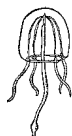


# DISTRIBUTION AND GROWTH IN JUVENILES OF THE SQUID *BERRYTEUTHIS MAGISTER* (CEPHALOPODA, GONATIDAE) IN THE WESTERN BERING SEA

ALEXANDER I. ARKHIPKIN, VYACHESLAV A. BIZIKOV & ANDREY V. VERKHUNOV

## SARSIA



ARKHIPKIN, ALEXANDER I., VYACHESLAV A. BIZIKOV & ANDREY V. VERKHUNOV 1998 03 13. Distribution and growth in juveniles of the squid *Berryteuthis magister* (Cephalopoda, Gonatidae) in the western Bering Sea. – *Sarsia* 83:45-54. Bergen. ISSN 0036-4827.

Seasonal distribution, size composition, age structure and growth of *Berryteuthis magister* juveniles (mantle length from 20 to 130 mm) were studied in the western Bering Sea (from 170°E to 179°W) between June and October 1994. According to the analysis of 1030 statoliths, the juveniles hatched from December to June with a peak in February and March. Growth data for different seasonally hatched groups were best fitted by an exponential function, summer-hatched juveniles demonstrated the fastest growth. *B. magister* attained the length at which it recruits (130 mm mantle length) at an age ranging from 140 to 200 days. Comparison of variability of both juvenile age structures and geostrophic currents in the region revealed that the Eastern Bering Slope Current (EBSC) was the main carrier of *B. magister* juveniles from the spawning grounds to the western Bering Sea. Seasonal variability of the EBSC determined the differences in juvenile migratory patterns. During its intense stage in May-June, the EBSC transported winter-hatched and spring-hatched juveniles first to the eastern part of the region and then westward along the slope. During its relaxed stage in July-September, the EBSC carried spring- and summer-hatched juveniles across the deep-water part of the Aleutian Basin directly to the western part of the region.

Alexander I. Arkhipkin, Atlantic Research Institute of Marine Fisheries and Oceanography (AtlantNIRO), 5 Dm. Donskoy street, Kaliningrad, 236000, Russia. – Vyacheslav A. Bizikov & Andrey V. Verkhunov, All-Russian Research Institute of Fisheries and Oceanography (VNIRO), 17 V. Krasnoselskaya street, Moscow, 107140 Russia.

KEYWORDS: Distribution; growth; squid; *Berryteuthis magister*; statoliths.

## INTRODUCTION

The gonatid squid *Berryteuthis magister* (BERRY, 1913) is one of the most abundant squids in the northern North Pacific, exploited commercially by Russian and Japanese bottom trawl fisheries (KASAHARA & al. 1978; FEDORETS 1986). Its distribution range coincides with the North Pacific Subarctic Gyre except the Sea of Japan, where an isolated subspecies of *B. magister* is found (NESIS 1987; OKUTANI & al. 1988). Many aspects of the biology of *B. magister* adults, such as distribution, feeding, size composition, and gametogenesis have been well studied (NAITO & al. 1977; KUZNETSOVA & FEDORETS 1987; OKUTANI & al. 1988). It has been shown that the population structure of *B. magister* is complicated and usually consists of either two or more size groups, which are believed to belong to several different annual cohorts (NATSUKARI & al. 1993). Estimations of the life span of *B. magister* determined by different methods vary from two years (YUUKI & KITAZAWA 1986; NESIS 1989; ARKHIPKIN & al. 1996) to four years (NATSUKARI & al. 1993). However, data on biology of *B. magister* paralarvae and juveniles remain scarce.

KUBODERA & JEFFERTS (1984) have revealed the general scheme of paralarvae distribution in the Northwest Pacific. ARKHIPKIN & al. (1996) have published the first results on age structure of *B. magister* juveniles caught in the western Bering Sea.

The habitat and vertical migrations of *B. magister* are well known only for adult squids. In the warm season (summer-autumn), slope and deepwater parts of the Bering Sea consist of four main water layers: surface warm mixed layer (depth ranging from 0 to 30-80 m), subsurface cold layer (from 30-80 to 200-250 m), intermediate warm layer (from 200-250 to 750-800 m), and deep-water cold layer (below 800-1000 m) (ARSENYEV 1967). Both in the Bering Sea and around the Kurile Islands, aggregations of adults are usually encountered in the intermediate warm layer near bottom in the daytime. At night, adults disperse throughout the water column up to the thermocline (FEDORETS 1979; 1983). KUBODERA & JEFFERTS (1984) have found *B. magister* paralarvae up to 30 mm mantle length (ML) in the surface warm layer. On the basis of data from pelagic and bottom trawl surveys in the Sea of Okhotsk, NESIS (1989) has proposed that *B. magister* juveniles become

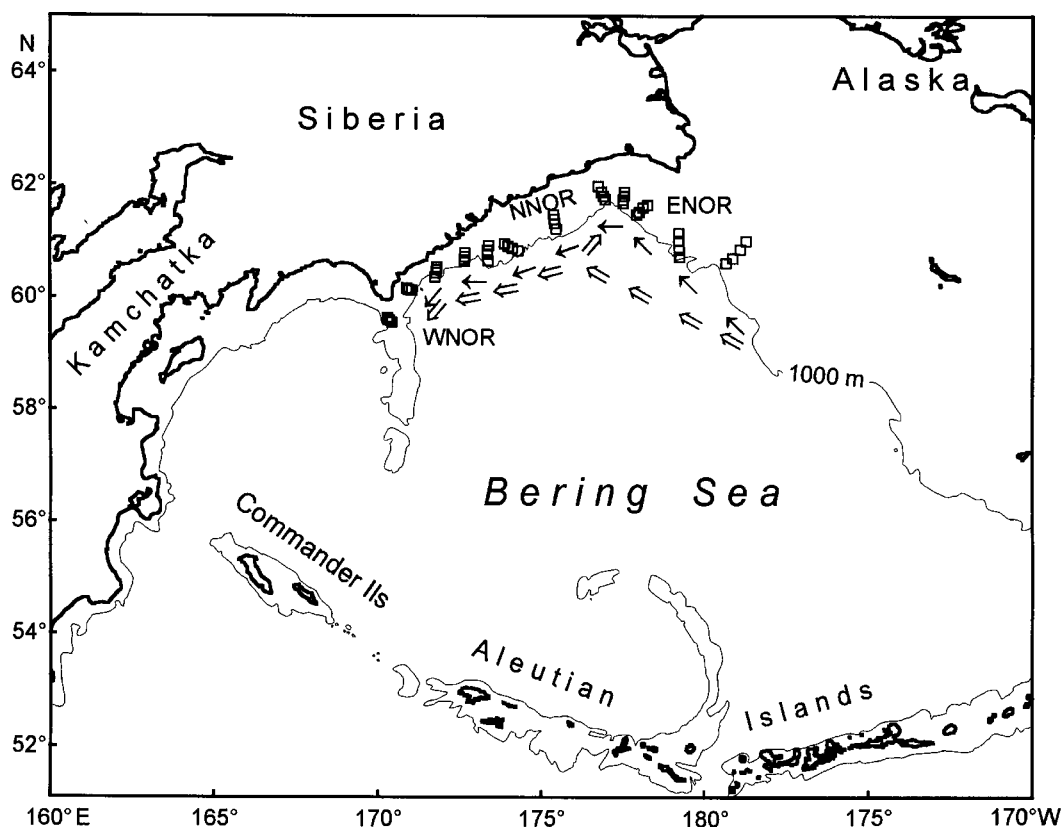


Fig. 1. Location of samples of *B. magister* juveniles (empty rectangles) in the Western Bering Sea. WNOR, NNOR and ENOR - western, northern and eastern parts of the Navarin-Olyutorsky Region. Schematic position of the intense (arrows) and relaxed (double arrows) phases of the Eastern Bering Sea Current (according to VERKHUNOV 1996).

vertically migrating like adults when they reach a mantle length  $> 140\text{--}160$  mm. However, he has noted that the smallest ML of *B. magister* from the bottom trawl catches was 46 mm (NESIS 1989). FEDORETS (1986) and NESIS (1995) have reported that juveniles with ML ranging from 40 to 120 mm have usually been found in bottom trawl catches at depths 300–450 m in the Bering Sea. GORBATENKO & al. (1995) noted that during a pelagic survey in the western Bering Sea in autumn, *B. magister* juveniles (ML from 38 to 78 mm) were found in the pelagic layer above the outer shelf and slope only at night (from 20.00 to 04.00) and disappeared from catches (descend to the near-bottom layer?) in the daytime. Thus, it is likely that juveniles start vertical migrations at smaller sizes (38–50 mm ML) than has been considered by NESIS (1989).

It is known that oceanic currents are the main carriers of paralarval and juvenile squid from their spawning grounds to feeding grounds (TRITES 1983; ROWELL & al. 1985). In the Bering Sea, the Slope Current System may be important for transport of *B. magister* paralarvae

and juveniles. It includes the Eastern Bering Slope Current (EBSC), or Bering Slope Current (after KINDER & al. 1975), and Kamchatka Current (ARSENYEV 1967). Interannual and seasonal variability of these systems is still poorly studied (VERKHUNOV & TKACHENKO 1992; VERKHUNOV 1995).

The purpose of the present article is to describe the size composition, age, and growth of *B. magister* juveniles occurring in the western Bering Sea in summer and autumn, and to study possible effects of oceanic currents on their migrations.

## MATERIAL AND METHODS

### *Squid sampling*

Squids were collected during four bottom trawl surveys (90 hauls) between June and October, 1994, performed by Japanese fishery trawlers *Tenryu-Maru N 57* and *Kayo-Maru N 28*. Each survey consisted of 10 transects conducted above the continental slope of Siberia from Cape Olyutorsky to Cape Navarin (Fig. 1). Each transect included three one-hour hauls

made at depth ranges of 190–250, 370–450, and 600–700 m in the daytime. The Japanese commercial bottom trawl with a horizontal opening of 42 m, vertical opening of 6 m and double mesh at the distal end of the cod-end (mesh size 70 mm) was used during the surveys. Hauling speed was 7.4–8.3 km/h. Squids were also sampled between the surveys from 22 commercial trawls of 3 to 9 hr duration.

*B. magister* juveniles (ML ranged from 20 to 130 mm) were taken both from the mesh and cod-end of the trawl. Their abundance was roughly estimated as number of specimens found in one trawl, using the following three categories: tens, hundreds and thousands. Sex of *B. magister* can rarely be determined by eye in specimens of ML < 130 mm. Therefore, *B. magister* with ML from 20 to 130 mm were considered as juveniles, and analyzed apart from adults (ML > 130 mm). As the catchability coefficient of the commercial trawl with a large mesh size varied for the juveniles of different size groups, the samples of juveniles could not be used for precise length-frequency analysis. In spite of this, as the probability of catching the same size groups of squids was always the same, it was possible to analyze relative abundance and frequencies of juveniles belonging to this size group in different regions and seasons. These data can be used for a qualitative analysis of juvenile distribution, as the appearance of a given size group in catches apparently reflects its appearance in the sampling region. Disappearance of the given size group could mean either its disappearance from the region or, for the large-size groups, their growth beyond ML 130 mm when they start to be analyzed as adults.

Some data on *B. magister* juveniles were also obtained from the stomach content analysis of halibut caught in the Navarin-Olyutorsky region (NOR) between September and October at depths ranging from 350 to 550 m. In total, 319 stomachs were analyzed, including 121 stomachs of the Pacific blue halibut (*Reinhardtius matsuurae*), body length (BL) from 440 to 830 mm (mode 640 mm); 95 stomachs of the Pacific white halibut (*Hippoglossus stenolepis*, 310 to 1650 mm BL (mode 730 mm) and 103 stomachs of the arrow-toothed halibut (*Atheresthes evermanni*, 300 to 950 mm BL (mode 540 mm).

To compare the near-bottom distribution of *B. magister* juveniles with that from mid-water, data on *B. magister* occurrence were analyzed from by-catches of 92 walleye pollock trawls made in the northern part of the Bering Sea (60°00'N–60°30'N; 179°00'E–178°30'W) in July. The hauls were made using commercial mid-water trawls (horizontal and vertical opening about 96 m) at an average speed of 8.3 km/h over depths ranging from 180 to 3100 m. The hauling depth varied from 40 to 300 m; duration of hauls ranged from 4 to 10 hours (average 8 hours).

### Size-frequency and age sampling

A random sample of one hundred juveniles was taken from each catch during the survey. All squids were analyzed if the total catch was < 100 specimens. Dorsal mantle length (ML) was measured to the nearest 1 mm. A total of 2167 juveniles were analyzed. Size-frequency histograms were plotted by pooling the catches together over each calendar month and separately for three subregions: western (WNOR, 171°00'E–175°30'E), northern (NNOR, 175°30'E–177°30'E) and eastern (ENOR, 177°30'E–180°00'E) parts of the NOR (Fig. 1).

The subregions were determined on the basis of differences observed in the size and age structure of juveniles in catches.

Age, growth and stock structure of juveniles were studied using statolith aging techniques (DAWE & NATSUKARI 1991). Statoliths were sampled and analyzed separately for different months and subregions. Each sample consisted of statoliths from 50–100 squids including 5–10 specimens for every 1-cm size class of ML. In June and August–October, samples were taken in the WNOR, NNOR and ENOR; in July – only in ENOR. A total of 1085 statoliths were sampled. They were washed in distilled water and placed for several days in 96 % ethanol for further examination on board ship.

### Statolith processing and reading

To study statolith microstructure, one statolith from each pair was attached with the concave (anterior) side up on a microscopic slide with Pro-texx mounting medium and ground on wet 1000-grit sandpaper. One side of the ground statolith was coated with a drop of glycerin and covered with a cover glass. Growth increments were examined under a compound microscope (Nikon 104) at 400x. From the total sample, 1030 statoliths were successfully read (94.9 %).

Earlier, daily deposition of the second-order growth increments within *B. magister* statoliths was validated by two independent methods (ARKHIPKIN & al. 1996). Moreover, during examination of statoliths from paralarvae and early juveniles of *B. magister* it was shown that the first check ('natal ring') was deposited not at hatching (as in NATSUKARI & al. 1993), but during the paralarval stage (in paralarvae 5–6 mm ML) (ARKHIPKIN & BIZIKOV in press). Hence, we counted only the second-order growth increments using an eye-piece micrometer (DAWE & NATSUKARI 1991) from the nucleus to the lateral part of the rostrum and further within the rostrum (ARKHIPKIN & al. 1996). Total number of growth increments for each specimen was considered to be equal to the age in days of squid, provided the mean of two counts by different readers did not deviate from individual counts by more than 5 %. Hatching dates were back-calculated. Hatching months were determined by grouping of squids over month of hatching (e.g. squids hatched from 1 to 30 September were regarded as the September-hatched squid etc.). It should be noted that squid grouped into different monthly groups of hatching are not separate monthly cohorts, but only temporal parts of continuous hatching. This grouping was done for further comparison of age structures of juveniles both in different regions and seasons. Growth data were analyzed separately for squids hatched in each of three seasons: winter (December–February), spring (March–May) and summer (June–August). Length-at-age data were fitted to each of five standard growth models (exponential, power, logistic, Gompertz and von Bertalanffy) using the method of iterative nonlinear least squares, and the curve with best fit was chosen. Daily growth rates (DGR) and instantaneous rate of growth (G) were calculated after RICKER (1958):

$$\begin{aligned} \text{DGR} &= (M_2 - M_1) / T \\ G &= (\ln M_2 - \ln M_1) / T \end{aligned}$$

where  $M_1$  and  $M_2$  are mantle length (mm) at the beginning and end of the time interval;  $T = 30$  days.

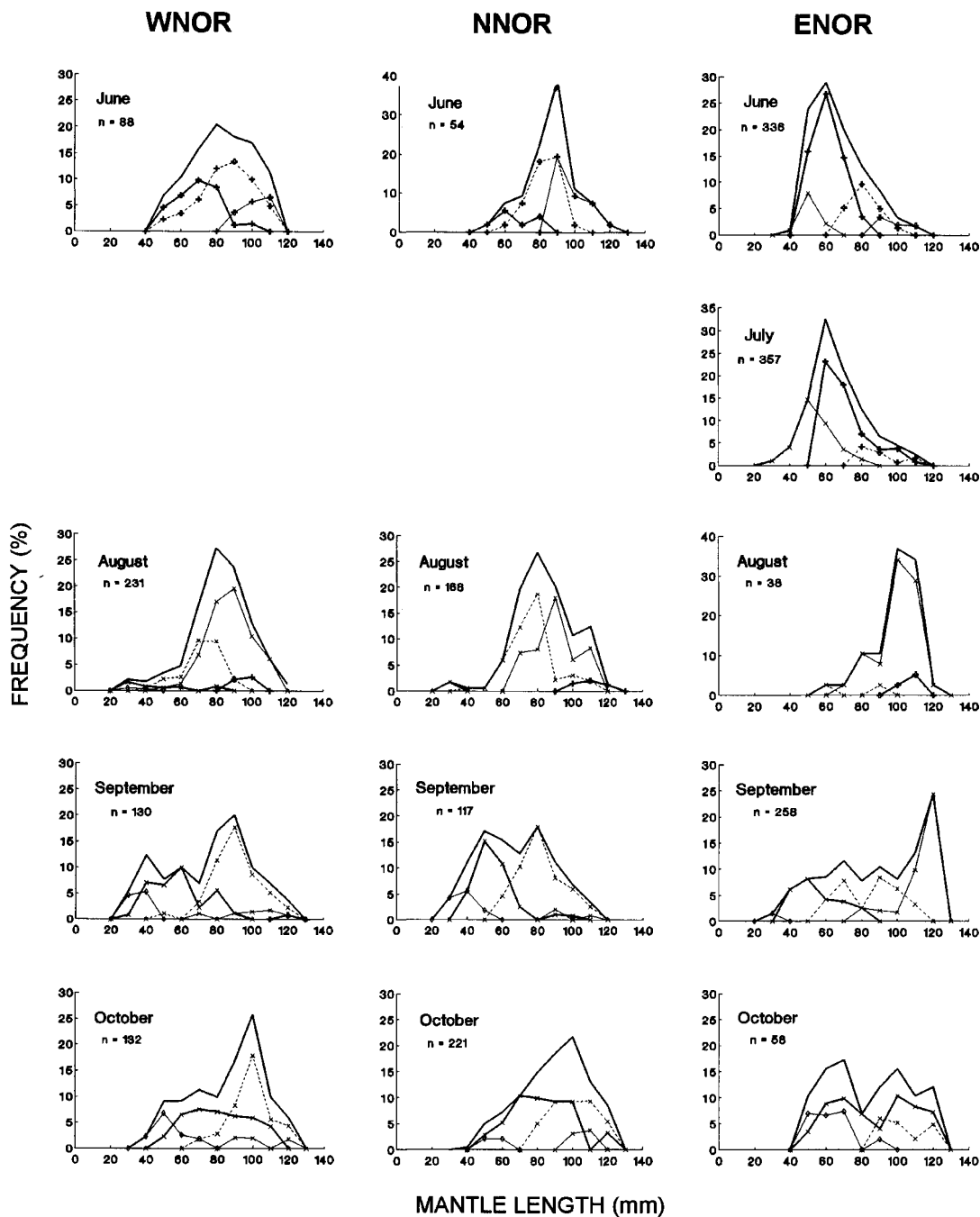


Fig. 2. Length compositions of *B. magister* juveniles in the Navarin-Olyutorsky region in June-October, 1994. Outer bold curve on each diagram - total length composition; inner curves - length compositions of different monthly-hatched groups. Symbols for monthly-hatched groups: 1. seasons: (+) - winter; (x) - spring; (◊) - summer; 2. months of hatching: solid line - the first month of a season, dotted line - the second month of the season, solid bold line - the third month of the season.

Monthly stock structure of *B. magister* juveniles occurring in a given region was defined by age-length key construction and its further application to length-frequency distribution (ARKHIPKIN 1993; ARKHIPKIN & al. 1996). The proportions of squids of each hatching month were calculated for every 1-cm size class of length-frequency distribution.

## RESULTS

### Vertical distribution

Juveniles were most abundant in the bottom trawl catches at depths of 380–500 m, while at depths < 350 m and > 500 m they were almost absent. Sometimes their abundance was so high that the wings of the trawls were strewn with enmeshed small squids, and they were also found in the catch taken from the cod-end. Their number in catches was greater in daytime and lower at night.

Analysis of the stomach contents of Pacific blue halibut (*Reinhardtius matsuurae*), white halibut (*Hippoglossus stenolepis*) and arrow-toothed halibut (*Atherestes evermanni*) in the NOR during September and October revealed that all three species preyed upon the squids. Partly digested *B. magister* occurred in 31 % of stomachs of *Reinhardtius matsuurae*, in 19 % of stomachs of *Atherestes evermanni* and in 9 % of *Hippoglossus stenolepis*. ML of partly digested squids ranged from 80 to 270 mm, the juveniles with ML less than 120 mm comprised about 10 % of all specimens. All halibuts were caught in daytime at a depth of 400–450 m.

Analysis of the data on the walleye pollock fishery in July, showed that *B. magister* juveniles were common in the upper pelagic layers. Young squids (ML 70 to 120 mm) were found in 11 trawls (mainly at night) at hauling horizons ranging from 80 to 200 m above depths ranging from 180 to 2000 m. Up to 150 specimens per hour were caught. In the daytime, *B. magister* juveniles disappeared from the pelagic catches.

### Seasonal distribution

In June, juveniles were highly abundant in the ENOR (hundreds and thousands per trawl), while in the WNOR and NNOR they occurred in rather small numbers (tens per trawl). Size distributions of juveniles were unimodal in all three subregions (Fig. 2). In July, abundance of juveniles as well as their modal size in the ENOR remained the same as in June. In August, abundance of juveniles was higher in the WNOR and NNOR (hundreds or thousands per trawl), than in the ENOR (tens or hundreds per trawl). Size distribution was unimodal in the WNOR and ENOR, whereas in the NNOR there were two modal classes. In September, abundance of juveniles was roughly the same in all parts of the NOR: from tens to hundreds per trawl. ML range of juveniles

became wide, being either bimodal (NNOR) or polymodal (WNOR and ENOR). In October, abundance of juveniles was the highest in the NNOR and WNOR (tens and hundreds per trawl). In the ENOR, it decreased to tens per trawl. Size distribution was unimodal in the NNOR and polymodal in the WNOR and ENOR (Fig. 2).

### Age and growth

Among 1030 aged juveniles, 236 were winter-hatched, 660 were spring-hatched and 134 were summer-hatched squids. They hatched from December to June. February and March-hatched juveniles were the most abundant. December and July-hatched squids were the least numerous, the former were only large-size juveniles (ML ranged from 93 to 130 mm), whereas the latter were small juveniles (ML from 22 to 40 mm). In June, the number of month-hatched groups was greater in the ENOR, from August to October it was greater in the WNOR.

In our samples, the youngest juvenile (53 days) was June-hatched (22 mm ML). The oldest juvenile (199 days) was a December-hatched squid (117 mm ML). Individual growth rates varied greatly, especially in spring-hatched juveniles. For example, among March-hatched squids at an age of 130 days both slow-growing (ML from 58 to 70 mm) and fast-growing specimens (ML from 100 to 110 mm) were found.

Length-at-age relationships were best described by an exponential function in all three seasonal groups of juveniles (Fig. 3A–C). The coefficient ‘a’ was the same in all three groups (11), whereas the exponential coefficient ‘b’ was smallest in winter-hatched squids (0.0141) and greatest in summer-hatched squids (0.0152). Exponential length-at-age relationships suggest that the three groups all experienced different instantaneous growth rates (G) during the ontogenetic period studied. The estimated values of the exponential coefficients indicate that the summer-hatched squids had the highest, and the winter-hatched squids the lowest growth rates. Spring-hatched juveniles had intermediate values of G and DGR (Fig. 3D).

### Length-at-age structure

Length-at-age structure of *B. magister* juveniles was described separately for each hatching month (Fig. 4).

December-hatched juveniles occurred in catches only in June, their abundance being the highest in the NNOR and the least in the ENOR. Size distribution was unimodal in all three subregions, the modes gradually increased from 90 mm in the ENOR to 110 mm in the WNOR. In July, December-hatched juveniles disappeared from the catches in the ENOR.

January-hatched juveniles were found both in June and July. In June, their abundance grew from the ENOR

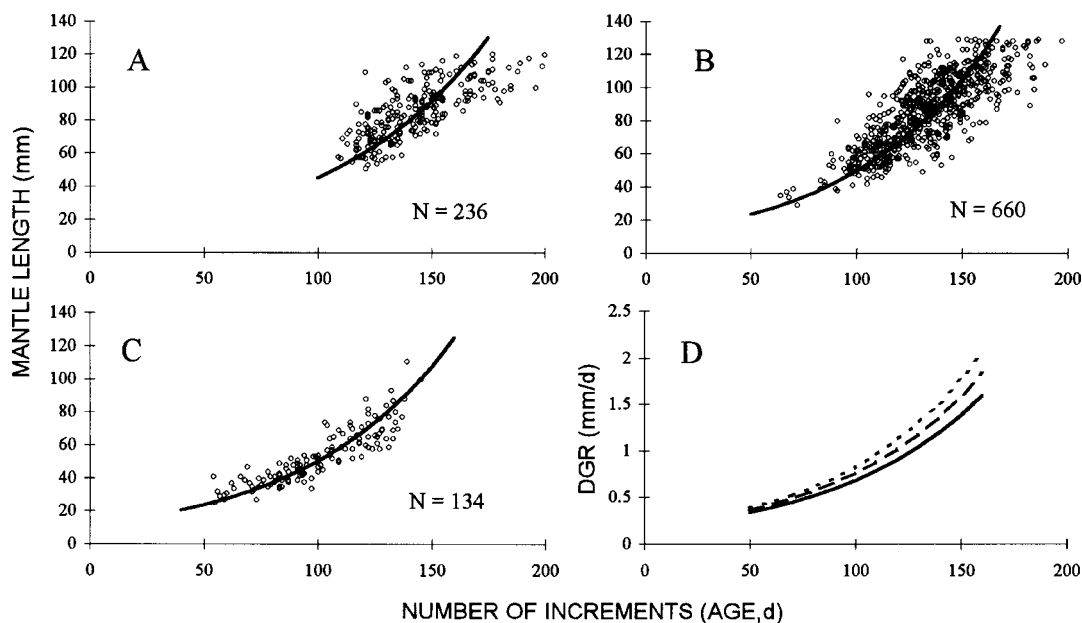


Fig. 3. Length-at-age data, exponential growth curves (A-C) and daily growth rates (D) for winter- (A, and solid line in D), spring- (B, and dashed line in D) and summer-hatched (C, and dotted line in D) *B. magister* juveniles in the Navarin-Olyutorsky region of the western Bering Sea.

to WNOR. In the WNOR and NNOR, this group ultimately dominated among juveniles. Size distribution was unimodal throughout the NOR, the modes slightly increased from the ENOR (80 mm) to WNOR (90 mm). In July, this group occurred in small numbers in the ENOR, their ML ranged from 80 to 120 mm. In August, January-hatched juveniles disappeared from catches.

February-hatched juveniles were the most abundant in June and July and almost disappeared in September. In June and July, this group comprised about 60 % of all juveniles in the ENOR, their ML ranged from 50 to 100 mm (modal ML of 60-70 mm). However, in the NNOR and WNOR they were less abundant in June. In August, February-hatched juveniles (modal ML of 100-110 mm) occurred in small numbers in all subregions. In September, large (120 mm ML) February-hatched juveniles were found occasionally in the WNOR only.

March-hatched juveniles were the second in terms of abundance. The first March-hatched juveniles (ML from 39 to 64 mm; mode of 50 mm) appeared in the ENOR in June. In July, their numbers had doubled in the ENOR. In August, they dominated in catches in all parts of the NOR. In this month, fast- and slow-growing groups appeared among March-hatched squids: the former (110 mm ML) dominated in the ENOR, the latter (80-90 mm) in the WNOR. In the NNOR, both groups occurred

in the catches. In September the slow-growing group almost disappeared from the WNOR and NNOR while the fast-growing one still dominated in the ENOR. In October, March-hatched squids (100-120 mm ML) occurred in small numbers in the WNOR and NNOR, but were absent in the ENOR.

April-hatched juveniles occurred from August to October. In August, these squids (modal ML of 60-70 mm) were the most numerous in the NNOR, less abundant in the WNOR and quite rare in the ENOR. In September, their numbers in the ENOR increased but remained less than in the WNOR and NNOR. Size distribution of April-hatched juveniles in September was unimodal (modal ML of 80-90 mm) in the WNOR and NNOR and bimodal (modal ML of 70 and 90 mm) in the ENOR. In October, these squids grew up to 100-110 mm ML, their abundance being gradually increased from the ENOR to WNOR.

May-hatched juveniles appeared first in the WNOR and NNOR in August (ML from 30 to 80 mm; mode 30-40 mm). In September, they spread eastward to the ENOR. Their size distribution was unimodal in the ENOR (modal ML of 50 mm) and bimodal in the WNOR and NNOR (50-60 mm and 80 mm). In October, the May-hatched juveniles were most abundant in the whole area. Two more or less distinct modes could be traced throughout the area: 70 mm and 100 mm ML.

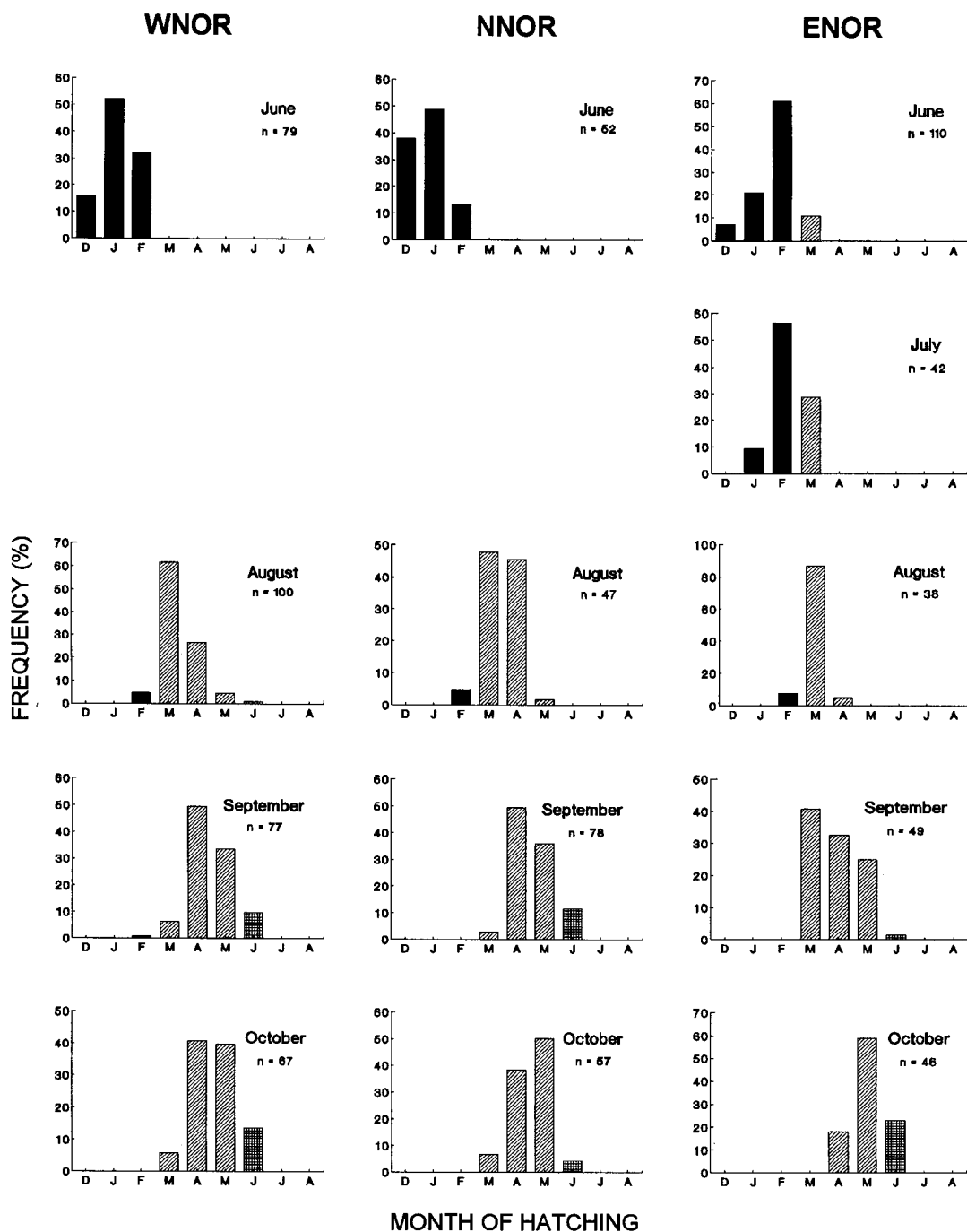


Fig. 4. Age structure of *B. magister* juveniles in the Navarin-Olyutorsky region, June-October, 1994. Black: winter-hatched. Dashed: spring-hatched. Checked: summer-hatched.

June-hatched juveniles were not numerous. They appeared first in the WNOR in August (20-40 mm ML). In September, they spread eastward to the NNOR and

appeared also in the ENOR. In October, they grew up to modes of 50-60 mm ML and were the most abundant in the WNOR and NNOR.

## DISCUSSION

### *Growth rates and age*

The results of the length-at-age data analysis showed that *Beryteuthis magister* in the western Bering Sea attains the length at recruitment (130 mm ML) at an age ranging from 140-170 days (spring-hatched juveniles) to 170-200 days (winter-hatched). Slower growth rates of winter-hatched juveniles compared to those of hatched in spring were apparently caused by lower water temperatures in winter in the Bering Sea.

Length-at-age data of different seasonally hatched groups of juveniles were best fitted by an exponential function as has been done for juveniles of other squids studied (FORSYTHE & VAN HEUKELEM 1987). However, *B. magister* juveniles grow rather slowly compared to other oceanic and neritic squids whose growth has been studied using statolith aging techniques. The growth rates of *B. magister* at age 60 to 190 days were considerably (2.5-3 times) lower than those of oceanic ommastrephids with a one-year life cycle (ARKHIPKIN 1989) as well as those of shelf loliginids with a 6-month or one-year life cycle (JACKSON & CHOAT 1992). Slow growth of *B. magister* juveniles was caused mainly by very low temperatures of their environment (3.0-3.7°C, our data). It is important to note that the differences between the growth rates of different seasonally hatched groups of *B. magister* juveniles were distinct but not so prominent as between summer and winter groups of the temperate *Illex argentinus* (Ommastrephidae) (ARKHIPKIN 1989) or tropical *Loligo chinensis* (Loliginidae) (JACKSON & CHOAT 1992). Inter-seasonal similarity in juvenile growth rates may be explained by greater stability of abiotic parameters at depths where they occur throughout the year in the Bering Sea (ARSENYEV 1967).

Our estimates of growth rates in *B. magister* juveniles are considerably greater than those obtained by length-frequency analysis (YUUKI & KITAZAWA 1986) or by earlier applications of statolith method (NATSUKARI & al. 1993). The reason for the difference in the latter case was the different interpretation of statolith increment periodicity (ARKHIPKIN & al. 1996).

### *Vertical distribution*

On the basis of our data, the former hypothesis on the epipelagic life of *B. magister* juveniles (KUBODERA & JEFFERTS 1984) cannot be confirmed. Occurrence of juveniles at depths of 380-500 m both in bottom trawl catches and in stomachs of near-bottom fishes agreed well with earlier reports on their presence in the bottom trawl catches (FEDORETS 1986; NESIS 1989, 1995). On the other hand, the report by GORBATENKO & al. (1995) and our data testified that *B. magister* juveniles in the

daytime occurred in pelagic layers above the outer shelf and the continental slope. Obviously, in the Bering Sea *B. magister* juveniles sink to the bottom and start vertical migrations at ML about 20-30 mm.

### *Possible migrations*

Comparative analysis of juvenile age structures in different months and NOR subregions provided the following data on their migrations.

**Winter-hatched group.** In June, older and larger juveniles of December- and January-hatched groups occurred mainly in the WNOR and NNOR while younger and smaller February-hatched squids were found in the ENOR (Fig. 4). Apparently this distribution reflected the ongoing westward transport of winter-hatched squids by the EBSC from the south-eastern part of the Bering Sea. In summer they fed in waters above the slope, and by August they exceeded 130 mm ML when they could be classified as adults. Certainly, some winter-hatched squids can be carried out of the NOR but the majority remained in the NOR and recruited to the adult stock. To verify this, the age structure of *B. magister* juveniles (the present paper) was compared to the age structure of adults occurring in the same region (ARKHIPKIN & al. 1996). It was found that the time of a given month-group's disappearance from the juvenile stock coincided with the time of its first appearance as adults: July for December-hatched squids, August and September for January- and February-hatched squids.

**Spring- and summer-hatched groups.** Spring-hatched juveniles demonstrated a different migratory pattern than winter-hatched juveniles. March-hatched juveniles appeared in the ENOR in June immigrating with the EBSC together with winter-hatched squids. In August, slow-growing March-hatched squids appeared also in the WNOR, and their size-distribution in this subregion became bimodal. From our data it is possible to suggest that fast-growing March-hatched juveniles entered the ENOR from the south-east with the EBSC while the slow-growing group entered the WNOR with an inflow from the deep sea between 173°30'E and 174°30'E (Fig. 1). In September, the slow-growing group almost disappeared from the WNOR and NNOR while the fast-growing one still dominated the ENOR. Taking into account the modal length of the slow-growing group in August (90 mm ML) and estimated growth rates, these squids could not grow from 90 to 130 mm during one month. Thus, we conclude that slow-growing March-hatched juveniles emigrated from the NOR with the slope current to the south-west. Fast-growing March-hatched



squids by October generally grew beyond 130 mm and recruited to the adult stock in the NOR (ARKHIPKIN & al. 1996).

April-, May-, and also June-hatched juveniles were carried to the NOR mainly with the deep-sea inflow from August to October. However, the presence of fast- and slow-growing groups among April- and May-hatched juveniles could also be explained by the second way of their migration with the EBSC. These groups did not exceed 130 mm ML in October.

Thus, the spring- and summer-hatched juveniles entered the NOR by two routes: from the south-west with the deep-sea inflow between 173°30'E and 174°30'E and with the EBSC. Squids migrating through the open sea had lower growth rates than those migrating along the slope. It is important to note that not all groups of *B. magister* juveniles found in summer and autumn 1994 in the western Bering Sea belonged to the recruitment of autumn-hatched adult squids that represented the main fishery stock in the region (ARKHIPKIN & al. 1996).

The pattern of age-size variability may be explained by possible seasonal changes in the regional circulation in the NOR (VERKHUNOV & TKACHENKO 1992; VERKHUNOV 1995; OVERLAND & al. 1994). According to the seasonal wind stress and cooling-warming changes, and in concordance with the results of synoptic cruises in the end of winter, general circulation in the Bering Sea Basin was most intense in late winter. Weakening of the regional atmospheric circulation and strong seasonal warming, leading to the decrease of baroclinity at the edges of the Basin, caused a relaxation of the current systems. Such a relaxation is expected to be most evident in August-September. The next current intensity enhancement caused by raising of the wind stress and seasonal cooling is believed to start in October-November. The developed stage of the system (spring and late fall) is characterized by a strong slope current, that tightly follows the line of the shelf-break, as observed in spring 1990 (VERKHUNOV & TKACHENKO 1992). The trajectories of the relaxed along-slope currents tended to deviate from the continental slope, causing the appearance of a pronounced counterclockwise eddy in the north of the Aleutian Basin. In this stage, the EBSC turned to the south-west, clinging to the Koryak coast in its central part rather than in the vicinity of the Vityaz' Canyon, that gives rise to the maximum size of the Navarin Clockwise Eddy. During this period (July-August), the expanded eddy is responsible for the mean easterly transport along the northern half of the Koryak continental slope.

Thus, the EBSC probably serves as the main carrier of *B. magister* juveniles from the spawning grounds to the NOR. Taking into account the path and average

speed of the EBSC on the horizons of juveniles transport (2-18 cm/sec after SCHUMACHER & REED 1992), the possible hatching region of winter-hatched juveniles found in the NOR in June might be somewhere on the southeastern continental slope between Unalaska and Pribilof Island. Seasonal variability of the EBSC determines differences in juvenile migration patterns. During its intense stage in spring, the EBSC transports winter-hatched and spring-hatched juveniles along the slope to the ENOR. Entering the NOR from the east, the juveniles are then transported westward with the slope current. During its relaxed stage (July-September), the EBSC carries spring- and summer-hatched juveniles across the deep part of the Basin delivering them to the WNOR between 173°30'E and 174°30'E. Entering the NOR from the west, these spring- and summer-hatched juveniles are later transported eastward by the Navarin Clockwise Eddy.

#### ACKNOWLEDGMENTS

We gratefully acknowledge the help of the officers and crews of the Japanese trawlers *Tenryu-Maru N 57* and *Kaiyo-Maru N 28*. We thank two anonymous referees whose comments helped to improve the manuscript. This research was funded by the Russian Federal Committee of Fisheries.

#### REFERENCES

- Arkhipkin, A.I. 1989. *Age and growth of squids of the family Ommastrephidae*. – Ph.D. Thesis, Shirshov Institute of Oceanography, Moscow. 134 pp. (in Russian)
- 1993. Age, growth, stock structure and migratory rate of pre-spawning short-finned squid *Illex argentinus* based on statolith ageing investigations. – *Fisheries Research* 16:313-338.
- Arkhipkin, A.I., V.A. Bizikov, V.V. Krylov & K.N. Nesin 1996. Distribution, stock structure and growth of the squid *Berryteuthis magister* (Berry, 1913) (Cephalopoda, Gonatidae) during summer and fall in the Western Bering Sea. – *Fishery Bulletin* 94(1):1-30.
- Arkhipkin, A.I. & V.A. Bizikov 1997. Statolith shape and microstructure in studies of systematics, age, and growth in planktonic paralarvae of gonatid squids (Cephalopoda, Oegopsida) from the western Bering Sea. – *Journal of Plankton Research* 19:1993-2030.
- Arsenyev, V.S. 1967. *Currents and water masses of the Bering Sea*. – Nauka, Moscow. 139 pp. (in Russian)
- Dawe, E.G. & Y. Natsukari 1991. Light microscopy. – Pp. 83-96 in: Jereb P., S.Ragonese & S. von Boletzky (eds). *Squid age determination using statoliths*. N.T.R.-I.T.P.P. Special publications, no.1, Mazara del Vallo, Italy.
- Fedorets, Y.A. 1979. Some results of the studies of the Commander squid *Berryteuthis magister* in the Bering Sea. – *Mollusks. Results of their studies. Abstracts of reports*. 6:122-123. (in Russian)

- 1983. Seasonal distribution of the squid (*Berryteuthis magister*) in the Western Bering Sea. – P. 129 in: Starobogatov Ya.I. & K.N. Nesis (eds). *Taxonomy and ecology of cephalopods*. Leningrad, Zoological Institute of AN USSR. (in Russian)
- 1986. Biology and resources of the squid *Berryteuthis magister* (Gonatidae) in the waters around the Commander Islands. – Pp. 57-66 in: Ivanov B.G. (ed.). *Resources and fishery potentials of the squids of the World Ocean*. VNIRO Press, Moscow. (in Russian with English abstract)
- Forsythe, J.V. & W.F. van Heukelem, 1987. Cephalopod growth. – Pp. 135-155 in: Boyle P.R. (ed.). *Cephalopod Life Cycles*, vol. 2. Academic Press, London.
- Gorbatenko K.M., V.I. Chuchukalo & G.A. Shevtsov 1995. Daily ration of two abundant species of squids in the Bering and Okhotsk Seas in autumn - winter time. – Pp. 349-357 in: Kotenev, B.N. & V.V. Sapozhnikov (eds). *Complex studies of the Bering Sea ecosystem*. VNIRO Press, Moscow. (in Russian)
- Jackson G.D. & J.H. Choat 1992. Growth in tropical cephalopods: an analysis based on statolith microstructure. – *Canadian Journal of Fisheries and Aquatic Sciences* 49:218-228.
- Kasahara, S., T. Nazumi, T. Shimizu & M. Hamabe 1978. Contribution of biological information useful for development of inshore squid fishery in Japan. II. A note on reproduction and distribution of *Berryteuthis magister* (Berry) assumed from biological observations on trawl catches in the waters around the Oki Islands, Japan Sea. – *Bulletin of Japanese Regional Fisheries Research Laboratory* 29:159-178. (in Japanese with English abstract)
- Kinder T.H., L.K. Coachman & J.A. Galt 1975. The Bering Sea Slope Current system. – *Journal of Physical Oceanography* 5(2):231-244.
- Kubodera T. & K. Jefferts 1984. Distribution and Abundance of the early Life Stages of squid, primarily Gonatidae (Cephalopoda, Oegopsida), in the Northern North Pacific. Parts 1-2. – *Bulletin of the National Scientific Museum, Tokyo, Serial A* 10(3-4):91-193.
- Kuznetsova N.A. & Y.A. Fedorets 1987. On feeding of Commander squid *Berryteuthis magister*. – *Biologiya Morya, Vladivostok* 1:71-73. (In Russian with English abstract)
- Naito, M., K. Murakami, T. Kobayashi, N. Nakayama & J. Ogasawara 1977. Distribution and migration of oceanic squid (*Ommastrephes bartrami*, *Onychoteuthis borealijaponicus*, *Berryteuthis magister* and *Gonatopsis borealis*) in the western subarctic Pacific region. – *Research Institute of the North Pacific Fisheries, Faculty of Fisheries, Hokkaido University, Special volume*:321-337. (in Japanese with English abstract)
- Natsukari, Y., H. Mukai, S. Nakahama & T. Kubodera 1993. Age and growth estimation of a gonatid squid, *Berryteuthis magister*, based on statolith microstructure (Cephalopoda: Gonatidae). – Pp. 351-364 in: Okutani, T., R.K. O'Dor & T. Kubodera (eds). *Recent advances in cephalopod fisheries biology*. Tokai University Press, Tokyo, Japan.
- Nesis, K.N. 1987. *Cephalopods of the world*. – Neptune City, T.F.H. Publications. 351 pp.
- 1989. Teuthofauna of the Okhotsk Sea. Biology of squids *Berryteuthis magister* and *Gonatopsis borealis* (Gonatidae). – *Zoologicheskij Zhurnal* 68(9):45-56. (in Russian with English abstract)
- 1995. Population dynamics of the Commander squid, *Berryteuthis magister* (Berry) in the Western Bering Sea during the autumn spawning season. – *Ruthenica* 1995, 5(1):55-69.
- Okutani, T., T. Kubodera & K. Jefferts 1988. Diversity, distribution and ecology of gonatid squids in the subarctic Pacific: a review. – *Bulletin of the Ocean Research Institute, University of Tokyo* 26 (Part I):159-192.
- Overland, J.E., M.C. Spillane, H.E. Hurlburt & A.J. Wallcraft 1994. A numerical study of the circulation of the Bering Sea Basin and the exchange with the North Pacific Ocean. – *Journal of Physical Oceanography* 24:736-758.
- Ricker, W.E. 1958. Handbook of computation for biological statistics of fish populations. – *Journal of the Fisheries Research Board of Canada* 119:1-300.
- Rowell, T.W., R.W. Trites & E.G. Dawe 1985. Distribution of the short-finned squid (*Illex illecebrosus*) larvae and juveniles in relation to the Gulf Stream frontal zone between Florida and Cape Hatteras area. – *NAFO Scientific Council Studies* 9:11-26.
- Schumacher, J.D. & R.K. Reed 1992. Characteristics of currents over the continental slope of the Eastern Bering Sea. – *Journal of Geophysical Research* 97, C6:9423-9433.
- Trites, R.W. 1983. Physical oceanographic factors and processes relevant to *Illex illecebrosus* spawning area in the Western North Atlantic and subsequent larval distribution. – *NAFO Scientific Council Studies* 6:39-55.
- Verkhunov, A.V. 1995. Climate change and variability of the Bering Sea current system. – *Canadian Special Publications in Fisheries and Aquatic Sciences* 121:73-80.
- Verkhunov, A.V. & Y.Y. Tkachenko 1992. Recent observations of variability in the Western Bering Sea Current System. – *Journal of Geophysical Research* 97, C9:14369-14376.
- Verkhunov, A.V. 1996. Hydrological situation in August and October 1995 in the Western Bering Sea. – Pp. 25-37 in: Jelizarov A.A. (ed.). *Commercial aspects of biology of Commander squid Berryteuthis magister and of fishes of slope communities in the western part of the Bering Sea*. VNIRO Publishing, Moscow. (in Russian)
- Yuuki, Y. & H. Kitazawa 1986. *Berryteuthis magister* in the Southern Japan Sea. – *Bulletin of the Japanese Society of Scientific Fisheries* 52:665-672. (in Japanese with English abstract)

Accepted 2 July 1997