfish stomachs from south to north can be accounted for on the basis of increasing size of the swordfish as shown by our data. This same relation was reported for swordfish examined by Scott & Tibbo (1968). In addition to increasing fish size, there is an increase in available prey biomass from the Middle-Atlantic Bight to Georges Bank (Clark & Brown 1977, Cohen & Grosslein (in press); Clark* pers. comm.). Available evidence shows that the levels of primary productivity between Cape Hatteras and the Gulf of Maine places this portion of the continental shelf among the most productive in the world, especially that area from the New York Bight to Georges Bank (O'Reilly & Busch 1984). The increased primary productivity and prey abundance from north of Hudson Canyon to Georges Bank would thus account for the larger stomach content volumes found in this region.

The use of the sword as a physical adaptation for incapacitating or killing prey has been recognized and accepted for many years (Goode 1883, Bigelow & Schroeder 1953, Scott & Tibbo 1968). There appears to be no consistent pattern, however, as to when prey is slashed (Tibbo et al. 1961, Scott & Tibbo 1968, present

study), nor does the kind of species seem to influence an onslaught since cut and whole individuals of the same species are often found in a stomach and show similar amounts of digestion. Scott & Tibbo (1968) point out that the sword is highly specialized for lateral slashing, and to be most effective must be used on prey that are oriented vertically in the water or the swordfish must be vertically oriented itself when ascending or descending. In recent years, evidence of vertical orientation by barracudinas (Houot 1958, Rofen 1966) and some pelagic squids (Toll & Hess 1981), including the Ommastrephidae, Thysanoteuthidae, Onychoteuthidae, and Histioteuthidae may explain why these taxa on occasion contribute significantly to the swordfish's diet.

Prey size (length) is probably not a limiting factor in food selection by the swordfish except to the extent where a prey item is too small to attract attention or so large that it cannot be cut into smaller pieces with the sword. Maksimov (1968) reported the occurrence of a 114 cm shark that was eaten whole by a 374 cm swordfish. He also reported that large Trachypteridae (king-of-the-herrings) up to 2.5 m in length are frequently found in swordfish stomachs. We have to assume that some of these were in pieces since it would seem an impossible feat for even a large swordfish to swallow prey of this size in one piece. Evidence from our data clearly shows that the swordfish is able to slash the thick mantle flesh of large squid into edible sized pieces.

It is generally accepted that large predatory fishes

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eat what is available in the greatest abundance in their immediate environment (Scott & Tibbo 1968, Palko et al. 1981). The diversity of prey species occurring in swordfish stomachs (Bigelow & Schroeder 1953, Tibbo et al. 1961, Scott & Tibbo 1968, Beckett 1974, this study) implies an opportunistic feeding pattern which allows swordfish to forage from various trophic levels during diurnal vertical migrations (DVM). First proof of the swordfish's ability to descend deep into the mesopelagic zone was provided by Zarudski (1967) and Church (1968) when visual observations of this species were made at 610 and 654 m, respectively. More recently, experiments by Carey & Robison (1981) demonstrated DVMs of swordfish ranging to 617 m. Information from one of these experiments conducted off North Carolina was used to illustrate the extent of the DVM by swordfish and how it overlaps the DVM of the mesopelagic fish and 10 families of squid found in our stomach samples (Fig. 3). The experiment showed that the average day-night depths approximated 510 and 90 m respectively with oscillations around these means varying from < 5 to about 100 m. These depths are well within the DVMs for most mesopelagic fishes (Marshall 1971) and pelagic squids occurring off the margins of the continental shelf (Voss 1967, Roper & Young 1975, Toll & Hess 1981). Although food may be a prime factor initiating these daily movements, sonic tracking experiments in the Atlantic and Pacific Oceans (Carey & Robison 1981) suggest that other variables, including oxygen, buoyancy, water depth, temperature, light intensity, and location, also affect the vertical movements of swordfish.

Consumption estimates from this study suggest swordfish require a minimum-maximum food biomass of 2,100 to 11,000 mt during their residency time on Georges Bank. Comparative estimates of consumption for all large pelagic fish (tunas, billfish) and sharks occurring on Georges Bank have been derived for the same time interval by Casey et al. (in press). These authors calculated a predator biomass ranging from 6,000 to possibly 60,000 mt, with corresponding estimates of consumption ranging from 9,000 mt to as high as 90,000 mt. A further comparison is made with the impact of marine mammals (cetaceans) on the available prey biomass of Georges Bank. Using data from a study by Scott et al. (1983) we were able to isolate information to show that during the summer and fall (corresponding closely to our swordfish residency time), the cetacean population consumes an estimated 240,000 mt of prey biomass. This figure may be an underestimate of at least 2 to 3 times (Scott et al. 1983). Total prey consumption (primarily finfish and squid) by the large predator species occurring in the Georges Bank region could thus approach 330,000 mt over an approximately 6 mo period. This amounts to about

15 % of the annual biomass of finfish and squid produced in the area based on a production estimate of 52 kcal m^{-2} yr^{-1} from data collected in the early 1970's (Cohen & Grosslein in press).

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