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Food Relations of Long-finned Squid, *Loligo pealei* Lesueur, in the Northwest Atlantic and its Position in Ecosystem

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#### Abstract

The ontogenetic, reproductive, seasonal and geographic variability in food spectrum of the long-finned squid on the USA shelf is shown. The information on the predators of this squid is given, and its position in the ecosystems of the Northwest Atlantic shelf and slope waters is analysed.

The long-finned squid, <u>Loligo pealei Le Sueur</u>, is a numerous species in the shelf waters between Cape Hatteras and Nova Scotia. The squid concentrations favourable for the fishery are formed on the overwintering grounds in the warm slope waters. In spring, with water heating the species migrates to the shallow waters for spawning and feeding (Summers, 1971; Vovk, 1972).

Due to a relatively short life cycle (1-2 years), protracted spawning period and presence of two populations with spawning peaks timed to the spring (peak in May) and fall (peak in August) periods the long-finned squid has a high level of survival. All the year round various size groups of squids which establish complex trophic relations with hydrocoles of the shelf waters exist in the populations.

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SPECIAL SESSION ON TROPHIC RELATIONSHIPS

Examination of feeding spectrum, its age variability, daily and seasonal rythmicities (Vovk, 1972, 1975) shows that owing to the numerous abundance, complicacy of food relations in the community, high adaptive features of populations the squid plays an important role in the formation of structure and functioning of the shelf ichthyocene (Vovk, 1975).

So, it is important to ascertain the role of existing "vertical relations" of squid, as a predator, and complex trophic relations of squid, as a competitor of fishes.

# Materials and Methods

The materials were collected during the eight trawl surveys carried out by the Soviet and U.S. research vessels under the joint program on the USA shelf between 35° and 42°N in the period from 1968 to 1978. Hauls of 30-min. duration were made by a bottom trawl at depths of 25, 50, 100 and over 150 m. Samples were collected during twenty-four hours in most cases. For studying of daily rythmicity of feeding a total of 33 samples were taken at diurnal stations within an interval of 3-4 hours.

The materials on feeding were collected and analysed according to the standard methods. Number of feeding squids was estimated in each catch and index of stomach fullness determined according to the 5-unit scale. Qualitative food composition was identified under the microscope MBS-1. Simultaneously, a biological analysis of each squid was made. The stomach fullness of 3791 specimens was analysed, and qualitative food composition identified and role of different food organisms in feeding evaluated for 745 specimens. The sizes of squids under study ranged between 1.2 and 32 cm.

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### Feeding spectrum

The feeding spectrum of squid is rather wide and includes various fish species, cephalopoda, crustaceans (copepoda, euphau-

siids, mysids, amphipoda, decapoda), chaetognaths, etc. Fishes belonging to 6 families namely Myctophidae, anchovy, young Sparidae, Clupeidae and Scombridae, hakes, sand eels (a total of 11 species) are of major importance in the feeding. In addition, juvenile squids of the same species predominate in the feeding, and young squids <u>Illex</u> <u>illecebrosus</u> and <u>Gonatus fabricii</u> are also found.

The largest species variety was recorded in the class of crustaceans: 23 species from 6. orders (7 species of copepods, 3 - amphipods, 4 - shrimps, 2 - euphausiids, etc.) (Vovk, 1972). Polychaetes and chaetognaths were represented by 2 and 1 species, respectively. Most stomachs contained food of one type, and the dominant item in the food mass could be determined according to its colour: dark-grey was characteristic of fishes, white of squids, light brown - of crustaceans, black - of polychaetes.

The four major items, such as squids, fishes, shrimps and euphausiids, predominate by frequency of occurrence in the food. A marked difference in frequency of occurrence of separate components is observed in various seasons. The squid occurred in every second stomach in fall and in every third stomach in spring. The fish was recorded nearly in equal frequency in both seasons (35 and 40%). Shrimps occupied the first place (43%) in spring and the fourth (26%) in fall. Euphausiids were found in the food half as many in spring than in fall (21 and 40%). All the other groups of animals were of minor importance in the diet. Among secondary food items copepods were most frequently recorded (5 and 14% respectively).

The occurrence of items in the stomachs does not characterize the real significance of these for the feeding. The ratio of various food items by a volume is more indicative. The occurrence and volume of food items were calculated for stomachs containing more than one component (table 1).

The fish occupy the first place by occurrence and volume. The squids are on the second place, and their significance in mixed feeding is half as much than that of fishes. Euphausiids occupy the third place and shrimps the fourth place by significance. These four groups constitute over 90% of food mass. Other animals are of minor importance in mixed feeding.

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### Change of feeding spectrum with age

<u>Feeding of juveniles.</u> Samples for feeding studies of juveniles were collected in November 1969. Of 322 stomachs 70 were empty, and 29, 30, 16 and 4% stomachs with fullness of 1, 2, 3 and 4 units respectively recorded. The number of stomachs without food or with small amount (1-2 units) constituted 80% that was indicative of a comparatively low feeding activity of juveniles in fall. This was probably associated with deterioration of feeding conditions (shortening of the daylight hours, decrease in food amount, etc.) and with peculiarities of the squid population structure in fall. A great number of juveniles of August spawning recruits to the populations (Macy, 1982; Mesnil, 1976).

The feeding spectrum of squid juveniles is represented by different systematic and ecological groups of animals, namely polychaetes, fishes, crustaceans, young squids, chaetognaths, etc. (a total of 15 items). Copepods, larval and young fishes are major food items while squids and all others are of minor and incidental importance respectively. The fish predominate by frequency of occurrence (43%). Among them are young representatives of families of Clupeidae, Myctophidae, hake, fry and juveniles of other fishes. Copepods occupy the first place by volume in the food mass. The large proportion of copepods in the diet of juveniles in comparison with the fish may be attributed to the abundant number and availability of these food items. Usually the stomach contents of squids 2-8 cm in size consisted completely of copepods (90%). According to their significance the representatives of genera of copepods were arranged as follows: Centropages, Candacia, Gaidus, Calanus, Scaphocalanus, Temora, Metridia. The representatives of 2-3 copepod species were found with obvious dominance of one of, these. Copepod eggs were recorded nearly in half of such samples, that is indicative of feeding of juveniles on the spawning concentrations of copepods. Copepods mentioned above are large,

in majority predatory, near-bottom and pelagic forms. The remains of young euphausiids and shrimps in addition to copepods were observed in every fourth stomach. So in fall the squid juveniles keep to the bottom and feed on different crustaceans.

According to the significance squid juveniles of the same species follow crustaceans and fishes, the remains of shortfin squid and representatives of Enoploteuthidae are recorded in 49 stomachs and 1 stomach respectively. All the remaining components are of little importance and may be regarded as random. The feeding spectrum and behaviour of juveniles change markedly with age (fig.1). Juveniles 1-4 cm in length feed mainly on small near-bottom organisms (copepods), and young euphausiids are of minor importance in the diet: 100 and 25% of occurrence respectively.

Squids of 4.1-6 cm in length turn from feeding on mesoplankton to macroplankton. The occurrence of copepods in their stomachs decreases sharply, and the proportion of sagittae and euphausiids increases.

Copepods eliminate completely from feeding spectrum of squids of 6.1-10 cm long, and young crabs, Anomura and Stomatopoda as well as shrimps and polychaetes appear for the first time. Young fish and squids were observed in the food mass composition of individuals 10.1-12 cm in length. Sagittae, crabs, euphausiids and shrimps are also of great importance in their diet. According to the peculiarities of the food mass the 12.1-16 cm size group may be regarded as a transitional one to the adult feeding type, which is characterized by prevalence of different fish species and squids in the food mass, however crustaceans also play a certain role in their feeding.

<u>Adult feeding</u>. Plankton and then euphausiids completely eliminate from feeding spectrum of squids of 16.1-19 cm and 19.1-23 cm in length respectively. In some cases only the representatives of decapods tend to increase their significance in the food. This may obviously be associated with feeding of large squids on shrimp concentrations. No representatives of decapods were found in the stomachs of squids above 30 cm. The role of its own juveniles in the feeding becomes higher than

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that of fishes for individuals greater than 25 cm. This difference is more clearly pronounced for squids above 30 cm long. A similar pattern of age differences in feeding of oceanic squids was reported by Nesis (1970) and Nigmatullin (1981).

So, the juveniles feed on plankton forms while with age longfin squids turn to feeding on near-bottom and then on nektonic organisms. A rather sharp change in the qualitative composition of feeding is recorded as squids attain 13-15 cm in length. In spring for squids with these sizes a marked increase in gonads is observed, and accelerated maturation of reproductive products commences. The replacement of components in the food mass becomes slower with age. The smaller sizes of animals the more rapid is such replacement. A relative stability of food item ratio in the diet is observed in feeding of squids above 16 cm in size.

# Relationship between sizes of squids and

## sizes of their preys

For each size group of squids there exists its own optimum size of preys. Copepods Candacia and Centropages predominate in the food of squids of 22-60 mm in size. Most of copepods were mature species having 2-3 mm in size, i.e. about 4-10% of the predator length.

Squids of 6.1-14 cm in size fed on young euphausiids and decapod larvae, adult euphausiids, shrimps, etc., in addition to copepods. Mean sizes of consumed organisms ranged between 9 and 25 mm. Relative sizes of preys increase and constitute about 15-20% of squid mantle length.

A considerable proportion of the diet for squids above 14 cm is represented by young fishes and young squids of the same species. Mean sizes of consumed organisms are increasing from 28 to 64 mm, i.e. 19-24% of mantle length.

A marked increase in amplitude of fluctuations of sizes of consumed animals with age of squid results mainly from increase in availability of larger organisms provided that a possibility of consuming small items remains (fig.2). This is closely associated with increasing possibility of capture larger preys with catching apparatus of predator as well as with a change in size of mouth, gullet and stomach volume. With increasing size of squids the sizes of food fragments in their stomachs increase (fig.3). Maximum length of fish from the squid stomach which was reconstructured by fragments reached 13 cm and was half the size of the predator length. Squids Loligo vulgaris and L.opalescens closely related to this species may consume preys of the same sizes as predators (Bidder, 1950).

# Quantitative aspects of feeding

According to preliminary estimates a daily food diet constitutes 3-15% of body weight (Shulman et al., 1981). The rate of food digestion by squid Loligo after one feeding is known to be equal to 4-6 hours (Bidder, 1950). So, the amount of food equal to 1-2% of squid body weight that corresponds to stomach fullness of 2-3 units is arbitrarily regarded as one portion. In this case, and better than at 1-4 units, the remains of animals, according to which eaten preys were counted, were preserved. The number of organisms including in one portion differs markedly from predators sizes (table 2).

The number of organisms forming one portion of food decreases sharply with age. About a hundred of copepods and euphausiids were found in the food of squids 3-15 cm in size whereas only a few organisms occurred in the stomachs of larger squids at the same fullness, however their body weight increased sharply.

According to the amount of organisms in one portion three groups of food items may be singled out: copepods and euphausiids - about 90 specimens; shrimps - about 10 specimens, and fishes and squids - up to 4 specimens. About 50 copepods make up approximately 2% of weight of squids 3-4 cm in length. The same amount of euphausiids was sufficient to constitute 2% of weight of the 11 cm squid. For squids of these sizes the number of shrimps required is 5-10 times lesser. One portion of adult squids feeding on shrimps and fishes consists of only 2-3 specimens.

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To reveal the use of prey by squids a ratio between reconstructured weights of consumed organisms and virtual weight of these organisms in the stomach was analysed. This index does not exceed 2 for copepods and euphausiids while reconstructured weights of other food groups exceed the virtual weights by 2.5-5.8 times. These differences may be attributed to the fact that as squids turn to feeding on larger animals the food items are less rationally utilized by squids.

Some parts of a prey (shrimp carapace, fish head and bones, etc.) are rejected by squids. The leavings are greater in eating of the fish than in consumption of squids. In most cases small crustaceans are completely consumed. Approximate estimate of number of consumed animals permits to calculate in future a daily diet for squids of different sizes. For juveniles <u>Sepietheutis</u> daily diet is known to constitute about half of animal weight (LaRoe, 1971).

On electivity of feeding. The squids with only one component found in the food constituted 68% of total number. Squid juveniles (20%), shrimps (12%), fishes (10%) and euphausiids (10%) were most frequently observed in feeding. In some cases the squids of different sizes fed exclusively on young cephalopods. Cannibamajority species of squids lism is a common phenomenon for including the long-finned squid (Nesis, 1975; Nigmatullin, 1981; Vovk, 1972). However, the feeding exclusively on young squids of the same species during a long period is observed for the first time. It seems that young squids of various sizes shifting to the continental slope area in fall, together with medium-sized and .... large squids, serve as a reliable source of food for the latter. The presence of squids with a wide size range (2-32 cm) in the catches in October may be explained by the protracted spawning period, by the presence of two peaks of reproduction (Mesnil, 1976).

Two components in the food were found in 22% of squids. The items were arranged by significance as follows: fish, squid, euphausiids, shrimps, polychaetes. The fragments of more than two items were recorded in the other stomachs (9%). Several stomachs contained skeletal remains belonging to 5 various items,

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namely fish, squids, euphausiids, amphipoda and polychaetes. Some of these items are the remains of previous food intake.

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The prevalence of uniform food in the stomach food mass indicates that the squid shows preference to one item which is the most numerous and available at a given moment although other food items have been recorded in great numbers in plankton and trawl catches from this area.

A mixed type of feeding is more indicative for medium-sized squids of 10-18 cm than for juveniles and large individuals.

### Rhythm of feeding

Two types of rhythm, namely daily and seasonal, may be singled out in squid feeding. The following pattern is observed in the daily rhythm (fig.4). Just 5% of stomachs contains food remains in the period from 0.00 to 6.00. Later, from 4.00 to 8.00 the number of stomachs containing food increases markedly, however every second stomach is to be empty. The degree of stomach fullness did not exceed 1-3 units. Up to 16.00 the feeding activity slightly increases although the specimens with stomach fullness in 4 units appear. From 16.00 to 20.00 the number of specimens with empty stomachs considerably decreases and constitutes about 8%. The greatest number of fed individuals (up to 30%) is recorded at this period. After 20.00 the number of stomachs containing food sharply drops and does not exceed 17%.

It may be affirmed that the squid is a day predator with main period of feeding activity reaching the maximum from 16.00 to 20.00. The feeding activity sharply drops in the night-time.

The second type of rhythm is the change in the feeding activity throughout a year (fig.5). A marked increase in feeding activity is observed between April and August. During this period the number of individuals with empty stomachs decreases by nearly 10 times (from 70 to 7%).

It seems that the peak of activity occurs in June-July (no data available), in any case, squids feed rather actively in the shallow waters in the summer months (Macy, 1982). The decrease in feeding activity is observed in September-November. At this period the number of fed specimens decreases to 2% while the amount of squids with empty stomachs increases to 68% by November. In the winter period (December-March) the degree of feeding activity is found to be nearly at the same level with insignificant deviation in January. At this time the number of squids with empty stomachs constituted more than half, while the stomachs with fullness in 1-2 units prevailed for the rest of squids.

From the pattern of changing of feeding activity of squids throughout a year three periods may be singled out: a) increase in feeding activity from April to August; b) a marked decrease in activity in fall (September-November); c) a relatively stable low activity in winter (December-March).

The highest activity of squid feeding is observed during the period of large length of the day-light hours and the highest light intensity in the year. The feeding activity decreases with decrease in light intensity in fall. In the winter period bad meteriological conditions and short day-light period are the most unfavourable for squid feeding. The influence of the light intensity factor on squid feeding activity is most probably realized through food items decreasing their availability. The impoverishment of food supply in the winter period results in local distribution of squids in canyons and migration of their aggregations along continental slope.

The food composition varies with feeding activity. For each month one or two food items prevailing in the feeding may be singled out. The fish and squids were used as a favourite food in October, squids in November and February, euphausiids in December, shrimps and other decapods in March, and the fish prevailed in April-May. These spatial-temporal changes in feeding activity and spectrum are stipulated by age peculiarities of population structure, by movements of squids in search of food patches, by ecology of food items, by hydrological conditions of environment, etc.

#### Geographic variability in feeding

#### spectrum

Shrimps and euphausiids were prevalent food items in the squid diet on Georges Bank in fall while the fish were of minor importance. The feeding spectrum of the squid markedly expands in the south in the areas of Hudson-Witch canyons at the same depths

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(100-150 m). Of major items the proportion of shrimps and euphausiids in the diet decreases due to increase in proportion of young squids, fish, polychaetes, etc. The importance of the fish (up to 60% of the food mass volume) for the feeding markedly increases especially near Hudson canyon.

Almost all the food items found were equally represented in the squid diet in the southernmost part of the area, near Norfolk. The amount of items in the feeding of squids from the southern regions is twice as large than that from the northern regions.

In fall the squid stomach fullness was twice as large in the shallow waters than in the continental slope waters. However, no difference was observed in the activity of squid feeding in the coastal waters of the northern and southern regions. Similar data were presented in Macy's paper (1982).

The following trend of geographic variability in the feeding of squids from the area under studying may be noted: a) in fall with migration along the slope to the south a marked expansion of feeding spectrum is observed at nearly equal degree of activity recorded in all the regions;

b) the squid feeding activity was twice as large in the shallow waters (up to 75 m) than in the continental slope waters;c) the squid feeding activity decreases with increase in the habitat depth.

#### Squid position in the ecosystem of pelagial

Owing to its numerous abundance and wide distribution the long-finned squid is of great importance in the biological interrelations and is one of the most important elements in the trophic structure of the shelf water biocenoses (Vovk, 1975; Summers, 1971; Tibbets, 1977). However, it is not ascertained yet how great is this role. Some trophic relations of the squid were analysed, and an attempt was made to evaluate its role and position in the ecosystem. The data on squid feeding on the one hand and on feeding of fishes and other animals preyed on the squid on the other hand were used. Among the items in the squid feeding are the organisms of at least three trophic levels, namely phytophagan (copepods, euphausiids, etc.), zooplankton-caters (various groups

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of invertebrates, young fishes and squids, plankton-eating fishes, etc.) and predators (young gadoids, sparids and squids) (Vovk, 1975).

In its turn the squid is a favourite food item for predators belonging to the third and fourth trophic levels. Among them are the representatives of gadoids, skates, Labridea, tunas, sharks, etc. as well as marine mammals and seabirds. A total of about 40 species are recorded according to our data.

A pattern of these interrelations at each level will be illustrated below by separate examples. The relationships between the squid and food items at the first three trophic levels are mainly connected with the predation by squid and attributed principally to vertical interrelations. The organisms of the first trophic level of consumers (crustaceans) are the major food items for young squids (2-10 cm) and partly for medium-sized squids (11-18 cm). So, the food relations between squid and these items are highly substantial, and form according to a predator-prey type. The most complex trophic interrelations are observed between squids and animals belonging to the second level of consumers. The greatest number of food groups for the squid is found there: from predatory copepods, the major food for fry, to relatively large fishes-plankton-eaters, the major food for large squids. A scheme of food relations between the squid and hake may exemplify the complex trophic interrelations at this level (Edwards, Bowman, 1978). In fall the major food items for silver hake and squids were the same four groups of animals, namely, fishes, shrimps, young squids, euphausiids (Vinogradov, 1970). Hence, the hake and squids of different size groups preying on the same item, e.g. on euphausiids, were in competitive relationships.

The winter-autumn aggregations of squids are to a considerable extent coincided with those of hake and most frequently kept to the spawning grounds of the latter. So, the hake is of great importance in the composition of the fish ration of the squid. In November-April large hakes of above 25 cm in length were observed in the Norfolk area. The hake aggregations were recorded at depths of 120-160 m and water temperature of 10-11° near the bottom. In the same place the squids were observed in the

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catches. The major food items for this hake were represented by squid (58%) and fish (42%). Immature individuals of silver hake below 25 cm in length fed mainly on macroplankton (Vinogradov, 1970). In this case hakes were the competitors for medium-sized squids. The competitor for large squids was large mature hake.

Taking into account the common migration routes and habitat conditions, and other peculiarities of biology both species keep together during a long period of the year and different size groups of these species enter into the complex trophic interrelations as competitors for the food and as enemies simultaneously. This fact increases the interdependence between these species and is one of the factors affecting the regulation of their abundance. The disturbance of dynamic equilibrium in abundance of one of the species due to either a poor year class or overfishing or other reasons may result in the outbreak in the abundance of the other.

The increase in the squid abundance necessarily results in the more intensive consumption of the squid by predators from the third and fourth levels and this entails the functional change in the structure of ichthyocene. Due to a complex food relations at each trophic level, food chains should be regarded as a "food web". While the squids and predator fishes from the third trophic level may to some extent have interrelations (reverse) as enemies, in the case of silver hake, trophic interrelations are established with predator of the higher order (sharks, tunas) according to the "predator-prey" type. These food relations of the squid are more pronounced at the ends of food chain of the first and fourth trophic levels. The interrelations of the squid at the second and third levels are the most complex and may be established according to the type "predator-prey" (vertical relations), "competitor for a food" (horizontal relations) and "enemies" (reverse relations).

Age peculiarities of the squid feeding allow the squids to be simultaneously at all the trophic levels. The individuals 2-10 cm in size feeding mainly on plankton belong to the second trophic level. The squids of 11-18 cm long preying on plankton-eaters and large squids of above 18 cm feeding on the fish and squids be-

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long to the third and fourth trophic levels, respectively. The mentioned types of trophic interrelations of squids occur all the year round because the squid population is represented by all size groups. The structure of food web changes with seasonal variability in the squid feeding.

The long-finned squid is one of the most important links in the transformation of energy between organisms from the first two trophic levels and animals from the third and fourth levels. Animals belonging to the last links of the food chain are usually large predators and valuable fishing objects.

### Conclusions

The four types of feeding spectrum for the long-finned squid may be singled out in the process of ontogenesis:

a) postlarval (1.1-8 cm) - multi-component composition of the food mass with predominance of small mesoplankton organisms (copepods - dozens of specimens), food intake is frequent;

b) juveniles (8.1-12 cm) - variety of food groups of nearbottom and pelagic complex with prevalence of macroplankton crustaceans and young fishes, the food portion is of 5-20 specimens;

c) transitional (12.1-16 cm) - the fish and squids prevail in the food diet, and euphausiids are present, the feeding takes place from time to time;

d) "adult" (above 16 cm) - micronektonic forms, fishes and squids are predominant food items, the food portion is of 1-3 specimens, rare food intake is observed.

So, with age the squid turns from the chase type of grazing predator to that of attacking predator. A ratio between sizes of preys and squids varies markedly with age and constitutes about 4-10% for juveniles and 20-25% for squids above 15 cm.

During the life history the squid belongs successively to a consumer of the second, third and fourth levels. At early growth stages the juveniles function as a competitor of plankton-eating fishes and other animals, and then of young near-bottom fish species, and at last the species compete with pelagic predators.

The squid is an important food item for majority commercial fishes and other animals (birds, mammals) in the Northwest Atlantic.

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Table 1 Food composition of Loligo pealei

Food item	Occurrence, %	Volume, %	Food item	Occurrence %	Volume %
Fish	63.5	38.4	Sagittae	5.9	0.9
Squids	50.5	18.6	Copepods	5.9	1.6
Euphausiids	43.5	21.7	Mysids	4.7	1.2
Shrimps	27.0	11.1	Hyperiids	2.7	+
Nonidentified remains	1 13.0	+	Lobsters 2.4		
Polychaetes	10.6	4.5	Gammaridae	1.2	+
Crabs	8.2	2.0			

Table 2 Change in number of preys with squid age

Squid sizes, cm			x or- ga- nisms	size of preys mm	Reconst- ructured index, <sup>5</sup> %		No.of stomachs examined
3.1	Copepoda	180	50/52/	2.5	210	1.2	2
13.2	Euphausiids	121	35/74/	18.0	224	1.9	10
16.0	Sagittae	29	10/10/	25.0	130	4.5	1
17.0	Shrimps	153	5/6/	36.0	900	5.8	3
18.4	Fish	213	2.8/4/	60.0	800	3.8	5
21.1	Squids	179	2.2/3/	41.0	440	2.5	6

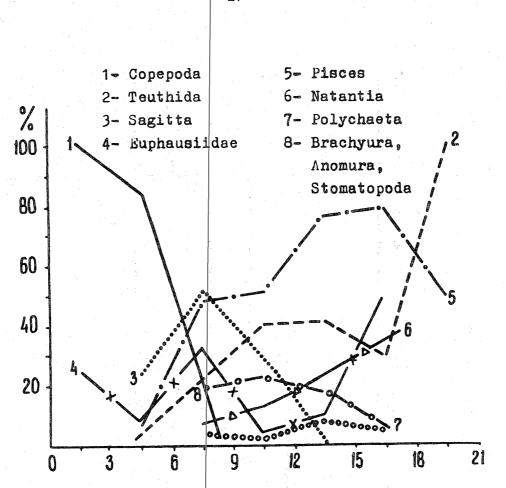
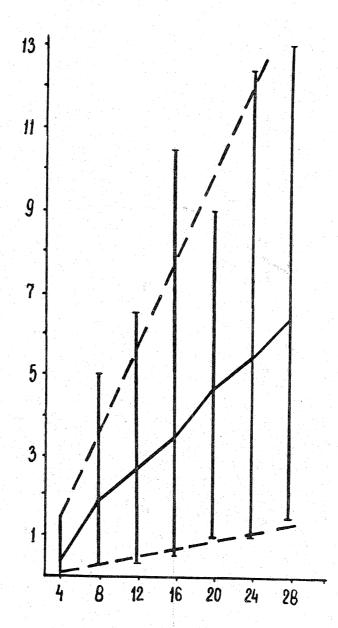
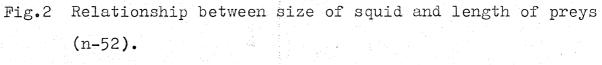


Fig.1 Age variability in feeding of squid juveniles. Horizontal scale - mantle length, cm Vertical scale - percent of occurrence of food components,

%

- 17 -





Horizontal scale - mantle length, cm Vertical scale - length of preys, cm

- 18 -

