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Food of Western North Atlantic Tunas (*Thunnus*) and Lancetfishes (*Alepisaurus*)

Frances D. Matthews, David M. Damkaer,
Leslie W. Knapp, and Bruce B. Collette

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Food of Western North Atlantic Tunas (*Thunnus*) and Lancetfishes (*Alepisaurus*)

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LESLIE W. KNAPP,[3] and BRUCE B. COLLETTE[1]

ABSTRACT

Stomach contents of 395 longline-caught specimens of *Thunnus* (281 *T. albacares*, 52 *T. t. thynnus*, 48 *T. alalunga*, 14 *T. obesus*) and 89 *Alepisaurus* were examined. About 45% of the tuna's food, by volume, was composed of fishes, 35% of cephalopods, 15% of crustaceans, and 5% of miscellaneous items. Fishes eaten by tunas ranged in length 9-360 mm SL ($\bar{x}$ 65 mm) and represented a minimum of 88 genera in 58 families. Fishes eaten by *Alepisaurus* were 8-846 mm SL ($\bar{x}$ 98 mm) and represented 40 genera in 34 families. Most forage fishes were immature forms of midwater and shore fishes, many of which are associates of the pelagic *Sargassum* community. Ten of the most frequently occurring families in *Thunnus* and *Alepisaurus* stomachs were Bramidae, Alepisauridae, Balistidae, Paralepididae, Scombridae, Sternoptychidae, Carangidae, Tetraodontidae, Gempylidae, and Syngnathidae.

Cephalopods were the most frequently occurring (80-90%) invertebrate group in the tuna stomachs, particularly the squid family Ommastrephidae. Crustaceans followed the cephalopods in frequency of occurrence (30-80% depending on tuna species). Larval decapods and hyperiid amphipods were the principal groups of crustaceans. In *Alepisaurus* stomachs, cephalopods occurred with 50% frequency, usually octopods and soft-bodied squids, families Cranchiidae, Histioteuthidae, and Bathyteuthidae. Crustaceans were present in 75% of *Alepisaurus* stomachs. Fewer decapod larvae were found than in the tunas, while amphipods were found more frequently. Pelagic polychaetes (Family Alciopidae), not found in any tunas, occurred in 38% of *Alepisaurus* specimens.

Differences in the relative importance of particular forage categories in the diet of different species of *Thunnus* and between the diets of *Thunnus* and *Alepisaurus* suggest interspecific differences in feeding, either anatomical (i.e., relative predatory ability) or behavioral, particularly the relative swimming speeds and feeding depths of different predators. The small-mouthed tunas consumed generally smaller prey fishes ($\bar{x}$ 98 mm SL) than did the large-mouthed lancetfishes ($\bar{x}$ 240 mm SL). Smaller sized yellowfin tunas generally consumed smaller prey than did larger yellowfins. Differences in swimming ability between tunas and *Alepisaurus* were reflected in the larger number of swift-moving muscular squids eaten by the tunas. Composition of the forage indicated that *T. albacares* fed at shallower depths than the other species of *Thunnus* and that *Alepisaurus* fed at greater depths than any of the tunas.

INTRODUCTION

In the past 20 yr, the tunas have become objects of intensified commercial and recreational fisheries. Heavy utilization of these fishes and subsequent concern about the limitation of stocks have made an understanding of their biology increasingly important. Because the tunas are peak predators in a vast part of the epipelagic zone, one important aspect of investigation is their feeding habits. Numerous forage studies have been carried out in all parts of the world for the tunas of the genus *Thunnus* and the skipjack genus *Katsuwonus*. Most information has been reported on a qualitative basis, however, and many studies have been based upon small samples. For the Atlantic Ocean, Dragovich (1969) reviewed the important literature on tuna feeding habits published until that time. Since then, several important contributions have been added for the Atlantic: Dragovich reported on the food of skipjack and yellowfin tuna in the Atlantic (1970a) and the bluefin tuna in the eastern tropical Atlantic (1970b); Dragovich and Potthoff (1972) compared the food of the yellowfin and skipjack off the coast of West Africa, and Borodulina (1974) reported on the feeding of bigeye tuna in the Gulf of Guinea.

Literature on Pacific tunas has not been similarly summarized. Important contributions include investigations on the feeding of yellowfin in the central Pacific (Reintjes and King 1953) and the comparison of the food of central Pacific bigeye and yellowfin (King and Ikehara 1956). Alverson (1963) compared the forage of yellowfin and skipjack in the eastern tropical Pacific. Iversen (1962) studied the food habits of albacore in the central and northeastern Pacific. Iversen (1971) reported on albacore and Pinkas (1971) reported on bluefin feeding habits in Californian waters.

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In the present study, we examined the stomach contents of four species of *Thunnus* in the western North Atlantic: *T. albacares* (Bonnaterre), the yellowfin; *T. alalunga* (Bonnaterre), the albacore; *T. t. thynnus* (Linnaeus), the Atlantic bluefin; and *T. obesus* (Lowe), the bigeye. The specimens examined were obtained during a series of exploratory longline cruises over the period 1957-64 by the Bureau of Commercial Fisheries (now National Marine Fisheries Service) MV *Delaware*, before a major fishery was established in the region. While fishing for tunas, lancetfishes of the genus *Alepisaurus* were often hooked by the longline. In this capacity at least, the lancetfishes were competing with tunas; being thus an apparent competitor, it seemed worthwhile to examine also the stomach contents of *Alepisaurus* taken with *Thunnus*. *Alepisaurus* forage has previously been investigated in the Atlantic by Haedrich (1964). Parin et al. (1967) reported on the feeding habits of *Alepisaurus* in the Indian Ocean. In the Pacific, lancetfish feeding habits have been reported on by Haedrich and Nielsen (1966), Kubota and Uyeno (1969), Rancurel (1970), and Kubota (1973).

Included in the present study are both species of lancetfishes, *Alepisaurus ferox* Lowe and *A. brevirostris* Gibbs. No distinction is made between species, however, because much of the data were collected before the latter was described by Gibbs (1960).

MATERIALS AND METHODS

We examined the contents of 395 *Thunnus* stomachs (281 *T. albacares*, 52 *T. t. thynnus*, 48 *T. alalunga*, and 14 *T. obesus*) and those of 89 *Alepisaurus*. Number, size range, and mean size of the *Thunnus* and *Alepisaurus* specimens are presented in Table 1. All specimens were collected by longline from the western North Atlantic off the eastern coast of the United States north of Bermuda and, on one cruise, east to the Azores (Figure 1). Specimens were taken from depths of 10-60 m. Longlin gear and methods used were described by Squire (1962 and Wilson and Bartlett (1967).

Most of the *Thunnus* stomach contents were collecte by Robert H. Gibbs, Jr. and Bruce B. Collette in con junction with a study of the anatomy and systematics c the genus *Thunnus* (Gibbs and Collette 1967). Method to obtain stomach contents were used that would no damage the tuna specimens. The stomach contents c *Thunnus* were obtained through a longitudinal ventra incision through which the stomach was pulled, the con tents were removed, and the emptied stomach pushe back into place. As a result, the total contents were no always obtained. The stomach contents that wer collected for each specimen were preserved in 10% For malin. Size (mm fork length (FL)) and weight of th tuna were usually recorded.

Alepisaurus stomach contents were obtained by shak ing the specimen head-down over a bucket, after th removal from the longline hook. The lancetfish's wid mouth, esophagus, and stomach allowed its stomac contents to fall out readily into the collection bucket Contents were then preserved in 10% Formalin.

Some stomach contents were identified at sea, record ed, and discarded; others were identified at the Wood Hole Oceanographic Institution and Boston University

Table 1.—Numbers, size ranges, and mean sizes of *Thunnus* spp. an *Alepisaurus* examined.

	N	Size range (cm FL)	$\bar{x}$
Thunnus albacares	281	74-166	114
Thunnus alalunga	48	96-106	101
Thunnus thynnus	52	158-232	188
Thunnus obesus	14	142-165	149
Alepisaurus sp.	89	48-138	—

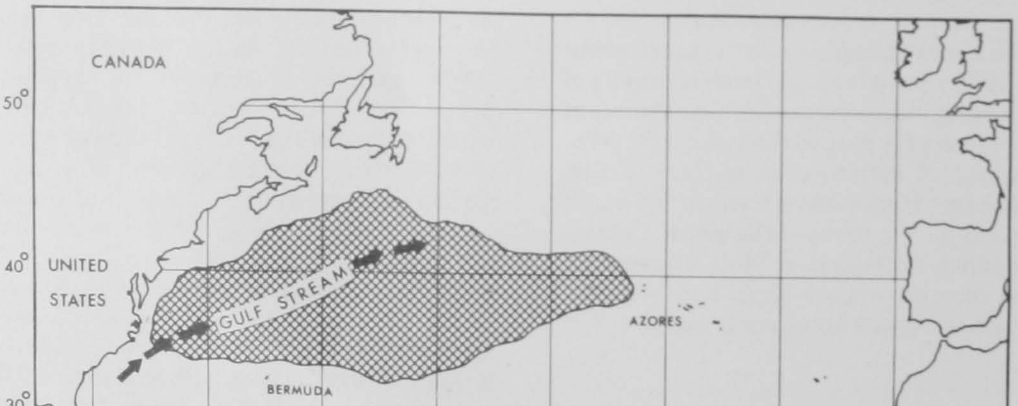

Figure 1.—Area sampled (crosshatched) for *Thunnus* and *Alepisaurus* by longline in the western North Atlantic.

Heteropods and pteropods from this collection were removed and reported on by Russell (1960). The bulk of the material was then transferred to the National Marine Fisheries Service Systematics Laboratory at the U.S. National Museum of Natural History. To facilitate identification, the stomach contents were divided into broad categories: fishes, cephalopods, other mollusks, crustaceans, jellyfish, and miscellaneous. D. M. Damkaer identified the crustaceans and, under the guidance of Clyde Roper (a specialist in cephalopod taxonomy), the cephalopods and the remainder of the invertebrates. Leslie Knapp (Smithsonian Oceanographic Sorting Center (SOSC)) supervised the identification of the fishes with the assistance of several specialists on the SOSC list. Representative specimens of forage species in good or fair condition have been deposited in the relevant collections of the National Museum of Natural History (worms, mollusks, crustaceans, and fishes).

The identification of forage specimens depended on the degree to which digestion had damaged the organism and on its stage of maturity, particularly in the crustaceans and cephalopods. Fishes were more completely identified than were other groups, usually to family and often to species. A large portion of the invertebrate forage could be identified only to order or superfamily. Therefore, the number of taxa from any one category of forage organisms, while giving a picture of the diversity of forage, should not be considered quantitatively.

The relative importance of a forage category can conveniently be thought of in terms of the amount of energy it affords its predator, measured by number and size of a particular organism eaten. The frequency with which an organism is eaten, furthermore, often gives a rough estimate of its general availability to a predator. To evaluate the composition of forage, therefore, we used these three measurements: 1) Frequency was calculated as percent frequency of occurrence, e.g., in what percentage of the total number of stomachs examined a particular organism was found. 2) The number of individuals per stomach from a particular forage group was compared numerically. 3) The size of a forage organism was expressed as length: crustaceans as mm total length, cephalopods as mm mantle length, and fishes as mm standard length (SL, tip of snout to the base of the caudal fin). Accuracy of measurement was dependent upon the degree to which the forage specimen had been digested; approximations were often made in cases where skeletons were incomplete, but suggestive of the organism's full size.

We considered a forage organism to be of greatest importance when it was eaten with relatively high frequency, was comparatively larger than other forage organisms eaten, and was consumed by an individual predator in larger numbers than the mean number of other forage groups present in that stomach. The less important a forage organism appeared in these three aspects, relative to the other organisms eaten, the less important it was considered to the predator's diet. No statistical tests were applied.

RESULTS

Taxonomic lists of forage components of *Thunnus* and *Alepisaurus* are presented in Appendix Table 1. Forage organisms which are additions to taxa listed for the Atlantic Ocean by Dragovich (1969) for *Thunnus* or by Haedrich (1964) for *Alepisaurus* are noted. Fishes, crustaceans, and mollusks made up the bulk of the collection. Medusae, salps, *Sargassum*, and parasitic nematodes and trematodes, which are not included in the forage lists, were also present. The forage composition for all *Thunnus* species consisted of, by volume, about 45% fishes, 35% cephalopods, 15% crustaceans, and 5% miscellaneous items.

Vertebrate Forage (Fishes)

Fishes occurred with a frequency of 66-100%, depending on the species of predator. Those consumed by tunas ranged in length 9-360 mm SL ($\bar{x}$ 65 mm) and represented 88 genera in 58 families. Fishes eaten by *Alepisaurus* varied over a greater size range (8-846 mm SL, $\bar{x}$ 98 mm) and represented 40 genera in 34 families. The majority of forage fishes in *Thunnus* and *Alepisaurus* were immature forms of midwater fishes and epipelagic post-larvae and juveniles of shore fishes.

Fish were present in 95% (266 stomachs) of the *T. albacares* stomachs examined. Evaluation of fish forage composition is based on 209 stomachs, however, in which fishes were identifiable. Of the 48 *T. alalunga* examined, 79% (38 stomachs) contained fish. Evaluation is based on 14 stomachs containing identifiable specimens. Seventy-three percent (38 stomachs) of the *T. thynnus* consumed fish. Forage composition analysis is based on 24 stomachs containing identifiable specimens. Forage fish were present in all 14 of *T. obesus* examined, but could be identified further in only eight.

The contents of *Alepisaurus* stomachs were generally in better condition than those from the tunas. Ninety-one percent (81 stomachs) of the *Alepisaurus* specimens examined had consumed fish, most of which were identifiable at least to family. The percent identifiable from *Alepisaurus* stomachs may be larger than from tunas because identification was easier, perhaps because digestion in *Alepisaurus* takes place mainly in the intestine, the stomach being used only for storage (Rofen 1966).

Thunnus albacares.—Forty families of fishes were found in the stomachs of yellowfin (Appendix Table 2). Those which occurred with at least 1% frequency are included in Figure 2.

Ten families occurred with 10% frequency or more: Balistidae, 41%; Carangidae, 31%; Bramidae, 24%; Chiasmodontidae, 21%; Syngnathidae, 18%; Priacanthidae, 13%; Tetraodontidae, 13%; Holocentridae, 12%; Acanthuridae, 11%; and Scombridae, 10%. Except for the Scombridae, none was outstanding in either size or number. In most families, one genus or one species was chiefly responsible for its high frequency: *Monacanthus* spp., *Caranx* sp., *Pterycombus* sp.,

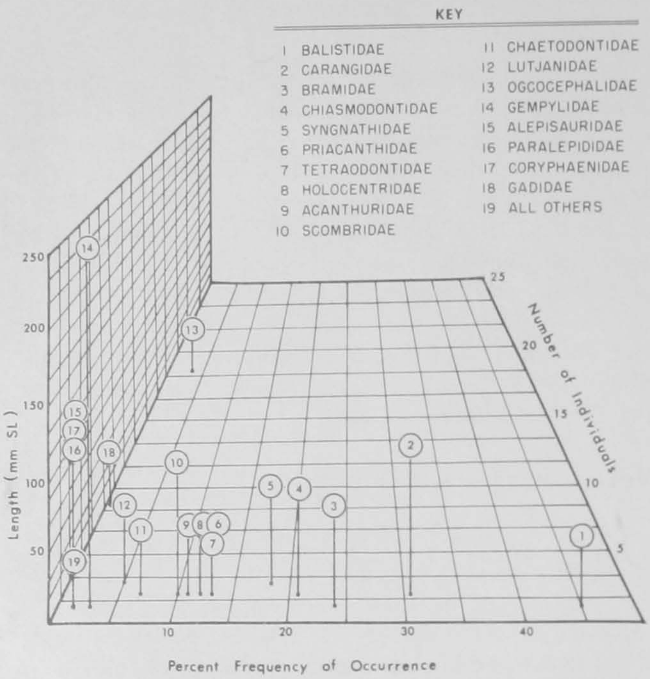

Figure 2.—Relative importance of families of fishes present in more than 1% of the stomachs of western North Atlantic *Thunnus albacares*. Percent frequency of occurrence is on the horizontal axis, mean length (mm SL) of forage family on the vertical axis, and mean number of individuals in a forage family on the third axis. The most important families are those that occur more frequently (to the right on the horizontal axis), average larger in size (lines coming up from the horizontal axis), and are the most numerous (displaced back into page on third axis).

Pseudoscopelus sp., *Hippocampus erectus*, *Cookeolus boops*, *Sphoeroides* sp., and *Auxis* sp. were of primary importance (Appendix Table 2). The occurrence of 32 *Cookeolus boops* (13-66 mm SL) in 26 stomachs of *T. albacares* is of interest because only 13 specimens of this species have previously been recorded from the western Atlantic (Anderson et al. 1972). One of these was identified by Caldwell (1962) from the stomach of one of the *T. albacares* collected during this study.

Fishes eaten by yellowfin varied in length 11-360 mm SL, $\bar{x}$ 45 mm SL. Gempylids ($\bar{x}$ 216 mm), *Coryphaena* ($\bar{x}$ 141 mm), *Alepisaurus* ($\bar{x}$ 120 mm), paralepidids ($\bar{x}$ 105 mm), and scombrids ($\bar{x}$ 96 mm) were the largest forage fishes. Except for the Scombridae, they were present in only a few stomachs and in small numbers. Ogcocephalidae, although eaten infrequently and among the smallest ($\bar{x}$ 17 mm SL) forage fishes, was the only family to occur in large numbers (43 in one stomach, average 19). No fishes which were eaten in large numbers, or which were outstanding in size, occurred with greater than 6% frequency, except for the Scombridae.

***Thunnus alalunga*.**—Fishes consumed by *T. alalunga* belonged to 21 families (Appendix Table 3). They averaged slightly smaller ($\bar{x}$ 40 mm SL) than fishes eaten by *T. albacares*. Gempylidae and Paralepididae were the most important forage families in terms of size and frequency of occurrence. Gempylids consisted mostly of *Diplospinus multistriatus* which was present in 36% of the stomachs and was the largest sized group ($\bar{x}$ 151 mm SL). Paralepididae occurred in 29% of the stomachs and averaged 101 mm SL. Bramidae were present in 64% of the stomachs examined, but were less important in terms of size. *Omosudis lowei* was also frequently eaten, although the family Omosudidae as a whole did not occur frequently. The only group to occur in large numbers was Ogcocephalidae, 40 of which were present in a single stomach.

***Thunnus thynnus*.**—The food of *T. thynnus* included 17 families of fishes (Appendix Table 4). Bramidae (38%) were the most frequently occurring, with *Collybus drachme* and *Taractes* spp. (both present with 8% frequency) being chiefly responsible for the high frequency of the whole family. Balistidae (17%) were also consumed frequently. *Alepisaurus* sp., *Auxis* sp., and *Hippocampus erectus* occurred relatively frequently, though the frequencies of their families were not particularly high.

The size range of forage fishes was 29-230 mm SL. No single family appeared to be unusually large in size, although *T. thynnus* forage fishes were larger on the average ($\bar{x}$ 107 mm SL) than those eaten by either *T. albacares* ($\bar{x}$ 45 mm SL) or *T. alalunga* ($\bar{x}$ 37 mm SL), while they were smaller than those of *T. obesus* ($\bar{x}$ 213 mm SL).

***Thunnus obesus*.**—Nine families and six genera of fishes were identified from 14 *T. obesus* stomachs: Alepisauridae, Balistidae, Belonidae, Bramidae, Caproidae, Melamphaidae, Nemichthyidae, Paralepididae, and Trachipteridae. Only two families occurred in more than one stomach: Paralepididae, in three (37% frequency), and Alepisauridae, in two (25% frequency). The fishes eaten by *T. obesus* were on the whole larger than those consumed by the other species of *Thunnus*. The smallest was 83 mm SL; others ranged up to 340 mm ($\bar{x}$ 213 mm SL).

***Alepisaurus*.**—Thirty-eight genera of fishes from 36 families were found in the stomach contents of *Alepisaurus* (Appendix Table 5). The five most common families included most of the largest fishes eaten. Paralepididae ($\bar{x}$ 124 mm SL) was the most frequently occurring family, present in 53% of the stomachs examined. Several *Paralepis coregonoides* measured 600-846 mm SL. Gempylidae ranked high in both size ($\bar{x}$ 105 mm SL) and occurrence (27%). Alepisauridae were the largest prey group eaten ($\bar{x}$ 213 mm SL) and were present in 12% of the stomachs. Sternoptychids were present in 27% of the stomachs. They were not outstanding in size but were often consumed in large numbers—as many as 54 in one stomach. Bramidae were present in 11% of the stomachs, although they were not important in either size or number.

Invertebrate Forage

Most taxa of invertebrate forage belonged to two groups, Mollusca and Crustacea (Appendix Table 1). Salps and scyphozoan medusae were also present, but were not identifiable.

Thunnus.—Cephalopods were the most frequently occurring invertebrates (80-90%) in the stomachs of all species of *Thunnus* (Appendix Tables 6-8). Crustaceans were present in 30-80% of the stomachs, depending on the species of tuna. In stomachs where the two groups co-occurred, the percent-volume ratios of cephalopods: crustaceans were about 75:25 (range 67-79:21-33). Cephalopods were, furthermore, more often the exclusive content of a stomach than were crustaceans (Appendix Table 10). Heteropods and pteropods were also abundant, more so than indicated in our tables because they were removed from many samples by Russell (1960).

Cephalopods were the largest invertebrates eaten (mantle lengths up to 200 mm). The most voluminous and abundant were species of the family Ommastrephidae. *Gonatus fabricii* (Gonatidae) was also common. The most common octopods were the species of *Argonauta* (including *A. argo*) and *Alloposus mollis*. Surface-dwelling *Argonauta* occurred far more often in the stomachs of *T. albacares* (36%) and *T. thynnus* (25%) than in *T. alalunga* (8%), and was not found in *T. obesus* (Appendix Table 11). The gelatinous octopod, *Alloposus mollis*, was frequently consumed by *T. thynnus* (48% frequency), but rare or absent in the diet of other species of tunas.

Even though abundant, pteropods and heteropods are not as important a component of the forage as are cephalopods and crustaceans because of the small size of these mollusks. They occurred in 52% of the *T. thynnus* stomachs examined (Appendix Table 8). Russell (1960) found the heteropod *Carinaria lamarcki* in *T. albacares* stomachs at 14 localities but gave no indication of either the number of heteropods found or the number of stomachs examined. He reported the pteropod *Cavolina tridentata* from *T. albacares* stomachs at three localities.

Crustaceans were generally smaller than cephalopods and were usually consumed in larger numbers, particularly amphipods and larval forms. The number of the hyperiid amphipod *Phrosina semilunata* (lengths of 20-30 mm) per single stomach sometimes exceeded 100 and constituted a considerable portion of the forage volume. *Phrosina semilunata* was present in the stomachs of 65% of the *T. alalunga*, and in 20-30% of the other tuna species. Although not in large numbers, various species of the hyperiid genus *Phronima* were also frequently utilized. They were found in 15% of *T. albacares* and *T. thynnus*, and in 9% of *T. alalunga*. Several other species of hyperiid amphipods collectively showed a high frequency of occurrence (10-20% depending on species of tuna).

Decapods were the largest crustaceans consumed. Portunids, represented by the sargassum crab (*Portunus sayi*), when identifiable, were eaten by 11% of *T. albacares*. Brachyuran and anomuran larvae were found in about 10% of *T. albacares* and *T. alalunga*, though rarely present in *T. thynnus* and absent from *T. obesus*. The large penaeid larva *Cerataspis petiti* comprised a significant portion of the crustacean volume in 5% of *T. albacares* stomachs. Scyllarid larvae and juveniles were also consumed by *T. albacares* and *T. alalunga*, although less frequently. Other decapods, mostly larvae, occurred in low frequency when considered separately, but were present in a sizeable percentage of tuna stomachs (about 10-30%) when considered as a group.

Isopods and copepods were not significant in either volume or frequency (1-2%). In one sample, it appeared that copepods had been eaten by another forage organism and were in the tuna stomach only secondarily. Also, the isopod, *Ceratothoa* sp., a parasite of exocoetids, was probably ingested only incidentally, in the capture of its host.

Alepisaurus.—Most of the invertebrates eaten by tunas were also consumed by *Alepisaurus* (Appendix Table 1). Forage composition differed, however, in the relative importance of different taxonomic groups. The percent-volume ratio of cephalopods:crustaceans was roughly 50:50 (Appendix Table 10). Crustaceans outranked cephalopods in frequency, however, in a ratio of 75:50. Deep-dwelling soft-bodied squids (Histioteuthidae, Bathyteuthidae, Cranchiidae; Roper and Young 1975) occurred more often in *Alepisaurus* (15%) than in any of the tunas. Other squids, although eaten less than by tunas, were still common (42%). Octopods were often present in *Alepisaurus* forage, *Argonauta* in 25%, *Alloposus* in 32%, and all others in 32% (Appendix Table 11).

Crustaceans were more often the exclusive content of an *Alepisaurus* stomach than were cephalopods. *Phronima* spp. (51%), other hyperiids (47%) (including two not found in the tunas), and anomuran larvae (22%) occurred in generally higher numbers and with higher frequency than in any of the tunas. No portunids were found in *Alepisaurus*, although two or three unidentified crab larvae were present.

Heteropods and pteropods were present in 14% and 12% of the *Alepisaurus* stomachs that we examined (Appendix Table 9) but the actual occurrence was much higher because Russell (1960) removed these mollusks from many of the *Alepisaurus* stomachs. Russell reported seven species of heteropods from three families and five species of pteropods from two families in his sample of *Alepisaurus* stomachs (Appendix Table 1). The heteropod *Carinaria lamarcki* and four species of the pteropod genus *Cavolina* were found at most stations, but Russell gave no numbers of forage organisms or of stomachs examined.

An important constituent of the *Alepisaurus* diet was the family of pelagic polychaetes, Alciopidae, present in 38% of the stomachs and forming much of the total food bulk. Gelatinous organisms (salps, pyrosomas, medusae, and siphonophores) were also more common in *Alepisaurus* stomachs than in tunas.

DISCUSSION

Planktonic and nektonic organisms comprising the diets of the tunas and lancetfishes ranged widely in size and form, suggesting that these predators feed opportunistically. Other data on the food of tunas show, worldwide, a large degree of consistency in forage composition, probably reflecting their association with a distinctive global epipelagic community (Haedrich and Nielsen 1966; Parin et al. 1969; Brodulina 1974). Fishes were consistently the largest and most frequently occurring taxonomic group and, where volumes were measured, constituted the largest forage volume. Cephalopods generally ranked second to fishes in all three measurements. Other invertebrates were generally much smaller but were often eaten in large numbers, particularly amphipods and larval crustaceans, probably encountered in swarms.

Despite such overall consistency, definite differences in the relative importance of certain forage categories do indicate some degree of feeding selectivity, either anatomical or behavioral. Some interspecific and intraspecific feeding differences can be traced to the anatomy of the predator. The size of the gill raker gap determines the minimum size of prey that can be captured and retained (Magnuson and Heitz 1971) and the maximum prey size is determined by the greatest distensibility of the predator's mouth and esophagus. Indeed, the small-mouthed tunas consumed generally smaller prey (mean forage fish length, 98 mm SL) than did the large-mouthed lancetfishes (mean forage fish length, 240 mm SL) .

A similar trend in forage utilization can be seen within a single tuna species. *Thunnus albacares* were divided into three size groups (60.0-99.9 cm FL, 100.0-119.9 cm FL, and 120.0-169.9 cm FL) to facilitate forage comparison. The largest fishes eaten (Gempylidae, $\bar{x}$ length 216 mm SL; Coryphaenidae, $\bar{x}$ length 141 mm SL; Alepisauridae, $\bar{x}$ length 120 mm SL; Paralepididae, $\bar{x}$ length 105 mm SL; Scombridae, $\bar{x}$ length 96 mm SL) were consumed most frequently by the largest sized tunas; among the prey families only the scombrids appeared in the smallest sized tunas. Conversely, the frequency of occurrence of the smallest forage organisms generally decreased with increasing tuna size, as shown by the overall mean frequency of occurrence for larval decapods in Appendix Table 6 ($\bar{x}$ 12.2% frequency of occurrence in 60.0-99.9 cm FL tunas; $\bar{x}$ 10.3% in 100.0-119.9 cm FL tunas; $\bar{x}$ 3.33% in 120.0-169.9 cm FL tunas). Similar trends were not apparent in the other tuna species (Appendix Tables 7-8).

A second limitation of forage composition is determined by the fish's predatory ability, particularly swimming speed. While the tunas are powerful, efficient swimmers, *Alepisaurus* is comparatively slow; this difference is reflected in the type of organism most frequently consumed. Swift-moving muscular squids (such as *Gonatus* and *Onychoteuthis*; Roper and Young 1975) were eaten much more frequently by tunas than by *Alepisaurus*; both capture squids more efficiently, however, than does the 10-foot Isaacs-Kidd midwater trawl. The predatory ability of tunas is further reflected in the frequency with which they consume such fast-swimming fishes as Belonidae, Scomberesocidae, Exocoetidae, Carangidae, and Coryphaenidae. The absence of these families from the *Alepisaurus* stomachs, however, may be due to the fact that they are found only near the surface, where *Alepisaurus* probably does not feed, rather than because *Alepisaurus* is unable to catch them.

Differences in depths at which predators feed probably constitute another mode of forage selectivity. In order to compare differences in feeding depth, we divided forage components somewhat arbitrarily into three categories according to their position in the water column: *Sargassum*-associates (strictly surface organisms associated with pelagic *Sargassum* in the upper 5 m of water); near-surface (the upper 20 m); and midwater (both vertical migrators and those which remain at depths).

Thunnus albacares evidently fed mainly at the surface, particularly on *Sargassum* associates. Bits of *Sargassum* present in stomachs were probably accidentally ingested in the process of capturing associated fauna, of which *Portunus sayi*, the sargassum crab, and large numbers of epipelagic decapod larvae were most frequently consumed (see Fig. 4). The most frequently occurring fishes in *T. albacares* stomachs were juveniles of reef and shore fishes, also associates of the *Sargassum* community.

The *Sargassum* community plays a similar role in the nutrition of other peak oceanic predators such as the dolphins *Coryphaena hippurus* and *C. equiselis* (Gibbs and Collette 1959). This utilization is reasonable to expect, as the *Sargassum* community provides the major concentration of forage organisms in the otherwise barren oceanic surface waters (see Fine 1970; Dooley 1972).

In contrast with the surface-oriented *T. albacares*, the diets of *T. alalunga*, *T. thynnus*, and *T. obesus*, composed mainly of midwater organisms, suggest that these tunas feed at somewhat greater depths. Forage compositions observed may be incomplete, however, because the samples examined were comparatively small.

The relatively small representation of epipelagic organisms and high frequency of occurrence of midwater fishes and invertebrates in the diet of *Alepisaurus* indicates that this predator feeds in the midwater layers (Figs. 3, 4). It might be noted in particular that *Alepisaurus* consumed the deeper-occurring gelatinous squids (Histioteuthidae, Bathyteuthidae, and Cranchiidae) and the gelatinous octopod, *Alloposus mollis* (family Alloposidae), much more frequently than did any of the tunas (except for *T. thynnus* feeding on *Alloposus mollis*). These cephalopods are probably not as abundant in the shallower levels, where tunas feed.

Relative feeding depths discussed above generally correspond to hooking depth records for tunas (Shomura and Murphy 1955; Yabe et al. 1963; Osipov 1968; Legand and Grandperrin 1973; Saito 1975) and lancetfishes. *Thunnus albacares* is generally the most shallow-occurring species; *T. alalunga* and *T. thynnus* occur

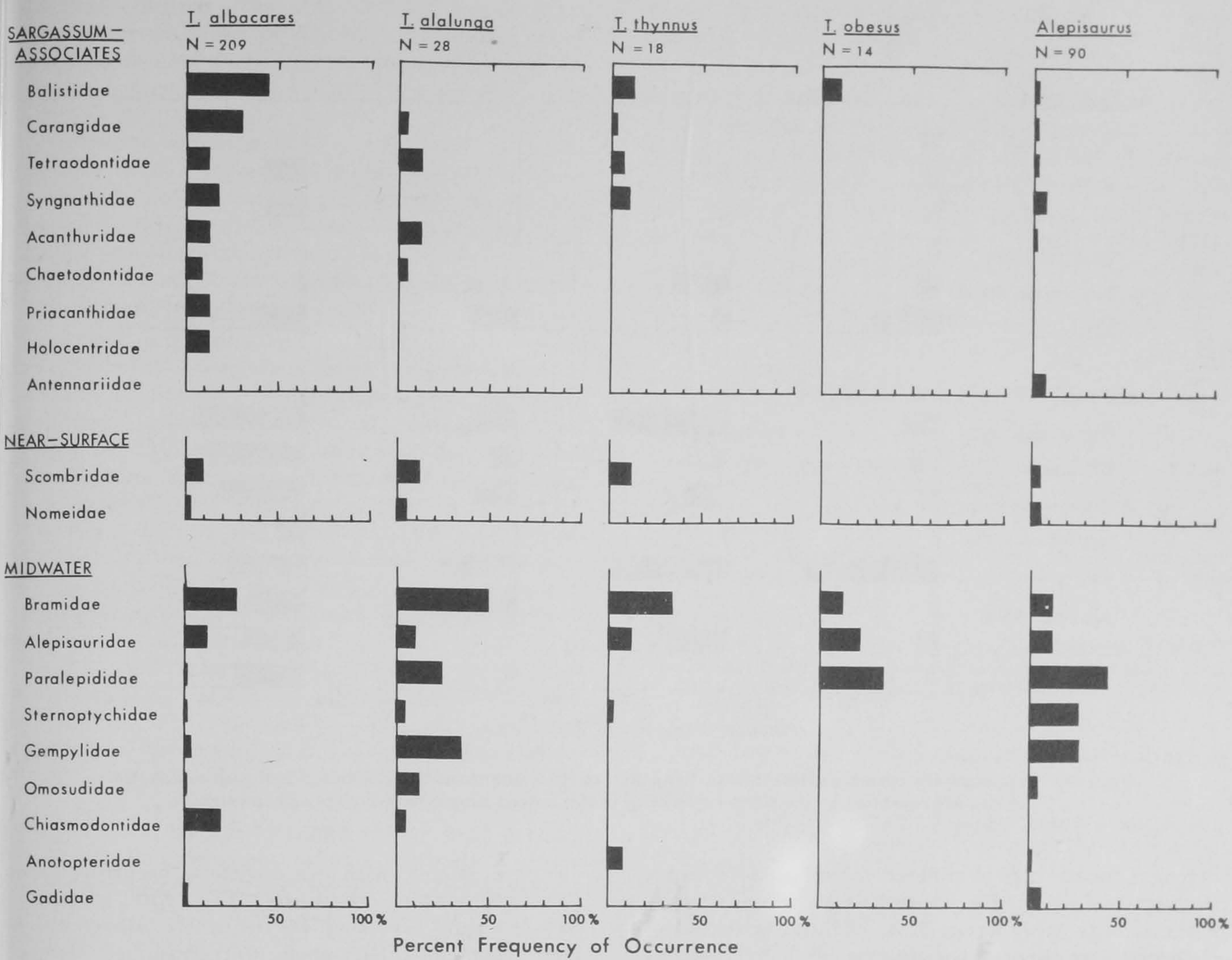

Figure 3.—Frequency of occurrence of the 20 most frequently occurring families of fishes in the stomachs of *Thunnus* and *Alepisaurus*. Families are separated into three categories: *Sargassum*-associates, near-surface, and midwater.

somewhat deeper and may have broader depth ranges; and *T. obesus* is recognized as the deepest swimming of the tunas. The distribution of the lancetfishes may be far broader than that of the tunas, although the lower depth limit is not established. Large specimens have been collected as shallow as 30 m, while small ones have been caught in open nets fished as deep as 2,000 m (Gibbs and Willimovsky 1966). Rancurel (1970) concluded that their primary feeding area is in the upper 300 m.

The following paragraphs summarize observations on forage composition reported in major studies from both the Atlantic and the Pacific for comparison with our data.. Forage composition in these studies may reflect differences in the geographical distributions of prey, local abundances of forage organisms, or local differences in either predator or prey swimming depths but the taxonomic composition of the major food components is similar in all of these studies.

Thunnus albacares.—Dragovich (1970a) reported on the food of yellowfin from the western North Atlantic. *Auxis* sp. (Scombridae) constituted 26.6% of the food volume and occurred in 24.9% of the stomachs. Bramidae and Gempylidae occurred frequently and were moderately important in volume and Balistidae were common. Other surface organisms (Carangidae and Priacanthidae), which were common in our study, were surprisingly absent in the study by Dragovitch (1970a). Serranids occurred frequently, 53.8%, and constituted 56.9% of the total volume. Other high-ranking families in terms of occurrence and volume were Scombridae, Carangidae (mainly *Decapterus* sp.), Dactylopteridae (*Dactylopterus volitans*), and Chaetodontidae. Dragovich and Potthoff (1972) reported that the fish forage of yellowfins caught by live bait and trolling off the coast of West Africa consisted by occurrence and volume mainly of the epipelagic juveniles of Acanthuridae, Carangidae, Dactylopteridae, Lutjanidae, and Mullidae, and the midwater Gempylidae and Gonostomatidae.

In the diet of yellowfin tunas in the central Pacific, acanthurids and bramids, particularly *Collybus*

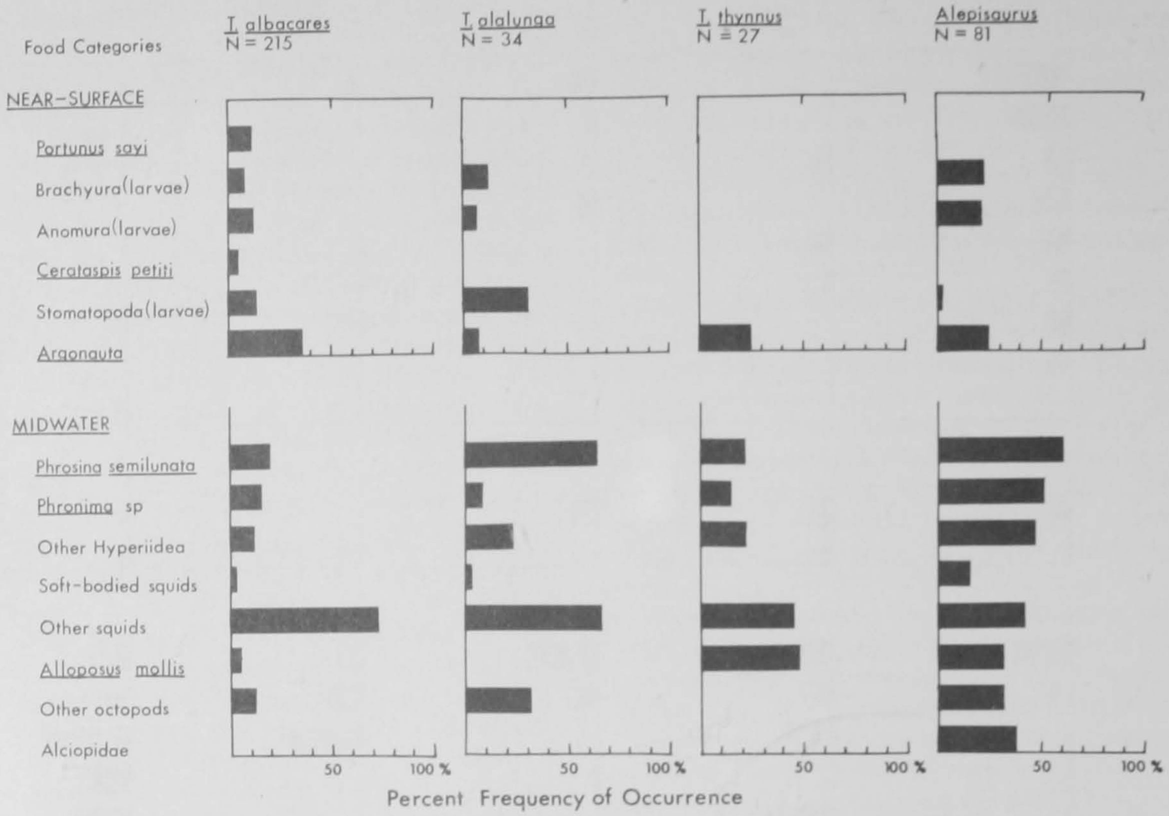

Figure 4.—Frequency of occurrence of invertebrate forage categories in the stomachs of *Thunnus* and *Alepisaurus*. Categories are separated by their general location in the water column: near-surface or midwater.

drachme, ranked high in number, volume, and frequency (Reintjes and King 1953). Exocoetids, scombrids (mainly *Katsuwonus pelamis*), and carangids (mainly *Decapterus* sp.) were important in volume, but were infrequently consumed. The most important fishes in the diet of central Pacific yellowfins were *Collybus drachme* and *Gempylus serpens* (King and Ikehara 1956). Scombridae and Mullidae were important in volume, though infrequently eaten. In the southwest Pacific, the families of fishes most frequently consumed by yellowfins were midwater Sternoptychidae (mostly *Argyropelecus* spp.), Paralepididae, and Bramidae, of which *Collybus drachme* was most important (Fourmanoir 1971). From the eastern tropical Pacific, Alverson (1963) reported Scombridae as the most important by volume (12.2%) followed in decreasing order of magnitude by Exocoetidae, Tetraodontidae, Carangidae, Myctophidae, and Serranidae.

Thunnus alalunga.—In stomachs of longline-caught albacore from the central and northeastern Pacific, the midwater families Gempylidae, Bramidae, Sternoptychidae, and Paralepididae were present most frequently (Iversen 1962). *Gempylus serpens* was the most frequently occurring species (9.9%) while *Collybus drachme* and *Sternoptyx* sp. were both present in 4.9% of the stomachs. In troll-caught albacore in California waters (Iversen 1971), however, the most important forage fishes in terms of both volume and frequency of occurrence were anchovies and sauries, with certain deeper-occurring fishes (*Tarletonbeania crenularis, Paralepis atlantica, Sebastes* spp.) occurring less frequently. Albacore from New Caledonia (Fourmanoir 1971) consumed Sternoptychidae, particularly *Sternoptyx diaphana*, and Bramidae, especially *Collybus drachme* most frequently.

Thunnus thynnus.—Dragovich (1970b) reported Bramidae (*Collybus drachme*) and the epipelagic Scombridae (particularly *Scomber scombrus* and *Auxis* sp.) and Syngnathidae (*Hippocampus erectus*) as the most frequently consumed fishes in western North Atlantic *T. t. thynnus*. In the stomachs of the northern Pacific bluefin, *T. thynnus orientalis*, however, Pinkas (1971) found that *Engraulis mordax* was the primary forage component (72.0% occurrence), followed by the red swimming crab, *Pleuroncodes planipes* (13.5% occurrence), and the saury, *Cololabis saira* (11.9% occurrence).

Thunnus obesus.—In her studies on the food of bigeye tuna from the Gulf of Guinea, Borodulina (1974) found midwater fishes, Paralepididae, Sternoptychidae, Gonostomatidae, Omosudidae, Scopelarchidae, and Alepisauridae most frequently consumed. Gempylidae and Diretmidae were only occasionally utilized, but occurred in large numbers when they were present. In the eastern tropical Atlantic, Gempylidae, Trichiuridae, Bramidae, Alepisauridae, and Myctophidae were most frequently utilized (Maksimov 1972). Northeast of Brazil, however, Maksimov found that shallower dwelling carangids and mackerels were frequently consumed, along with *Alepisaurus*.

Alepisaurus spp.—In the western North Atlantic, Haedrich (1964) reported findings similar to ours: paralipidids, sternoptychids, and alepisaurids were the most frequently occurring fishes. The midwater myctophids, gonostomatids, stomiatids, and chauliodontids that we observed, however, either occurred infrequently or were completely absent.

The most important food organisms in *Alepisaurus* from the Indian Ocean (Parin et al. 1969) were fishes of the families Sternoptychidae (*Sternoptyx diaphana*), Bramidae, Alepisauridae, Nomeidae, Paralepididae, and Gempylidae. Myctophidae, Gonostomatidae, and other fishes that make daily vertical migrations were missing. They suggsted that *Alepisaurus* feeds in the depths between the daytime and nighttime accumulation levels of migrating fishes, and passage of these interzonal populations may be quite rapid through the depths where the *Alepisaurus* were located, explaining the paucity of vertically migrating organisms.

In the southeastern Pacific, epipelagic fishes were more frequently eaten by *Alepisaurus* than midwater forms (Haedrich and Nielsen 1966), although some deeper living fishes such as *Dolichopteryx* were also occasionally present. *Alepisaurus* stomachs from Suruga Bay, Japan, contained fishes from surface, midwater, and bottom zones (Kubota and Uyeno 1969; Kubota 1973). The four dominant fishes in both studies were *Gephroberyx japonicus*, *Lophius litulon*, *Trichiurus lepturus*, and *Engraulis japonica*. In *Alepisaurus* from New Caledonia (Grandperrin and Legand 1970), the most frequently consumed fishes were *Diplospinus multistriatus* (30%) and *Sternoptyx diaphana* (24%). Cephalopods were present in 15% of the stomachs, crustaceans in 10%, and annelids in 12%, most often in young *Alepisaurus* specimens.

Most studies on tuna food have been limited either to qualitative analysis or to quantitative analysis based on a relatively small number of stomach samples from a limited area. The accumulation of such data has made evident the currently acknowledged opportunistic feeding pattern in tunas. A better understanding of interspecific differences in forage utilization might be met through large-scale quantitative analyses of tuna forage in comparison with in situ fauna and oceanographic conditions; there seems little need, however, for additional qualitative studies of tuna food in the future.

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Appendix Table 1.—Forage components of *Thunnus* and *Alepisaurus*. (A) eaten by *Alepisaurus*; (T) eaten by *Thunnus*; (A*) addition to forage list of Haedrich (1964); (T*) addition to forage list of Dragovich (1969).

Phylum Arthropoda
Class Crustacea
  Subclass Copepoda (T)
    Order Calanoida
      Family Aetideidae
        Euchirella sp. (T*)
      Family Candaciidae
        Candacia sp. (T*)
  Subclass Malacostraca
    Order Isopoda (A) (T)
      Suborder Flabellifera
        Family Cirolanidae
          Cirolana sp. (T*)
        Family Cymothoidae
          Ceratothoa sp. (T*)
      Suborder Valvifera
        Family Idoteidae
          Idotea sp. (T)
    Order Amphipoda
      Suborder Hyperiidea (A) (T)
        Family Lanceolidae
          Lanceola sp. (A) (T)
        Family Vibiliidae
          Vibilia sp. (A*) (T)
        Family Hyperiidae
          Hyperia galba (A*) (T)
          Parathemisto gaudichaudii (A*) (T)
        Family Phronimidae
          Phronima sp. (A) (T)
          Phronima atlantica (incl. *solitaria*) (A) (T)
          Phronima sedentaria (A) (T)
        Family Phrosinidae
          Phrosina semilunata (A) (T)
        Family Lycaeidae
          Brachyscelus crusculum (A) (T)
          Lycaea serrata (A*)
        Family Oxycephalidae
          Oxycephalus clausi (A*)
        Family Platyscelidae
          Platyscelus ovoides (A) (T)
    Order Stomatopoda (larva) (T)
          Lysiosquilla (larva) (A*) (T)
    Order Euphausiacea (A) (T)
          Meganyctiphanes norvegica (A*) (T)
    Order Decapoda (larva and adult) (A) (T)
      Superfamily Penaeidea (A*) (T)
          Cerataspis petiti (larva) (T)
      Superfamily Caridea (larva) (A*) (T); (adult) (T)
          Hippolyte zostericola (T*)
          Notostomus sp. (T*)
          Periclimenes (*Harpilius*) *americanus*? (T*)
        Family Scyllaridae (larva) (A) (T)
          Scyllarides sp. (T)
          Scyllarus sp. (A*) (T)
      Superfamily Nephropsidea (larva) (T)
      Section Anomura (larva) (T)
        Family Diogenidae (larva) (A*) (T)
          Paguristes ? (larva) (A*) (T)
      Section Dromiacea (larva) (A*) (T)
      Section Brachyura (larva) (A) (T); (adult) (T)
        Family Portunidae (T)
          Portunus sayi (T*)

Phylum Mollusca
Class Gastropoda (A) (T)
    Order Heteropoda (A) (T)
        Family Atlantidae
          Atlanta peronii (A)
          Oxygyrus keraudrenii (A)
        Family Carinariidae
          Carinaria lamarcki (A) (T)
          Cardiapoda placenta (A)
        Family Pterotracheidae
          Pterotrachea hippocampus (A)
          Pterotrachea scutata (A)
          Pterotrachea coronata (A)
    Order Pteropoda (A) (T)
        Family Cavoliniidae
          Cavolina tridentata (A) (T)
          Cavolina uncinata (A)
          Cavolina gibbosa (A)
          Cavolina trispinosa (A)
        Family Pneumodermatidae
          Pneumoderma atlanticum (A)
    Order Nudibranchia
        Family Phylliroidae
          Phyllirhoe sp. (A*)
Class Cephalopoda (A) (T)
    Order Teuthoidea
      Suborder Oegopsida (A) (T)
        Family Gonatidae (T)
          Gonatus fabricii (T)
        Family Enoploteuthidae (T)
          Abraliopsis sp. (A)
          Enoploteuthis sp. (A*) (T*)
          Enoploteuthis anapsis (A*)
          Pterygioteuthis giardi (A*)
        Family Onychoteuthidae (A) (T)
          Onychoteuthis sp. (T)
          Onykia ? sp. (T)
        Family Lepidoteuthidae (T)
          Tetronychoteuthis dussumieri (T*)
        Family Brachioteuthidae (A*) (T)
          Brachioteuthis riisei (A*) (T)
        Family Histioteuthidae (A*) (T)
          Histioteuthis sp. (T)
          Histioteuthis elongata (A*)
        Family Bathyteuthidae (A)
          Bathyteuthis abyssicola (A*)
        Family Ommastrephidae (A) (T)
          Hyaloteuthis pelagica (T*)
          Illex sp. (A*) (T)
          Ommastrephes spp. (A*) (T)
          Ommastrephes caroli (T*)
          Ornithoteuthis antillarum (T*)
        Family Thysanoteuthidae (T)
          Thysanoteuthis rhombus (T*)
        Family Cranchiidae (A) (T)
          Cranchia scabra (T)
          Leachia sp. (A*) (T*)
          Megalocranchia ? sp. (A)
    Order Octopoda (A) (T)
        Family Bolitaenidae
          Eledonella pygmaea (A*) (T*)
        Family Alloposidae
          Alloposus mollis (A*) (T)
        Family Ocythoidae
          Ocythoe tuberculata (T)
        Family Octopodidae
          Octopus sp. (A*) (T)
          Danoctopus schmidti (A*)
          Scaeurgus unicirrhus (A*) (T*)
        Family Argonautidae
          Argonauta sp. (A) (T)
          Argonauta argo (A) (T*)

Phylum Coelenterata
Class Scyphozoa (Medusae) (A) (T)

Appendix Table 1.—Forage components of *Thunnus* and *Alepisaurus*. (A) eaten by *Alepisaurus*; (T) eaten by *Thunnus*; (A*) addition to forage list of Haedrich (1964); (T*) addition to forage list of Dragovich (1969).—Continued.

Class Hydrozoa
  Order Siphonophora (A*)

Phylum Annelida
Class Polychaeta
    Family Alciopidae
      Greeffia sp. (A*)
      Vanadis sp. (A*)

Phylum Chordata
 Subphylum Tunicata
  Salpida (A) (T)
Class Osteichthyes
  Order Anguilliformes
    Family Muraenidae
      Uropterygius diophus (A*)
    Family Ophichthidae
      Myrophis punctatus (T*)
      Pisodonophis cruentifer (A*)
    Family Nemichthyidae (T)
      Nemichthys scolopaceus (T)
  Order Clupeiformes
    Family Clupeidae (T)
  Order Salmoniformes
    Family Argentinidae (A)
    Family Gonostomatidae (A) (T)
      Gonostoma sp. (A) (T)
      Maurolicus sp. (T)
    Family Sternoptychidae (A) (T)
      Argyropelecus aculeatus (A) (T)
      Sternoptyx diaphana (A) (T)
    Family Stomiatidae (T)
      Eustomias sp. (T*)
    Family Aulopidae (T)
      Aulopus nanae (T*)
    Family Paralepididae (A) (T)
      Lestidiops sp. (T*)
      Lestidiops affinis (A)
      Lestidium atlanticum (A) (T*)
      Macroparalepis sp. (A)
      Notolepis rissoi (T)
      Paralepis sp. (T)
      Paralepis atlantica (A)
      Paralepis coregonoides (A) (T)
      Paralepis elongata (A) (T*)
      Stemonosudis sp. (T*)
    Family Omosudidae (A) (T)
      Omosudis lowei (A) (T)
    Family Alepisauridae (A) (T)
      Alepisaurus sp. (A) (T)
      Alepisaurus brevirostris (A) (T*)
      Alepisaurus ferox (A) (T)
    Family Anotopteridae (A) (T)
      Anotopterus pharao (A) (T)
    Family Myctophidae (A) (T)
      Gonichthys coccoi (T*)
      Lampanyctus sp. (A)
  Order Lophiiformes
    Family Lophiidae (A)
      Lophius americanus (A)
    Family Antennariidae (A) (T)
      Antennarius radiosus (A) (T)
    Family Ogcocephalidae (A) (T)
      Dibranchus atlanticus (T*)
      Halieutichthys aculeatus (A)
   Suborder Ceratioidei
    Family Ceratiidae
      Borophryne sp. (T*)
    Family Linophrynidae (T*) (A)
      Linophryne sp. (T*) (A)

Order Gadiformes
    Family Moridae
      Laemonema barbatula (A*)
    Family Bregmacerotidae (A)
      Bregmaceros sp. (A)
    Family Gadidae (A) (T)
      Melanogrammus aeglefinus (A) (T*)
      Merluccius bilinearis (T)

Order Atheriniformes
    Family Belonidae (T)
      Tylosurus acus (T*)
    Family Scomberesocidae (T)
      Scomberesox saurus (T)
    Family Exocoetidae (T)
      Cypselurus sp. (T)
      Cypselurus heterurus (T)
      Exocoetus obtusirostris (T)
    Family Hemiramphidae
      Hyporhamphus sp. (T)

Order Beryciformes
    Family Melamphaidae (T*)
    Family Anoplogasteridae (A) (T)
      Anoplogaster cornutus (A) (T)
    Family Monocentridae (T*)
    Family Holocentridae (T)
      Holocentrus sp. (T)
      Holocentrus ascensionis (T)

Order Zeiformes
    Family Caproidae (T)
      Antigonia capros (T)
      Capros aper (T)

Order Lampridiformes
    Family Lophotidae (T*)
    Family Trachipteridae (A) (T)
      Trachipterus sp. (A) (T)

Order Gasterosteiformes
    Family Fistulariidae (T)
      Fistularia sp. (T)
    Family Syngnathidae (A) (T)
      Hippocampus sp. (T)
      Hippocampus erectus (A) (T*)

Order Scorpaeniformes
    Family Scorpaenidae (A)
    Family Triglidae
      Peristedion gracile (T)
      Peristedion greyae ? (T)
      Peristedion miniatum (T)

Order Dactylopteriformes
    Family Dactylopteridae (T)
      Dactylopterus volitans (T)

Order Perciformes
    Family Serranidae (A) (T)
      Serranus sp. (T*)
    Family Priacanthidae (T)
      Cookeolus boops (T*)
      Pseudopriacanthus sp. (T)
    Family Echeneidae (T)
      Remora osteochir (T*)
    Family Carangidae (T)
      Caranx sp. (T)
      Selar crumenophthalmus (T)
      Seriola dumerili (T*)
      Seriola rivoliana (T*)
      Trachurus sp. (T)
      Trachurus lathami (T)
      Vomer setapinnis (T)
    Family Coryphaenidae (T)
      Coryphaena equiselis (T*)
      Coryphaena hippurus (T)

Appendix Table 1.—Forage components of *Thunnus* and *Alepisaurus*. (A) eaten by *Alepisaurus*; (T) eaten by *Thunnus*; (A*) addition to forage list of Haedrich (1964); (T*) addition to forage list of Dragovich (1969).—Continued.

Family Bramidae (T)
- *Collybus drachme* (T)
- *Pteraclis* sp. (A) (T)
- *Pterycombus* sp. (A) (T)
- *Taractes* sp. (T)

Family Lutjanidae (A) (T)
- *Pristipomoides* sp. (A) (T)
- *Pristipomoides aquilonurus* (T)

Family Chaetodontidae (T)
- *Centropyge argi* (T*)

Family Pomacentridae (T*)

Family Trichodontidae (T*)

Family Uranoscopidae (A)
- *Kathestoma averruncus* (A)

Family Chiasmodontidae (T)
- *Pseudoscopelus* sp. (T*)

Family Acanthuridae (A) (T)
- *Acanthurus chirurgus* (T)
- *Acanthurus coeruleus* (T)

Suborder Scombroidei (A) (T)

Family Gempylidae (A) (T)
- *Diplospinus multistriatus* (A) (T*)
- *Gempylus serpens* (T)
- *Nealotus* sp. (A)
- *Nealotus tripes* (A) (T*)
- *Nesiarchus nasutus* (A) (T)

Family Trichiuridae (T)

Family Scombridae (A) (T)
- *Auxis* sp. (A) (T)
- *Euthynnus alletteratus* (T)
- *Katsuwonus pelamis* (T)
- *Scomber japonicus* (A*) (T)
- *Thunnus atlanticus* (T)

Family Xiphiidae
- *Xiphias gladius* (T*)

Suborder Stromateoidei (A) (T)

Family Stromateidae (A)
- *Peprilus triacanthus* (A)

Family Centrolophidae (A) (T)
- *Hyperglyphe* sp. (T*)
- *Hyperglyphe perciformis* (A) (T)

Family Nomeidae (A) (T)
- *Nomeus* sp. (A) (T)
- *Psenes maculatus* (T*)
- *Psenes pellucidus* (A) (T*)

Family Tetragonuridae (A) (T)
- *Tetragonurus cuvieri* (A) (T)

Order Pleuronectiformes

Family Bothidae (A) (T)

Order Tetraodontiformes

Suborder Balistoidei (T)

Family Balistidae (incl. Monacanthidae) (A) (T)
- *Aluterus* sp. (T)
- *Balistes* sp. (T)
- *Balistes capriscus* (T)
- *Cantherhines* sp. (T)
- *Canthidermis* sp. (T)
- *Canthidermis maculatus* (T*)
- *Monacanthus* sp. (T*)
- *Monacanthus ciliatus* (T)
- *Monacanthus hispidus* (T*)
- *Monacanthus tuckeri* (A) (T)
- *Xanthichthys ringens* (T)

Family Tetraodontidae (A) (T)
- *Lagocephalus* sp. (T)
- *Sphoeroides* sp. (T)

Family Diodontidae (T)
- *Chilomycterus* sp. (T*)
- *Diodon* sp. (T)

Family Molidae (T)
- *Mola mola* (T*)
- *Ranzania laevis* (T*)

Appendix Table 2.—Precent frequency of occurrence of food fish categories identified from 266 stomachs of western North Atlantic *Thunnus albacares* by size range.

Food fish categories	Size (cm FL): No. of specimens:	60.0-99.9 58	100.0-119.9 90	120.0-169.9 63	Unknown 55	Total 266
Sternoptychidae (unid.)					3	< 1
Sternoptyx diaphana			1			< 1
Aulopidae						
Aulopus nanae			1			< 1
Paralepididae (unid.)			1	5		2
Omosudidae						
Omosudis lowei					2	< 1
Alepisauridae						
Alepisaurus brevirostris				3		1
A. ferox				2		< 1
Ogcocephalidae (unid.)		3	1	4		2
Halieutichthys aculeatus					2	< 1
Ceratioidei (unid.)			1			< 1
Ceratiidae						
Borophryne sp.					2	< 1
Gadidae						
Melanogrammus aeglefinus			1			< 1
Belonidae						
Tylosurus acus		2				< 1
Exocoetidae					4	1
Cypselurus sp.					2	< 1
C. heterurus					2	< 1
Exocoetus obtusirostris					2	< 1
Hemiramphidae						
Hyporhamphus sp.					2	< 1
Scomberesocidae						
Scomberesox saurus			2	2		1
Anoplogasteridae						
Anoplogaster cornutus		2			4	1
Holocentridae (unid.)			13	8		6
Holocentrus sp.			2			1
H. ascensionis					2	< 1
Caproidae						
Antigonia capros		3				1
Fistulariidae						
Fistularia sp.					2	< 1
Syngnathidae (unid.)			4	2		2
Hippocampus sp.		5	6	11	2	6
H. erectus		2	2	14		5
Triglidae						
Peristedion greyae			1		1	1
P. gracile			1			< 1
P. miniatum				2		< 1
Dactylopteridae						
Dactylopterus volitans			2	2		1
Perciformes (unid.)		2				< 1
Serranidae (unid.)		2	1			1
Priacanthidae						
Cookeolus boops		16	10	5		9
Pseudopriacanthus sp.					3	< 1
Echeneidae						
Remora osteochir		3				1
Carangidae (unid.)		5	7	3		4
Caranx sp.		7	20	11		11
Selar crumenophthalmus		5	2			2
Seriola dumerili					2	< 1
S. falcata					4	1
Trachurus sp.		7	2			2
Vomer setapinnis		3	6	6		4

Appendix Table 2.—Percent frequency of occurrence of food fish categories identified from 266 stomachs of western North Atlantic *Thunnus albacares* by size range.—Continued.

Food fish categories	Size (cm FL): No. of specimens:	60.0-99.9 58	100.0-119.9 90	120.0-169.9 63	Unknown 55	Total 266
Coryphaenidae						
Coryphaena equiselis				3	2	1
Coryphaena hippurus		2	6	6	4	5
Bramidae (unid.)		3	1	2		2
Collybus drachme		5	2	6		3
Pteraclis sp.					4	1
Pterycombus sp.		26	13	3		11
Taractes sp.					3	< 1
Lutjanidae						
Pristipomoides sp.			1			< 1
Chaetodontidae (unid.)		10	1	2		3
Centropyge argi		5	1	2		2
Chiasmodontidae (unid.)					11	2
Pseudoscopelus sp.		16	11	3		8
Acanthuridae (unid.)		9	7	2		5
Acanthurus coeruleus					4	1
Acanthurus chirurgus					2	< 1
Trichiuridae (unid.)			1			< 1
Gempylidae (unid.)				2		< 1
Diplospinus multistriatus					6	2
Gempylus serpens					3	1
Nealotus tripes					3	1
Neasiarchus nasutus					2	< 1
Scombridae						
Auxis sp.		5	3	8	7	5
Euthynnus alletteratus				2		< 1
Katsuwonus pelamis		2	4			2
Thunnus atlanticus				2		< 1
Xiphiidae						
Xiphias gladius				2		< 1
Stromateoidei (unid.)			2	2		2
Nomeidae (unid.)		2	1			1
Tetragonuridae						
Tetragonurus cuvieri			1			< 1
Bothidae (unid.)		2				< 1
Tetraodontiformes (unid.)		3	3			2
Balistoidei (unid.)			3	3		2
Balistidae (including Monacanthidae)		19	24	27	3	12
Aluterus sp.				3	5	2
Balistes sp.			1	10	3	3
Balistes capriscus		2	2		9	3
Cantherhines sp.				2		< 1
Canthidermis sp.		5	1			2
Canthidermis maculatus		2				< 1
Monacanthus sp.			6	17	5	7
Monacanthus ciliatus				2		< 1
Monacanthus hispidus					3	< 1
Xanthichthys ringens			2	3		2
Tetraodontidae (unid.)		5	2			2
Lagocephalus sp.				5	4	2
Sphoeroides sp.		3	8			3
Diodontidae						
Diodon sp.		2	2	3	2	2
Molidae (unid.)		2				< 1
Mola mola				2		< 1
Ranzania laevis		2	6		2	3
Unidentified fishes		21	17	25	67	30

Appendix Table 2.—Precent frequency of occurrence of food fish categories identified from 266 stomachs of western North Atlantic *Thunnus albacares* by size range.

Food fish categories	Size (cm FL): No. of specimens:	60.0-99.9 58	100.0-119.9 90	120.0-169.9 63	Unknown 55	Total 266
Sternoptychidae (unid.)					3	<1
Sternoptyx diaphana			1			<1
Aulopidae						
Aulopus nanae			1			<1
Paralepididae (unid.)			1	5		2
Omosudidae						
Omosudis lowei					2	<1
Alepisauridae						
Alepisaurus brevirostris				3		1
A. ferox				2		<1
Ogcocephalidae (unid.)		3	1	4		2
Halieutichthys aculeatus					2	<1
Ceratioidei (unid.)			1			<1
Ceratiidae						
Borophryne sp.					2	<1
Gadidae						
Melanogrammus aeglefinus			1			<1
Belonidae						
Tylosurus acus		2				<1
Exocoetidae					4	1
Cypselurus sp.					2	<1
C. heterurus					2	<1
Exocoetus obtusirostris					2	<1
Hemiramphidae						
Hyporhamphus sp.					2	<1
Scomberesocidae						
Scomberesox saurus			2	2		1
Anoplogasteridae						
Anoplogaster cornutus		2			4	1
Holocentridae (unid.)			13	8		6
Holocentrus sp.			2			1
H. ascensionis					2	<1
Caproidae						
Antigonia capros		3				1
Fistulariidae						
Fistularia sp.					2	<1
Syngnathidae (unid.)			4	2		2
Hippocampus sp.		5	6	11	2	6
H. erectus		2	2	14		5
Triglidae						
Peristedion greyae			1		1	1
P. gracile			1			<1
P. miniatum				2		<1
Dactylopteridae						
Dactylopterus volitans			2	2		1
Perciformes (unid.)		2				<1
Serranidae (unid.)		2	1			1
Priacanthidae						
Cookeolus boops		16	10	5		9
Pseudopriacanthus sp.					3	<1
Echeneidae						
Remora osteochir		3				1
Carangidae (unid.)		5	7	3		4
Caranx sp.		7	20	11		11
Selar crumenophthalmus		5	2			2
Seriola dumerili					2	<1
S. falcata					4	1
Trachurus sp.		7	2			2
Vomer setapinnis		3	6	6		4

Appendix Table 2.—Percent frequency of occurrence of food fish categories identified from 266 stomachs of western North Atlantic *Thunnus albacares* by size range.—Continued.

Food fish categories	Size (cm FL): / No. of specimens:	60.0-99.9 / 58	100.0-119.9 / 90	120.0-169.9 / 63	Unknown / 55	Total / 266
Coryphaenidae						
Coryphaena equiselis				3	2	1
Coryphaena hippurus		2	6	6	4	5
Bramidae (unid.)		3	1	2		2
Collybus drachme		5	2	6		3
Pteraclis sp.					4	1
Pterycombus sp.		26	13	3		11
Taractes sp.					3	< 1
Lutjanidae						
Pristipomoides sp.			1			< 1
Chaetodontidae (unid.)		10	1	2		3
Centropyge argi		5	1	2		2
Chiasmodontidae (unid.)					11	2
Pseudoscopelus sp.		16	11	3		8
Acanthuridae (unid.)		9	7	2		5
Acanthurus coeruleus					4	1
Acanthurus chirurgus					2	< 1
Trichiuridae (unid.)			1			< 1
Gempylidae (unid.)				2		< 1
Diplospinus multistriatus					6	2
Gempylus serpens					3	1
Nealotus tripes					3	1
Neasiarchus nasutus					2	< 1
Scombridae						
Auxis sp.		5	3	8	7	5
Euthynnus alletteratus				2		< 1
Katsuwonus pelamis		2	4			2
Thunnus atlanticus				2		< 1
Xiphiidae						
Xiphias gladius				2		< 1
Stromateoidei (unid.)			2	2		2
Nomeidae (unid.)		2	1			1
Tetragonuridae						
Tetragonurus cuvieri			1			< 1
Bothidae (unid.)		2				< 1
Tetraodontiformes (unid.)		3	3			2
Balistoidei (unid.)			3	3		2
Balistidae (including Monacanthidae)		19	24	27	3	12
Aluterus sp.				3	5	2
Balistes sp.			1	10	3	3
Balistes capriscus		2	2		9	3
Cantherhines sp.				2		< 1
Canthidermis sp.		5	1			2
Canthidermis maculatus		2				< 1
Monacanthus sp.			6	17	5	7
Monacanthus ciliatus				2		< 1
Monacanthus hispidus					3	< 1
Xanthichthys ringens			2	3		2
Tetraodontidae (unid.)		5	2			2
Lagocephalus sp.				5	4	2
Sphoeroides sp.		3	8			3
Diodontidae						
Diodon sp.		2	2	3	2	2
Molidae (unid.)		2				< 1
Mola mola				2		< 1
Ranzania laevis		2	6		2	3
Unidentified fishes		21	17	25	67	30

Appendix Table 3.—Percent frequency of occurrence of food fish categories in 38 stomachs of western North Atlantic *Thunnus alalunga* by size range.

Food fish categories	Size (cm FL): No. of specimens:	80.0-99.9 13	100.0-110.0 15	Unknown 10	Total 38
Sternoptychidae					
Sternoptyx diaphana			7		3
Paralepididae (unid.)			7	30	11
Omosudidae					
Omosudis lowei				20	5
Alepisauridae				20	5
Myctophidae				10	3
Ogcocephalidae (unid.)		8			3
Caproidae					
Antigonia capros				10	3
Triglidae					
Peristedion gracile		8			3
Perciformes (unid.)		8			3
Serranidae (unid.)			7		3
Carangidae					
Vomer setapinnis			7		3
Bramidae					
Collybus drachme				10	3
Pteraclis sp.				30	8
Pterycombus sp.			23		8
Chaetodontidae (unid.)		8			3
Pomacentridae (unid.)				10	3
Chiasmodontidae				10	3
Acanthuridae				20	5
Gempylidae				10	3
Diplospinus multistriatus				30	8
Nealotus tripes				10	3
Nesiarchus nasutus				10	3
Scombridae					
Auxis sp.		15			5
Scomber japonicus		8			3
Nomeidae					
Psenes pellucidus			7		3
Bothidae		8			3
Tetraodontidae		8		10	5
Diodontidae					
Chilomycterus sp.			7		3
Unidentified fishes		77	67	40	63

Appendix Table 4.—Percent frequency of occurrence of food fish categories in 38 stomachs of western North Atlantic *Thunnus thynnus*.

Food fish categories	% freq.	Food fish categories	% freq.
Ophichthidae		Bramidae	
Myrophis punctatus	3	*Collybus drachme*	8
Sternoptychidae		*Pteraclis* sp.	5
Argyropelecus aculeatus	3	*Taractes* sp.	8
Alepisauridae		Trichiuridae	3
Alepisaurus sp.	8	Scombridae	
Anotopteridae		*Auxis* sp.	8
Anotopterus pharao	5	Balistidae (incl. Monacanthidae)	
Scomberesocidae		*Aluterus* sp.	3
Scomberesox saurus	5	*Monacanthus hispidus*	5
Anoplogasteridae		*Xanthichthys ringens*	3
Anoplogaster cornutus	5	Tetraodontidae	
Lophotidae	3	*Sphoeroides* sp.	5
Syngnathidae		Diodontidae	5
Hippocampus erectus	8	Molidae	
Carangidae	3	*Mola mola*	6
		Unidentified fishes	37

Appendix Table 5.—Percent frequency of occurrence of food fish categories in 81 stomachs of western North Atlantic *Alepisaurus*.

Food fish categories	% freq.	Food fish categories	% freq.
Ophichthidae		Moridae	
Pisodonophis cruentifer	1	*Laemonema barbatula*	4
Muraenidae		Anoplogasteridae	
Uropterygius diopus	1	*Anoplogaster cornutus*	2
Argentinidae	1	Trachipteridae	
Gonostomatidae		*Trachipterus* sp.	1
Gonostoma sp.	1	Syngnathidae	
Sternoptychidae		*Hippocampus erectus*	6
Argyropelecus aculeatus	2	Scorpaenidae	2
Sternoptyx diaphana	25	Serranidae	2
Aulopidae		Carangidae	
Aulopus nanae	2	*Trachurus lathami*	1
Paralepididae	5	*Vomer setapinnis*	1
Lestidium affine	1	Bramidae	2
Lestidium atlanticus	1	*Pteraclis* sp.	4
Macroparalepis sp.	4	*Pterycombus* sp.	5
Notolepis rissoi	5	Lutjanidae	1
Paralepis sp.	6	*Pristipomoides* sp.	1
Paralepis brevirostris	4	Uranoscopidae	
Paralepis coregonoides	33	*Kathestoma averruncus*	1
Paralepis elongata	4	Acanthuridae	1
Omosudidae	2	Gempylidae	1
Omosudis lowei	1	*Diplospinus multistriatus*	14
Alepisauridae		*Neolotus* sp.	1
Alepisaurus sp.	4	*Neolotus tripes*	7
Alepisaurus brevirostris	5	*Nesiarchus nasutus*	5
Alepisaurus ferox	4	Scombridae	
Anotopteridae		*Auxis* sp.	1
Anotopterus pharao	1	*Scomber japonicus*	2
Myctophidae		Stromateidae	2
Lampanyctus sp.	1	*Peprilus triacanthus*	1
Lophiidae		Centrolophidae	
Lophius americanus	1	*Hyperglyphe perciformis*	4
Antennariidae		Nomeidae	
Antennarius radiosus	6	*Nomeus* sp.	2
Ogcocephalidae	1	*Psenes pellucidus*	2
Halieutichthys aculeatus	2	Tetragonuridae	
Linophrynidae		*Tetragonurus cuvieri*	1
Linophryne sp.	2	Bothidae	2
Bregmacerotidae		Balistidae	1
Bregmaceros sp.	1	*Monacanthus tuckeri*	1
Gadidae		Tetraodontidae	2
Melanogrammus aeglefinus	5		

Appendix Table 6.—Percent frequency of occurrence of principal invertebrate groups in 215 stomachs of western North Atlantic *Thunnus albacares* by size range.

Food categories — Size (cm FL): / No. of specimens:	60.0-99.9 59	100.0-119.9 91	120.0-169.9 65	Total 215
Portunidae	12	7	15	11
Brachyura larvae	8	10	5	8
Anomura larvae	19	14	2	12
Cerataspis larvae	5	7	3	5
Scyllaridae (incl. larvae)		3	2	2
Other Decapoda (incl. larvae)	12	8	5	8
Stomatopoda larvae	17	20	3	14
Euphausiacea	5			1
Phrosina semilunata	29	16	17	20
Phronima spp.	12	15	17	15
Other Hyperiidea	15	9	11	11
Isopoda	2	3		2
Copepoda	2	2	3	2
Heteropoda	10	10	11	10
Pteropoda				< 1
Other Gastropoda	3			
Cephalopoda	83	77	82	80

Appendix Table 7.—Percent frequency of occurrence of principal invertebrate groups in 34 stomachs of western North Atlantic *Thunnus alalunga* by size range.

Food categories — Size (cm FL): / No. of specimens:	80.0-99.9 15	100.0-110 19	Total 34
Brachyura larvae	20	5	12
Anomura larvae	13		6
Scyllaridae (incl. larvae)	7	11	9
Other Decapoda (incl. larvae)	20	37	29
Stomatopoda larvae	13	47	32
Euphausiacea	7	11	9
Phrosina semilunata	60	68	65
Phronima spp.	7	10	9
Other Hyperiidea	20	26	24
Cephalopoda	93	84	89

Appendix Table 8.—Percent frequency of occurrence of principal invertebrate groups in 27 stomachs of western North Atlantic *Thunnus thynnus* by size range.

Food categories — Size (cm FL): / No. of specimens:	100.0-149.9 10	150.0-199.9 10	200.0-231.9 7	Total 27
Other Decapoda (incl. larvae)		20	14	11
Euphausiacea	10	10	14	11
Phrosina semilunata		50	14	22
Phronima spp.	10	30		15
Other Hyperiidea	10	40	14	22
Heteropoda; Pteropoda	70	50	29	52
Cephalopoda	90	90	71	85

Appendix Table 9.—Percent frequency of occurrence of principal invertebrate groups in 81 stomachs of western North Atlantic *Alepisaurus* spp.

Food categories	% freq.
Brachyura larvae	23
Anomura larvae	22
Scyllaridae (larvae)	5
Other Decapoda (incl. larvae)	4
Stomatopoda larvae	2
Euphausiacea	17
Phrosina semilunata	60
Phronima spp.	51
Other Hyperiidea	47
Isopoda	1
All Crustacea combined	75
Heteropoda	14
Pteropoda	12
Other Gastropoda	4
Polychaeta	38
Salpa and Pyrosoma	16
Cephalopoda	49
Medusae	6

Appendix Table 10.—Occurrence and co-occurrence of crustaceans and cephalopods in the stomachs of western North Atlantic *Thunnus* and *Alepisaurus* species.

Species	Number of exclusive occurrences		Number of co-occurrences	Co-occurrence, estimated average percent-volume	
	Crustaceans	Cephalopods		Crustaceans	Cephalopods
T. albacares	28	89	125	31	69
T. alalunga	7	8	30	33	67
T. obesus	1	7	7	21	79
T. thynnus	3	26	14	23	77
Alepisaurus spp.	30	9	31	54	46

Appendix Table 11.—Percent frequency of occurrence of cephalopod groups in stomachs of western North Atlantic *Thunnus* and *Alepisaurus* species.

	T. albacares	*T. alalunga*	*T. obesus*	*T. thynnus*	*Alepisaurus* spp.
Specimens containing cephalopods (Percent of total)	214 (77)	38 (79)	14 (100)	40 (77)	40 (49)
Soft-bodied squids,[1] % with	2	3	0	0	15
Other squids, % with	72	66	86	45	42
Argonauta spp., % with	36	8	0	25	25
Alloposus mollis, % with	5	0	0	48	32
Other octopods, % with	12	32	0	0	32

[1]Bathyteuthidae, Cranchiidae, and Histioteuthidae.