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Feeding Spectrum of Longfin Squid (*Loligo pealei*) in the Northwest Atlantic and its Position in the Ecosystem*

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Abstract

The feeding spectrum of longfin squid (*Loligo pealei*) was quite diverse and changed considerably with age. Fish, squid and crustaceans were the main components of the diet, being dominant by their frequency of occurrence in the stomachs and constituting about 90% of the food mass. The feeding spectrum of juveniles (1–16 cm ML) consisted of different systematic groups of animals than that of adults (>16 cm ML). Each size-group of squid had its own optimum size of prey which varied from 4 to 24% of predator length. The amount of food consumed in a feeding was approximately 1–2% of the body weight of squid, and the number of organisms varied inversely with size of predator. Diel variation in the number of stomachs with food was great, indicating that longfin squid is a daytime predator and does not feed extensively at night. Feeding intensity was higher in summer than in winter, and the composition of the diet also varied seasonally.

Introduction

The longfin squid (*Loligo pealei*) occurs in abundance on the continental shelf from the Gulf of Maine-Georges Bank region to Cape Hatteras (NAFO Subareas 5 and 6). The squid concentrations favorable for the fishery form on the overwintering grounds in the warm water along the continental slope. With the warming of shelf water in the spring, squid migrate to shallow areas for spawning and feeding (Summers, 1971; Vovk, 1972).

Various size groups of squid in the population establish complex trophic relations with fish and other organisms on the continental shelf. Because of their great abundance, the protracted spawning period and the complexity of food relationships, longfin squid play an important role in the structure and functioning of the ecosystem on the continental shelf (Vovk, 1972, 1975). The purpose of this paper is to review the results of studies on feeding of longfin squid and ascertain its position in the ecosystem.

Materials and Methods

The data, which form the basis of this paper, were derived from field observations and laboratory analysis of squid samples from eight bottom-trawl surveys of the continental shelf off the United States between 35° N and 42° N latitude in 1968–69 and 1978, under a joint Soviet Union-United States research program. Trawl hauls (each of 30-min duration) were made at depths of 25, 50, 100 and 150+ m on the shelf and slope, and samples were collected during both day and night operations in most cases. Diurnal variation in the feeding of longfin squid was studied from 33 samples (1,331 specimens) which were obtained at 4-hr intervals during 9–19 October 1969 from catches in 50–120 m at stations off New Jersey (38° 00′N to 40° 30′N). Samples for the study of feeding by juveniles were also collected in October 1969.

The materials for the feeding studies of longfin squid were collected and analyzed according to the methods suggested by Turpaeva (1953). Observations on stomach fullness were noted for 3,791 specimens. Quantitative analysis of the stomach contents and the role of different food types in the diet were evaluated from 745 specimens. The food items, by which species-specificity was determined and the size of prey organisms reconstructed, were sketched, counted and measured. The sizes of longfin squid under study ranged from 1.2 to 32 cm ML (mantle length).

Results

Feeding spectrum

The food composition of longfin squid was quite diverse and included a variety of fishes, cephalopods, crustaceans, chaetognaths, and other invertebrates. Of major importance in the diet were fishes which belong to six families (Myctophidae, Engraulidae, young Sparidae, Clupeidae, Scombridae and Merluccidae). Cephalopods were next in importance, the dominant component being young *L. pealei* although young *Illex illecebrosus* and *Gonatus fabricii* were also found among the stomach contents. The largest variety of species was recorded for crustaceans (23 species of 6 orders): copepods (7), amphipods (3), mysids

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(2), decapods (8), euphausiids (2) and stomatopods (1). Polychaetes and chaetognaths were represented by 2 and 1 species respectively. In general, the individual stomachs contained food of mainly one type, and the dominant item in the food mass could be determined by its characteristic color: dark grey for fish, white for squid, light brown for crustaceans, and black for polychaetes.

Four major food types (fish, squid, euphausiids and shrimps, in descending order of importance) predominated by their frequency of occurrence in the stomachs (Table 1). The other groups of animals were of minor importance in the diet, the most frequently recorded groups being polychaetes and crabs. In terms of the quantity of food in the stomachs, the four types (fish, euphausiids, squid and shrimps, in descending order of importance) constituted 90% of the food mass. The remaining 10% consisted of polychaetes, crabs, copepods, mysids and arrow worms (*Sagitta*). The four major types varied seasonally in their relative importance. Squid occurred in about 50% of the stomachs during autumn and in about 35% during spring, whereas fish were recorded in about equal frequency in both seasons. Shrimps occurred in nearly half of the stomachs in spring (being the dominant group at that time) and in about one-quarter of the stomachs in autumn. Euphausiids, on the other hand, were only half as frequent in spring as in autumn.

Selective feeding

Stomachs with only one food component constituted 68% of the total number containing food, the most frequently observed components being young squid (20% of stomachs), shrimps (12%), fish (10%) and euphausiids (10%). In some cases, longfin squid of different sizes fed exclusively on cephalopods, including their own young. Cannibalism is a common phenomenon for most species of squids including longfin squid (Nesis, 1970; Vovk, 1972; Nigmãtuallin *et al.*, 1983; Macy, 1982). However, the exclusive feeding of longfin squid on their own young during a long period, as observed in the present study, has not been reported previously. It seems that young squid of various sizes, which migrate to the continental slope area in autumn, together with medium-sized and large squids, serve as a reliable source of food for the latter. The presence of a wide size range (2–32 cm ML) in the catches in October may be explained by a protracted spawning period with two or more peaks of reproduction (Mesnil, 1977).

TABLE 1. Incidence and relative volume of various food types in the stomachs of longfin squid from the Northwest Atlantic.

Class	Food type	Percent occurrence	Percent volume
Pisces	Various fishes	63.5	38.4
Cephalopoda	Squids	50.5	18.6
Crustacea	Euphausiids	43.5	21.7
	Shrimps	27.0	11.1
	Crabs	8.2	2.0
	Copepods	5.9	1.6
	Mysids	4.7	1.2
	Hyperiids	2.7	+
	Lobsters	2.4	+
	Gammarids	1.2	+
Polychaeta	Worms	10.6	4.5
Chaetognatha	*Sagitta* sp.	5.9	0.9
Unidentified remains		13.0	+

Stomachs with two food components constituted 22% of those examined, the significant items being fish, squid, euphausiids, shrimps and polychaetes. Fragments of more than two food types were recorded for 9% of the stomachs, several containing skeletal remains of five types (fish, squid, euphausiids, amphipods and polychaetes), some of which were from previous feedings. A mixed type of feeding was more indicative of medium-sized squid (10–18 cm ML) than of smaller and larger individuals.

Of 322 stomachs of juvenile longfin squid, which were collected in October 1969, 21% were empty, and fullness grades of 1, 2, 3 and 4 were recorded for 29, 30, 16 and 4% respectively. The number of stomachs without food or with small amounts (grades 1 and 2) constituted 80% of the total, indicating comparatively low feeding activity by juveniles in the autumn. This was probably associated with a deterioration of feeding conditions (shortening of daylight hours, decrease in availability and quantity of suitable food, etc.).

The feeding spectrum of juvenile longfin squid consisted of different systematic and ecological groups of animals than that of adults and changed markedly with age (Fig. 1). The smallest juveniles (1–4

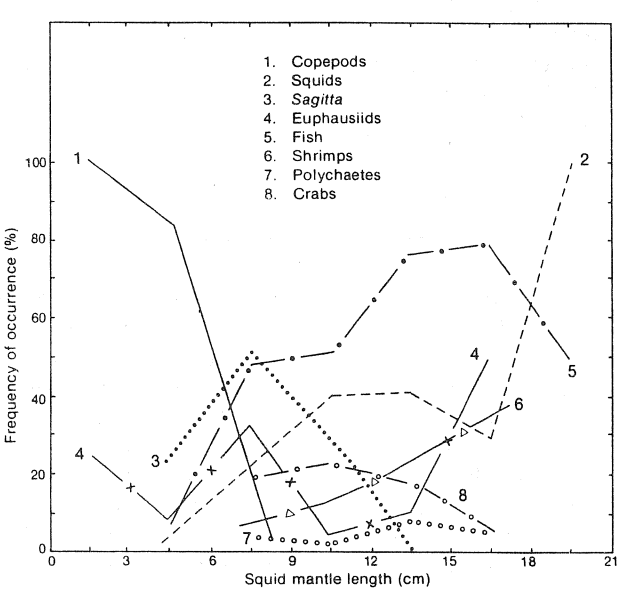

Fig. 1. Variability in feeding of longfin squid from the Northwest Atlantic with size.

cm ML) fed mainly on copepods, with young euphausiids being of much less importance (100% and 25% occurrence respectively). The copepods, ranked in descending order of their abundance as food, were *Centropages*, *Candacia*, *Gaidius*, *Calanus*, *Scophocalanus*, *Temora* and *Metridia*. These copepods are mostly large pelagic and near-bottom forms. Larger juveniles (4–8 cm ML) turn from feeding on mesoplankton to macroplankton. The occurrence of copepods in the stomachs decreased sharply and the proportions of *Sagitta* and euphausiids increased. Also, at this size range, the young longfin squid began feeding on fish larvae and exhibited a cannibalistic tendency.

Copepods disappeared completely from the feeding spectrum of 8–12 cm ML longfin squid and *Sagitta* decreased in importance. Young crabs (Brachyura and Anomura), shrimps (Natantia) and polychaetes appeared in the diet for the first time. However, young fish and squids dominated as the major components. Among the fish remains, young representatives of the families Clupeidae, Myctophidae, Merlucciidae and Gadidae were identified. The 12–16 cm ML size-group may be regarded as a transitional one toward the adult feeding type, which is characterized by the prevalence of different fish species and squids in the food mass, with other types being insignificant or disappearing altogether. The occasional feeding on concentrations of shrimps increased the apparent significance of decapods in the diet. No representatives of decapods were found in the stomachs of squid larger than 30 cm ML. The role of its own young in the feeding of longfin squid becomes more significant than that of fish for individuals larger than about 20 cm ML. A similar pattern of change in feeding of oceanic squids with size (age) was reported by Nesis (1970) and Nigmãtullin *et al.* (1983), whereby a significant change in food composition was noted when the squids were 13–15 cm ML.

Predator and prey size

Each size-group of squid has its own optimum size of prey. Copepods (*Centropages* and *Candacia*) predominated in the food of 2–6 cm ML squid and most of them were mature stages (2–3 mm in length), i.e. about 4–10% of predator mantle length. For 6–14 cm ML squid (Fig. 2), the mean prey sizes ranged from 9 to 30 mm, or 15–20% of predator length. Much of the diet of larger squid (14–28 cm ML) consisted of young fish and squid, the mean sizes of which increased from 30 to 64 mm, i.e. 19–24% of predator length.

A marked increase in the range of prey size with age (size) of predator results mainly from increased availability of larger organisms while retaining the choice of consuming small items (Fig. 2). This is associated closely with increasing opportunity of capturing larger prey with the tentacles as the predator grows, as well as with the change in size of mouth, gullet and

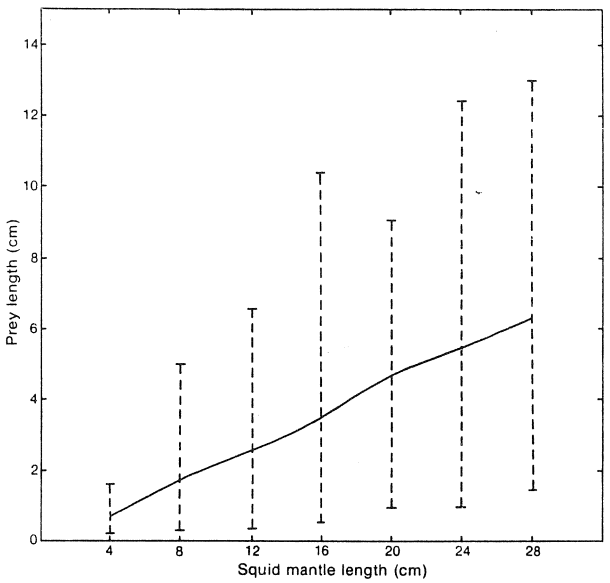

Fig. 2. Relationship between size of predator and size of prey, based on stomach contents of 52 longfin squid from the Northwest Atlantic.

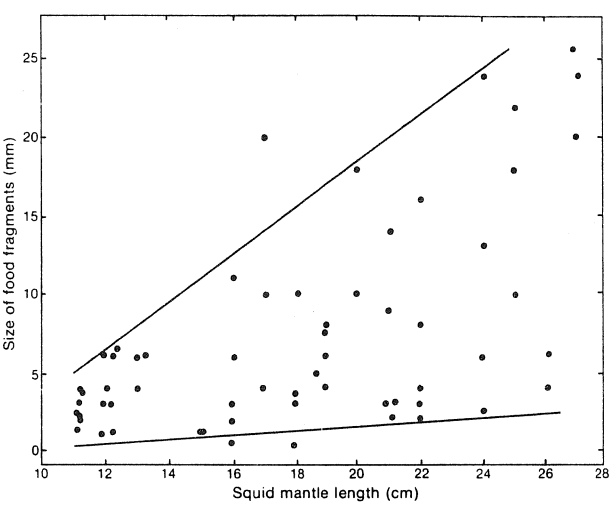

Fig. 3. Relationship between size of predator and size of food fragments in the stoamchs of 58 longfin squid from the Northwest Atlantic.

stomach. With increasing size of predators, the size of food fragments in the stomachs also increased (Fig. 3). The maximum length of a fish which was reconstructed from fragments in the stomach of a 28 cm ML longfin squid was 13 cm. According to Bidder (1950), closely related longfin squid (*Loligo vulgaris* and *L. opalescens*) may consume prey approximately equal to their own sizes.

Quantitative aspects of feeding

The contents of some longfin squid stomachs which contained only one type of food were analyzed to estimate the extent of utilization of prey by predators

TABLE 2. Variation in number and size of prey of longfin squid from the Northwest Atlantic in cases where the stomach contained primarily one food type.

Squid mantle length (cm)	No. of stomachs examined	Food types	(A) Stomach fullness index[a] (%)	No. of items in food mass		Mean prey size (mm)	(B) Recon-structed index[a] (%)	Ratio of indices (B/A)
				Mean	Max.			
3.1	2	Copepods	1.80	50	52	2.5	2.10	1.2
13.2	10	Euphausiids	1.21	35	74	18.0	2.24	1.9
16.0	1	*Sagitta* sp.	0.29	10	10	25.0	1.30	4.5
17.0	3	Shrimps	1.53	5	6	36.0	9.00	5.8
18.4	5	Fish	2.13	2.8	4	60.0	8.00	3.8
21.1	6	Squid	1.79	2.2	3	41.0	4.40	2.5

[a] Weight of food mass as percent of body weight.

of various sizes by comparing the weights of the reconstructed organisms with the actual weights of the fragments found in the stomachs, with both parameters expressed as percentages of prey weight to weight of predator (Table 2). The ratios of the reconstructed and actual indices did not exceed 2.0 for copepods and euphausiids but ranged from 2.5 to 5.8 for other food types. These differences may be attributed to less efficient utilization of prey when the squid feed on larger organisms.

The daily food diet of squids has been estimated to constitute 7-12% of body weight (Shulman *et al.*, 1983). According to Bidder (1950), it takes 4-6 hr for squid to digest the food after a feeding. Thus, the amount of food consumed in a feeding is approximately 1-2% of the squid's body weight, and the number of organisms varies inversely with predator size (Table 2). About 50 copepods make up approximately 2% of the weight of 3-4 cm ML squid, and the same number of euphausiids constitute about 2% of the weight of 13 cm ML squid. However, only 5-6 shrimps constituted a feeding for 17 cm ML squid, and 2-3 prey were found in the stomachs of larger squid which fed primarily on fish and squid.

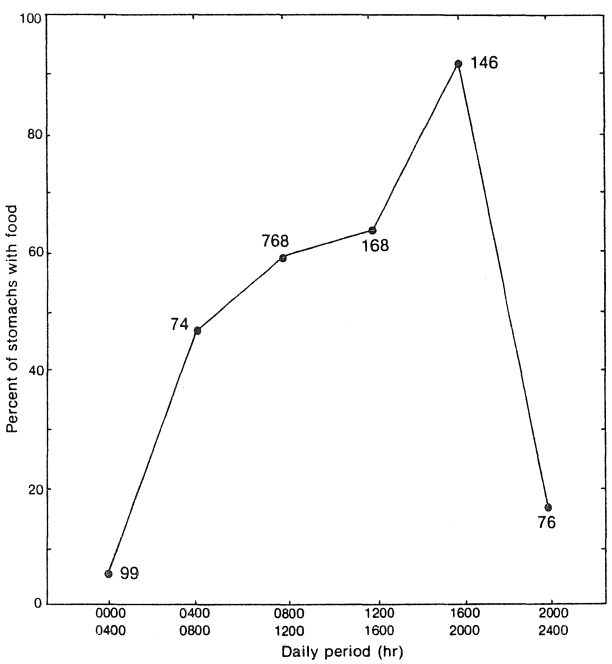

Fig. 4. Diel viariability in the feeding of longfin squid from the Northwest Atlantic. (Number of squid examined is given for each period.)

Diel and seasonal variation in feeding

Two types of variation in feeding of longfin squid have been observed, namely daily and seasonal (Vovk, 1972). Observations on 1,331 squid, examined during 4-hr intervals in October 1969, showed that feeding activity was high during daylight hours and very low at night (Fig. 4). The proportion of stomachs with food increased markedly from 5% during 0000-0400 hr to 47% during 0400-0800 hr. Feeding intensity continued to increase during 0800-1600 hr and reached a peak (92%) during 1600-2000 hr, following which there was a sharp decline to 17% during 2000-2400 hr. At times when less than 50% of the stomachs contained some food, none of the stomachs were more than half full. However, during the peak feeding period, about 30% of the squid had full stomachs. It is evident that the longfin squid is a daylight predator and does not feed extensively at night.

The second type of variation is the seasonal change in feeding activity, as indicated by observations on 2,680 stomachs during 10 months of the year (Fig. 5). There was a marked increase in feeding activity from April to August when the proportion of stomachs with food increased from 35 to 93%. A rapid decrease in feeding activity was observed during September-November when the proportion of stomachs with food decreased to 32%. During the winter (December-April), feeding activity was generally low, with more than 50% of the squid having empty stomachs (except the slight deviation in January) and the remainder with relatively small quantities of food (less than one-quarter full). Although no data were available for June and July (Fig. 5), peak feeding activity evidently occurs during the summer months. Macy (1982) observed that longfin squid feed actively in shallow waters during this period.

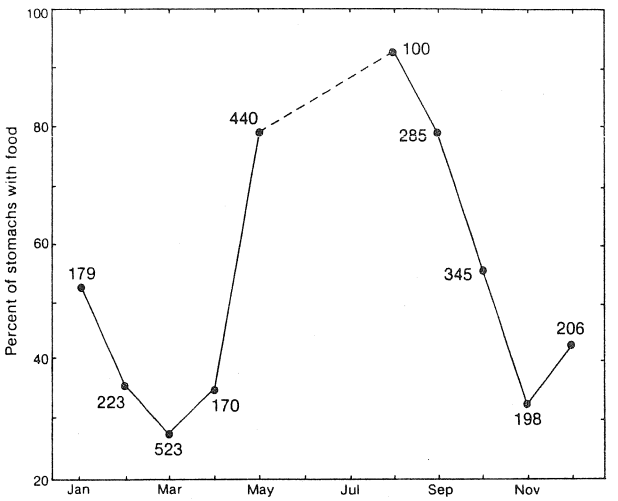

Fig. 5. Seasonal variability in the feeding of longfin squid from the Northwest Atlantic. (Number of squid examined is given for each month.)

The composition of the diet also varies seasonally, with different food items being prevalent in different months. Fish and squid were the dominant types in October, squid in November and February, euphausiids in December, shrimps and other decapods in March, and fish in April and May. These spatial-temporal changes in feeding activity and food spectrum result from changes in the size composition of the squid population, movements of squid in search of food concentrations, seasonal abundance of prey, and environmental conditions which affect both prey and predator.

Geographic variability in feeding

Shrimps and euphausiids were the prevalent food types in the diet of squid from Georges Bank in the autumn, with fish being of minor importance. There was a marked expansion in the feeding spectrum of squid in the Hudson and Witch Canyon areas at the same depth range (100–150 m), the major food types being young squid, fish and polychaetes. Fish was particularly important (up to 60% of the food mass) in the diet of squid near Hudson Canyon. In the southernmost part of the area surveyed (off Norfolk, Virginia), the number of food types in the stomachs was twice as many as in the northern areas and almost all of the types were well represented in the diet. In autumn, the stomach fullness was twice as large in squid from shallow areas as in those from the continental slope. However, there was no difference in the feeding activity of squid from coastal waters of the northern and southern regions. Similar observations were reported by Vinogradov and Noskov (1979) and Macy (1982).

Discussion

Because of their great abundance and wide distribution, longfin squid represents one of the most important elements in the trophic structure of the continental shelf ecosystem in Subareas 5 and 6 (Summers, 1971; Vovk, 1975; Tibbetts, 1977). Studies on the feeding of squid show that organisms of at least three trophic levels are present in the stomachs, namely phytophages (copepods, euphausiids, etc.), zooplankton-eaters (various young fishes, squids and other invertebrates) and predators (gadids, sparids and squids) (Vovk, 1975). In turn, squid is a favorite food of many predators belonging to the third and fourth trophic levels. Among them are gadids, skates, lambrids, tunas and sharks, as well as marine mammals and seabirds.

The relationship between squid and food organisms at the first three trophic levels mainly involves predation by squid and consists principally of vertical (predator-prey) interactions. Organisms of the first trophic level of consumers (crustaceans) are the major food items of young squid (1–10 cm ML) and partly so for medium-sized squid (11–18 cm ML). Thus, the food relations between squid and these organisms are of the predator-prey type. The most complex trophic relationships exist between squid and organisms belonging to the second level of consumers, which contains the greatest number of food groups, from predatory copepods (the main food of young fish) to relatively large fish and plankton eaters (the major food for squid). A summary of the interactions between squid and silver hake (Edwards and Bowman, 1978) may be used to illustrate the complex trophic interactions at this level. In autumn, the major food items of silver hake and squid were the same four groups of animals, namely fish, shrimps, young squid and euphausiids (Vinogradov, 1970). Hence, the silver hake and squid of different size groups, which preyed on the same food item (e.g. euphausiids), were in mutual competition. The winter aggregations of squid also coincide to a considerable extent with those of silver hake and most frequently are located on the spawning grounds of the latter. In November–April, aggregations of large silver hake (>25 cm in length) were observed off Norfolk, Virginia, at depths of 120–160 m and near-bottom temperatures of 10° to 11°C, and squid were also taken in the catches. The stomach contents of these hake consisted of squid (58%) and fish (42%). Smaller silver hake (<25 cm) fed mainly on macroplankton (Vinogradov, 1970). In this case, silver hake and medium-sized squid were competitors. In view of the common migration routes, habitat conditions, and other aspects of the two species, squid and silver hake inhabit the same areas for a long period of the year, and different size-groups of those species enter into complex relationships simultaneously as competitors for food or as enemies. The interdependence of these species is one of the factors which regulate their abundance. Disturbance of the dynamic equilibrium in abundance of one of the species, due to poor year-class survival, overfishing or other reasons, may result in increased abundance of the other.

Increased abundance of squid results in more intensive consumption of the species by predators of the third and fourth trophic levels, and this, in turn, involves a functional change in the structure of the pelagic ecosystem. Although squid and predatory fish of the third trophic level may to some extent interact as enemies, relationships in the case of silver hake are established with higher order predators (sharks and tunas). The interrelations of squid at the second and third levels are the most complex and may be of three types (predator-prey, competitor and enemies).

Differences in the food items consumed by different size-groups allow squid to be represented at all trophic levels. Small squid (2–10 cm ML), which feed mainly on plankton, belong to the second trophic level. Larger squid (11–18 cm ML) which prey on plankton-eaters and those (>18 cm ML) which feed on fish and squid belong to the third and fourth trophic levels respectively. All three types of relationships occur throughout the year because the squid population is represented by all size-groups. The structure of the food web also changes with the seasonal variability in squid feeding. Therefore, longfin squid represents one of the most important links in the transfer of energy between animals of the first two trophic levels and those of the third and fourth levels.

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