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Feeding Spectrum and Trophic Relationships of Short-finned Squid (*Illex illecebrosus*) in the Northwest Atlantic*

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Abstract

The feeding spectrum of short-finned squid was investigated from material collected in the southern part of the Northwest Atlantic from the Scotian Shelf to Cape Hatteras. Organisms belonging to 4 phyla and 13 orders were identified mostly to the family level. The most prevalent groups were euphausiids, fish and squid, which on the average constituted 62, 18 and 12% of the food mass respectively. *Meganyctiphanes norvegica* predominated among the euphausiids, myctophids and merlucciids prevailed among the fish, and cannibalism was evident from time to time, particularly at night. The food composition changed with increasing squid size from mainly euphausiids in the smaller animals to fish and squid in the larger individuals. The squid functions as a predator at the second and third trophic levels and are preyed upon extensively by predators of higher trophic levels (fish, birds and mammals). A unique role of squid in the ecosystem of the continental shelf and slope is that they appear to ingest considerably less than half of the biomass of the organisms killed, the discarded parts being available as food for near-bottom and benthic animals.

Introduction

The short-finned squid is an important part of the ecosystem in the Northwest Atlantic, ranging from the Newfoundland area southward to at least the latitude of Cape Hatteras and probably as far south as Florida (Squires, 1957; Mercer, MS 1965; Clarke, 1966; Roper *et al.*, 1969; Mercer and Paulmier, MS 1974). The spawning grounds are as yet unknown, but larvae and small juveniles are found during winter and spring in Slope Water and along the northern edge of the Gulf Stream from Cape Hatteras to the southern tip of Grand Bank (Fedulov and Froerman, MS 1980; Froerman, MS 1980; Froerman *et al.*, MS 1981; Dawe *et al.*, MS 1981, MS 1982; Hatanaka *et al.*, MS 1982). The squid migrate to the continental shelf in late spring (Fedulov and Amaratunga, MS 1981) and are extensively exploited during summer and autumn, as indicated by catches of 108,000-180,000 (metric) tons in 1977-79 (ICNAF, 1979, 1980; NAFO, 1981). During various phases of their life history, squid perform extensive vertical and horizontal migrations (Roper and Young, 1975; Lu and Roper, 1979; Minet and Dupouy, MS 1980; Hurley and Dawe, MS 1980; Dawe *et al.*, 1981, MS 1982).

Short-finned squid are active predators and feed on a great variety of marine organisms, with crustaceans, fishes and squids being the major components of their diet (Squires, 1957; Mercer, MS 1965; Burukovsky and Froerman, 1974; Mercer and Paulmier, MS 1974; Ennis and Collins, 1979; Vinogradov and Noskov, 1979; Amaratunga *et al.*, MS 1979; O'Dor *et al.*, 1980; Amaratunga, MS 1980; Wallace *et al.*, 1981). On the other hand, many fish species, marine mammals and birds prey on *Illex* (Templeman, 1944; Vladykov, 1946; Sergeant and Fisher, 1957; Squires, 1957, 1967; Sergeant, 1962; Scott and Tibbo, 1968; Zuev and Nesis, 1971; Vinogradov, 1972; Katona *et al.*, 1978; Dupouy *et al.*, MS 1982).

The objective of this paper is to describe the feeding spectrum of short-finned squid during various phases of growth from juveniles to maturing adults and to elaborate the role of this species in the ecosystems of the Northwest Atlantic both as predator and prey.

Materials and Methods

The feeding spectrum of short-finned squid was determined from specimens collected during bottom-trawling by USSR research vessels on the continental shelf and slope areas and midwater-trawling in the open sea from Cape Hatteras to the Scotian Shelf during 1968-81. Depth of sampling ranged from 30 to 500 m. A total of 1,012 stomachs were analyzed, most of which contained some food. Samples were taken during all seasons of the year, but most of the material was collected during summer and autumn (628 and 200 stomachs respectively).

The contents of each stomach were examined under a binocular microscope. The components were

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sorted according to their systematic category. The remains of food organisms, by which species specificity could be identified and their size estimated, were sketched, and, if possible, measured. Where possible, food organisms were identified to the lowest taxonomic level, but this could not be done in all cases because the food was macerated by the squid beak and radula. The methods of Shorygin (1952) and Turpaeva (1953) were generally followed in the analysis of stomach contents.

The role of different food components in the feeding spectrum was examined by determining the frequency of occurrence (%) and the relative volume (%) of the organisms in the stomachs. All stomachs containing food were utilized for analysis of frequency of occurrence. Only those stomachs more than three-quarters full of freshly eaten food were utilized for the analysis of contents by volume.

Food of Short-finned Squid

The organisms found in the stomachs of short-finned squid belong to four major taxonomic groups (Table 1), namely Arthropoda (crustaceans), Mollusca (cephalopods and gastropods), Chaetognatha (arrow worms) and Chordata (fishes). Most of the organisms were identified to the family level, and 12 types were identified to the genus and/or species level. Addition-

TABLE 1. List of food components found in the stomachs of short-finned squid from Subareas 4, 5 and 6 of the Northwest Atlantic (Scotian Shelf to Cape Hatteras), including food items reported by other researchers.

Phylum	Class	Order	Family	Species
Arthropoda	Crustacea	Amphipoda	Gammaridae	?
			Phronimidae	*Phronima atlantica*
			Hyperiidae[1]	*Parathemisto* sp.[1]
		Anisopoda	?	?
		Copepoda	Candacidae	*Candacia armata*
			Centropagidae	*Centropages* sp.
			Scolecithricellidae	*Scolecithrix danae*
			Aetideidae[1]	*Euchirella rostrata*[1]
			Euchaetidae[2]	*Euchaeta norvegica*[2]
		Decapoda (Brachyura)	?	?
		Decapoda (Natantia)	Crangonidae	?
			Pandalidae	?
			Sergestidae	?
			Pasiphaeidae[3]	?
		Euphausiacea	Euphausiidae	*Meganyctiphanes norvegica*
				Thysanoessa sp.
		Stomatopoda	?	?
Mollusca	Cephalopoda	Sepioidea	Sepiolidae	?
		Teuthoidea	Ommastriphidae	*Illex illecebrosus*
			Loliginidae	*Loligo pealei*
			Histioteuthidae[2]	?
	Gastropoda	Pteropoda	?	?
Chaetognatha	—	—	—	*Sagitta* sp.
Chordata	Pisces	Clupeiformes	Astronesthidae	?
			Gonostomatidae	?
			Osmeridae[3]	*Mallotus villosus*[3]
		Gadiformes	Macrouridae	?
			Merlucciidae	*Merluccius bilinearis*
			Gadidae[3]	*Gadus morhua*[3]
				Melanogrammus aeglefinus[3]
		Myctophiformes	Myctophidae	?
		Perciformes	Chilodipteridae	?
			Zoarcidae	*Macrozoarces americanus*
		Scorpaeniformes	Cottidae[3]	*Triglops pingeli*[3]
			Scorpaenidae	*Sebastes marinus*

[1] Reported by Mercer and Paulmier (MS 1974).
[2] Amaratunga *et al.* (MS 1979).
[3] Squires (1957).

ally, the list contains seven species which have been identified as food of *Illex illecebrosus* by other researchers.

Arthropoda (Crustacea)

This phylum (class) was represented by six orders in the food spectrum of short-finned squid (Table 1), but identification to the family level was achieved only for amphipods, copepods, decapods (shrimps) and euphausiids.

Amphipoda. This order was represented by two families, Gammaridae and Phronimidae (Table 1), the latter belonging to the suborder Hyperiidea. Among the amphipods that were identified, the larvae of Gammaridae with their unsegmented cephalothorax were readily counted and they predominated in the food mass (96% occurrence). The average number of gammarid larvae was 137 in the stomachs containing amphipods, the maximum number being 240 in a single stomach. The remains of adult amphipods were most frequently represented by a typical chela of Phronimidae. The hyperiid, *Parathemisto* sp., was reported by Mercer and Paulmier (MS 1974) to be a component of the diet of short-finned squid.

Copepoda. This order was represented by three genera belonging to three different families (Table 1). The average number of copepods found in the squid stomachs was 2, with 12 being the maximum number in a single stomach. In most cases, the copepods were not macerated, and it is possible that they were present in the stomachs of larger organisms which were eaten by the squid. Two other copepods have been reported as food of short-finned squid: *Euchaeta norvegica* of the family Euchaetidae by Amaratunga *et al.* (MS 1979), and *Euchirella rostrata* of the family Aetideidae by Mercer and Paulmier (MS 1974).

Decapoda. This class was represented by two tribes (Brachyura and Natantia), but identification to the family level could be achieved only for three families of shrimps (Table 1). Among the shrimps, the remains of Sergestidae, which live pelagically, were most frequently found (75% occurrence) in the squid stomachs. They were readily identified from mandibles and appendages, and the maximum number found in a single stomach was 6. Bottom-inhabiting shrimps of the families Crangonidae and Pandalidae were rarely found. Besides the common remains of shrimps such as mandibles and appendages, Caridea eggs were found in some stomachs, indicating that mature females were sometimes eaten. Squires (1957) noted that short-finned squid fed on shrimps of the family Pasiphaeidae in the Newfoundland area. Among the remains of Brachyura, fragments of carapaces and appendages were frequently found in the squid stomachs, but it was not possible to identify the crabs to a lower taxonomic level.

Euphausiacea. This order was represented by two genera, *Meganyctiphanes* and *Thysanoessa*, in the feeding spectrum of short-finned squid (Table 1). Euphausiids were identified mainly by well-preserved mandibles and eyes and by fragments of appendages, carapaces, telsons and maxillae. Of all identified euphausiids, *Meganyctiphanes norvegica* was most frequently observed (95% occurrence). The squid appeared to use two different strategies in feeding on euphausiids. In certain cases, the number of sperm globules of euphausiids in the squid stomachs was 3-4 times greater than the number of eyes and 6-7 times grater than the number of mandibles, indicating that the squid bit through the abdominal region of the euphausiid and ingested much of the copulatory mechanism. In other cases, the number of eyes and mandibles in the squid stomachs was much larger than the number of fragments from the middle and posterior parts of the euphausiids, indicating that the squid ingested mainly the cephalothorax. A maximum of 114 euphausiids were recorded from a single squid stomach (see Fig. 1). Estimation of the sizes of individual euphausiids from the sizes of their mandibles indicated that, when squid preyed on dense concentrations of euphausiids, they ingested about 20–40% of the prey biomass. The remainder was probably utilized as food by benthic and near-bottom organisms.

Other crustaceans. Representatives of the orders Anisopoda and Stomatoda were recorded rarely in the stomach contents (Table 1), and the fragments did not permit identification to lower taxonomic levels.

Mollusca

This phylum was represented by the classes Cephalopoda and Gastropoda (Table 1). The latter occurred only rarely and belonged to the order Pteropoda.

Cephalopoda. This class was represented by two orders, Sepiolidea and Teuthoidea, the latter accounting for nearly all of the food mass in the short-finned squid stomachs containing cephalopod remains (Table 1). Eggs of Sepiolidea were found in one stomach. Teuthoidea was represented in the stomachs by two families (Ommastriphidae and Loliginidae). The ommastriphid *I. illecebrosus* was the dominant type in samples from the Scotian Shelf and both *I. illecebrosus* and the loliginid *Loligo pealei* were prevalent in samples taken off northeastern United States (Georges Bank to Cape Hatteras). Amaratunga *et al.* (MS 1979) found squid of the family Histioteuthidae in the stomachs of short-finned squid from the Scotian Shelf.

Fragments of mantles, arms, tentacles with suckers, gladii, beaks and lenses were frequently found in the squid stomachs. Occasionally, fragments of liver, ink sac, stomach, heart, male gonads and spermatophores were found in large prespawning females (24–29 cm ML) with stomachs completely full of recently-ingested squid. Fragments of mantles were as large as 12 x 7 mm. Although the average number of beaks found in the stomachs was two, the presence of as many as nine beaks and five pairs of lenses in individual stomachs indicated that several squid may be eaten during a single feeding period. Reconstruction of the sizes of consumed squid from their beaks, suckers, gladii, lenses and spermatophores indicated that their mantle lengths were generally 5–6 cm shorter than those of the predators.

Chaetognatha

This phylum was represented by arrow worms of the genus *Sagitta* in a few stomachs of short-finned squid larger than 13 cm ML and in most of the stomachs of 4–11 cm ML specimens (see Table 2).

Chordata (Pisces)

Fishes were represented in the stomachs of short-finned squid by five orders and nine families, of which only three were identified at the level of species (Table 1). The stomach remains consisted of vertebrae, fin rays, gill arches, jaws, lenses and soft tissues. Of the fish identified at the family level, Myctophidae (45% occurrence) and Merlucciidae (20%) were the dominant types. According to Squires (1957), the food of short-finned squid contained representatives of the families Osmeridae (*Mallotus villosus*), Gadidae (*Gadus morhua* and *Melanogrammus aeglefinus*) and Cottidae (*Triglops pingeli*).

Silver hake (*Merluccius bilinearis*) eggs were observed in four stomachs, one of which was completely full of eggs at maturity stage IV (ripening). It is quite possible that the squid had eaten a gonad which was discarded from a fishing vessel. Large fragments of spinal columns (as large as 12 x 6 mm) and guts of myctophids were found in the stomachs of squid larger than 23 cm ML. These fish guts contained mainly euphausiids and copepods. The presence of several guts, jaws, lenses and caudal fins of myctophids in a stomach indicated that the squid ate these small fish completely or almost completely. The remains of other fish species consisted mainly of pectoral vertebrae, with no guts or caudal fins being recorded. This latter observation is consistent with published reports that a squid, upon capturing a fish with its tentacles, makes some bites behind the head in the pectoral area and rejects other parts (Zuev and Nesis, 1971) or eats only the head and soft parts (Wallace *et al.*, 1981). The average number of fish found in the stomachs containing fish food was 2, with 13 being the maximum for a single stomach (see Fig. 1). Measurements of jaws, lenses, vertebrae and otoliths indicated that the approximate sizes of the consumed fish were in the range of 3–12 cm, with rare occurrence of larger fish up to 20 cm in length.

In August 1973 on the northeastern slope of Georges Bank, the author observed a short-finned squid (25–30 cm ML) attacking a 23-cm herring (*Clupea harengus*) which was placed in the water as bait. The squid, swimming backwards, circled the suspended herring three times and then changed direction and attacked the fish. The squid held and fed on the herring for 15–17 min and then released the remains and swam away. Examination of the herring showed 16 bites in the area behind the head. About 55–60 g of the fish biomass was consumed.

Feeding Spectrum of Short-finned Squid

Crustaceans (mainly euphausiids) predominated in the feeding of short-finned squid throughout the Northwest Atlantic region from the Scotian Shelf to Cape Hatteras (Table 2). They occurred in 74% of the stomachs of all 11–29 cm ML squid examined and constituted 67% by volume of the food mass in the stomachs which were more than three-quarters full of recently-ingested food. Fish and squid occurred less frequently (40 and 24%) and constituted smaller proportions of the food mass (18 and 14% respectively).

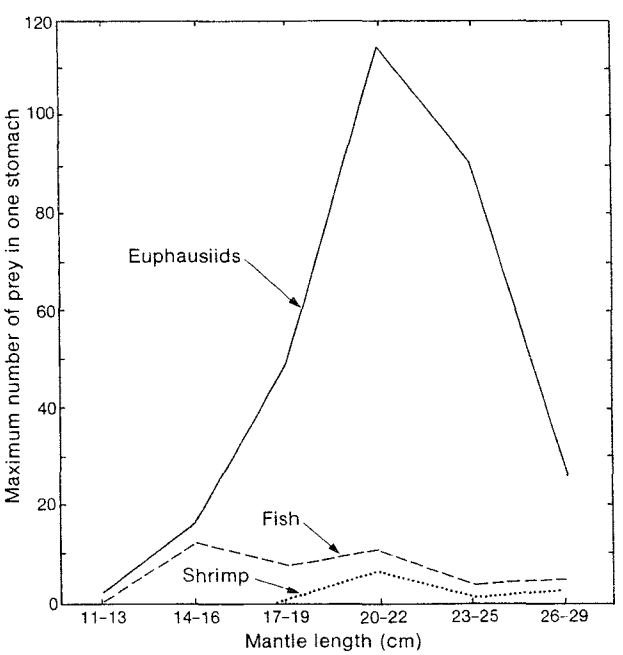

Fig. 1. Variation in maximum number of three types of prey found in the stomachs of individual short-finned squid by size group.

TABLE 2. Variation in stomach contents of short-finned squid by size-group in samples from Subareas 4, 5 and 6.

Food components	Food composition by squid size-group (cm ML)							
	4–10	11–13	14–16	17–19	20–22	23–25	26–29	11–29
Percentage occurrence of food components[a]								
Crustacea	58.8	97.4	100.0	68.8	72.9	54.0	47.2	74.1
Amphipoda	17.6	7.9	9.0	0.4	1.0	1.4	1.4	2.9
Anisopoda	—	—	1.4	—	—	—	—	0.3
Copepoda	—	—	0.5	—	2.0	2.9	2.8	1.3
Decapoda	5.9	2.6	5.2	6.1	6.1	7.2	11.1	6.3
Euphausiacea	11.8	86.8	84.8	60.6	63.7	42.4	31.9	63.0
Stomatopoda	—	—	—	0.9	—	—	—	0.2
Cephalopoda	17.6	2.6	6.7	20.8	31.9	30.2	52.8	24.1
Sepioidea	—	—	—	0.9	—	—	—	0.2
Teuthoidea	17.6	2.6	6.7	19.9	31.9	30.2	52.8	23.9
Chaetognatha	76.5	—	1.0	2.2	1.0	0.7	—	1.1
Pisces	11.8	13.2	21.0	36.8	41.7	61.2	72.2	40.0
Clupeiformes	—	—	—	—	0.3	1.4	2.8	0.5
Gadiformes	—	—	—	0.4	2.4	3.6	2.8	1.5
Myctophiformes	—	—	—	—	3.1	5.8	13.9	2.7
Perciformes	—	—	—	0.4	0.7	0.7	4.2	0.7
Fish eggs	—	—	—	0.9	0.3	0.7	—	0.4
Unidentified remains	17.6	—	1.0	2.6	—	1.4	2.8	1.2
No. of stomachs	17	38	210	231	295	139	72	985
Percentage food composition by volume[b]								
Crustacea		94.8	93.2	68.4	60.1	34.2	11.1	67.4
Amphipoda		8.3	10.4	0.6	0.2	—	—	3.2
Copepoda		—	—	—	0.1	—	—	—
Decapoda		—	2.1	3.7	1.3	2.4	0.2	2.1
Euphausiacea		86.5	80.7	64.1	58.6	31.8	10.9	62.1
Cephalopoda		0.2	0.9	16.5	20.3	27.7	19.8	14.1
Pisces		5.0	5.8	14.3	19.6	38.1	68.4	18.2
No. of stomachs		24	136	134	170	45	28	537

[a] All stomachs examined.
[b] Stomachs more than three-quarters full of freshly-eaten food.

Feeding spectrum by size

During the first 3–4 months of their life (winter and spring), young short-finned squid occur in the epipelagic and mesopelagic zones of Slope Water eastward of the continental shelf in Subareas 3 to 6. No data on feeding of larvae and juveniles less than 35 mm ML are yet available. Generally, the stomachs from such small squid were found to be empty, except for fat droplets and the remains of crustaceans and chaetognaths in a few specimens. The stomach contents of 4–10 cm ML juveniles are still being analyzed, and only some general information on their feeding is given (Table 2). The remains of chaetognaths, crustaceans (amphipods, euphausiids and shrimps), cephalopods and fish were recorded from several stomachs, with chaetognaths being the dominant food type.

On attaining sizes of 11–16 cm ML, the juveniles migrate toward the continental shelf. During this phase of growth (Table 2), they feed mainly on euphausiids (85–87% occurrence), with fish (13–21%), amphipods (8–9%), squid (3–7%) and decapods (3–5%) being rather minor components of the diet. As the squid grew in size from 14–16 to 26–29 cm ML, the occurrence of euphausiids declined from about 85 to 32%. This was accompanied by increase in the frequency of fish food from 21 to 72%, squid food from 7 to 53%, and decapods from 6 to 11%. Most of the fish remains could not be identified very specificially, but traces of clupeids, macrourids, merlucciids, myctophids, percids and fish eggs were found in the stomachs of the larger squid.

Data on the maximum number of organisms found in the stomachs by size-group indicate a rapid increase in the consumption of euphausiids as the squid grow from 14–16 to 20–22 cm ML, followed by a rapid decline for larger squid (Fig. 1). Although the maximum number of fish prey tended to decline for squid larger than 14–16 cm ML, it is evident from measurements of fish lenses (Fig. 2) that larger fish prey were consumed as the squid grew from about 17 to 29 cm ML.

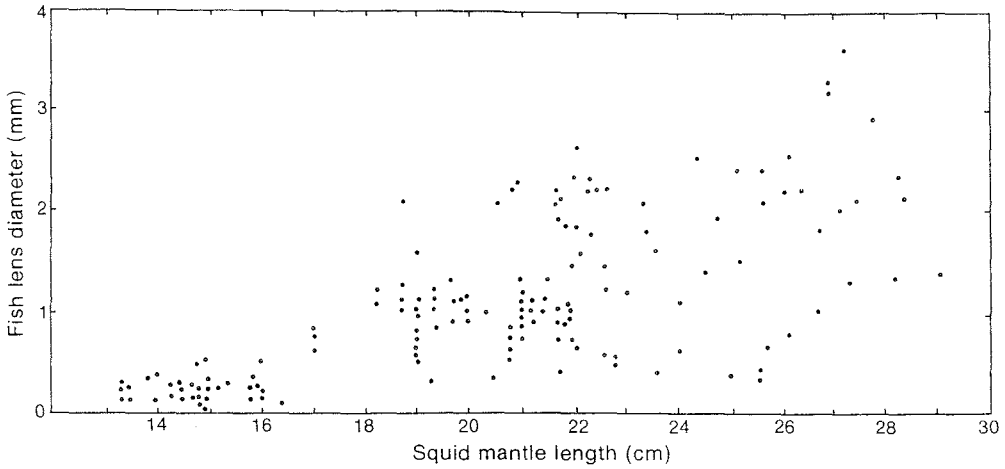

Fig. 2. Diameters of fish lenses from the stomachs of short-finned squid relative to mantle lengths of the predator.

Feeding sepctrum by season

In spring, summer and winter, euphausiids prevailed as the dominant component of the diet of short-finned squid both in frequency of occurrence and as a proportion of the food mass (Fig. 3). Fish food, which was second in importance during spring and summer, became dominant in autumn but was much less prevalent in winter. In this latter period, fish remains were observed in 30% of the stomachs but the volume did not exceed 5% of the food mass. Squid remains were present in the stomachs during all seasons but cannibalism increased in autumn and winter and was particularly evident off the United States coast where squid of all size-groups were recorded. Shrimps occurred most frequently in autumn but were rather insignificant as a component of the food mass.

Diurnal variation in feeding

The daily rhythm of feeding was studied from material collected during the period when short-finned squid are active feeders (i.e. May–October). Euphausiids predominated as food from 0400 to 2000 hr (Fig. 4). During this daylight period when light penetration of the water is greatest, euphausiids become densely concentrated in the near-bottom layer, forming a suitable food supply for *Illex*. During twilight and darkness when the euphausiids become dispersed in the upper water layers, the squid feed to a larger extent on fish. Peak cannibalism evidently occurred at night (0001–0400 hr).

Predators of Short-finned Squid

During three spring expeditions (1980–82) aimed at studying the biology and abundance of juvenile short-finned squid in the Slope Water and Gulf Stream areas of Subareas 4–6 before they migrate to the continental shelf, an attempt was made to record the predators that may be feeding on *Illex illecebrosus*. The midwater trawl catches contained none of the fish species which prey on squid. However schools of dolphins (20–30 per school) were observed occasionally along the northern edge of the Gulf Stream in March–April 1982 and schools of small whales were recorded in an area bounded by 42° 30′–43° 11′N and 46° 30′–46° 50′W in April, the largest being observed on 21 April. This school occupied an area of about 35 km², and the surface water temperature was about 15° C. Juvenile *Illex* were caught by midwater trawl in the area at depths to 500 m (Dawe *et al.*, MS 1982). It is possible that the dophins and whales were feeding on the juvenile squid, but no confirmable data were acquired. In Newfoundland waters and on the Grand Bank, pilot whales (*Globicephala melaene*) have been reported to prey almost exclusively on *Illex* during summer and autumn (Squires, 1957; Sergeant, 1962; Mercer, MS 1965). White whales (*Delphinapterus leucas*) and white-sided dolphins (*Lagenorhynchus acutus*) have also been reported to feed on squid (Vladykov, 1946; Sergeant and Fisher, 1957; Katona *et al*, 1978).

Among the fish species which have been reported to prey on short-finned squid are *Thunnus thynnus* (Butler, 1971), *Squalus acanthias* (Templeman, 1944), *Xiphias gladius* (Scott and Tibbo, 1968), *Merluccius bilinearis* and *Urophycis chuss* (Vinogradov, 1972), *Melanogrammus aeglefinus*, *Sebastes mentella*, *Pollachius virens*, and *Gadus morhua* (Dupouy *et al.*, MS 1982), and *Raja radiata* (Templeman, 1982).

The short-finned squid is an important component of the diet of seabirds. In the Georges Bank area, squid remains were found in the stomachs of six species: *Puffinus gravis*, *P. diomedea*, *P. griseus*, *Fulmarus glacialis*, *Larus marinus* and *L. argentatus* (Tsygankova, 1981, and pers. comm.). *Illex* occurred in more than 80% of the stomachs of the first three species and in

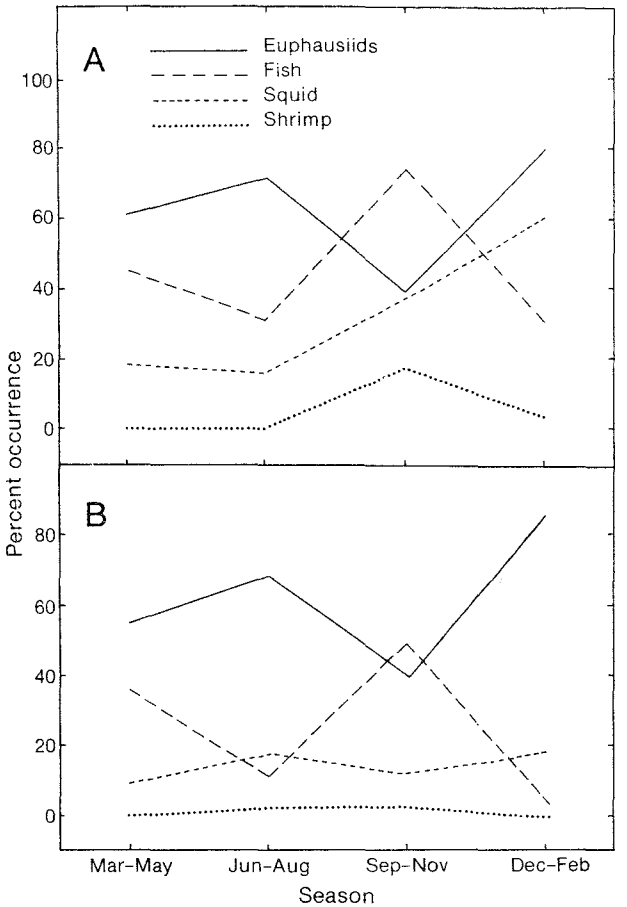

Fig. 3. Seasonal changes in feeding of short-finned squid by (**A**) frequency of occurrence and (**B**) relative volume of the food mass.

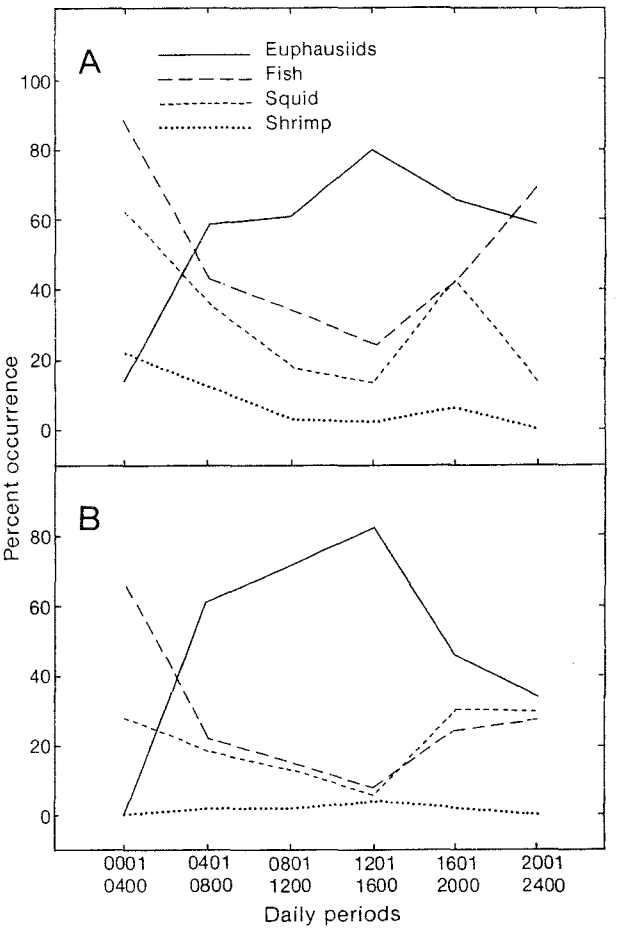

Fig. 4. Diurnal variation in feeding of short-finned squid by (**A**) frequency of occurrence and (**B**) relative volume of food mass.

70% of the stomachs of *F. glacialis* and accounted for 50–60% of the total biomass of sea organisms consumed by these birds. Squid remains (beaks only) were found rarely in the stomachs of *L. marinus* and *L. argentatus*, which may have acquired them through eating fish. In the Grand Bank area, *P. gravis*, *P. diomedea* and F. *glacialis* prey on short-finned squid (Z. K. Tsygankova, pers. comm., 1983). The maximum size of *Illex* in the bird stomachs was 18–19 cm ML, but the bulk of the squid consisted of juveniles about 11–12 cm ML. Because the above-mentioned seabirds feed from the ocean surface and do not dive deeper than a few meters, juveniles are evidently abundant in the near-surface layer of the epipelagic zone. This should be taken into account when surveys are being carried out to evaluate the distribution and abundance of juveniles.

Trophic Relations of Short-finned Squid

From about the second month of life until they die, short-finned squid function as typical predators in the epipelagic and mesopelagic zones of the open ocean and in continental slope and shelf waters. The feeding spectrum is represented by a great variety of marine organisms belonging to four phyla and 14 orders, with crustaceans, cephalopods and fishes being the important types. These are planktonic and nektonic organisms which constitute much of the pelagic (copepods, arrow worms, and larvae of amphipods, euphausiids, stomatopods, shrimps and various fishes), the near-bottom and pelagic (adult euphausiids, shrimps, young squid, and juvenile fishes), and the bottom (shrimps, crabs, etc.) complexes of the ecosystem in different parts of the distributional range of short-finned squid. During development from larvae to adults, *Illex* may feed on phytoplankton, zooplankton and fish and are thus consumers of the third and fourth trophic levels.

In the open ocean away from the shelf and slope areas, the young squid function principally as a predator of the third trophic level. At this stage of the life cycle, the squid have many potential predators, but, since these predators tend to concentrate in the shelf and slope areas, mortality of squid due to predation during their habitat in the open ocean is probably quite low.

Upon migrating to the continental slope and shelf areas, the young squid find an abundance of food items (mainly euphausiids and small fish), but there are also numerous predators of the fourth trophic level which prey on squid. The transition from one ecosystem, where squid have practically no predators and competitors, to another ecosystem, where competition for food is intense and squid are prey for many predators, very likely results in a significant increase in squid mortality. For example, when the young squid arrive on the Scotian Shelf in late spring, they encounter silver hake as a major predator and competitor. Mixed aggregations of both species feed on euphausiids and they also eat each other. As the squid grow from juveniles to maturing adults, the pattern of feeding changes and larger pelagic and near-bottom fishes, including secondary predators, become increasingly important in their diet. Simultaneously, large fish, such as cod, haddock and pollock, prey actively on squid.

A high degree of cannibalism apparently occurs in short-finned squid from time to time as indicated by the presence of beaks and other squid remains in the stomachs. It is likely that this occurs during the formation of anomalously dense aggregations and may be termed "anomalous cannibalism". Additionally, large prespawning females may sometimes eat mature males during or after copulation, as indicated by the presence in their stomachs of male reproductive organs and spermatophores, and this may be termed "forced-expedient cannibalism" (Yu. M. Froerman, unpublished data).

The unique role of short-finned squid, and perhaps other squids, in the trophic interrelationships of shelf ecosystem is that they, unlike other predators, neither swallow nor eat their prey completely. More than 50% of the prey animals killed by squid, except perhaps the smallest organisms, are discarded and these remains become food for fish and other animals which live near or on the bottom. Although the spawning grounds of short-finned squid are presently unknown and spawning has not been observed in nature, it is probable that they die after spawning and thus play an important role in the energy balance of the shelf and slope communities by the transmission of energy from the pelagic to the benthic zones.

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