

**Abstract.**—Distribution, abundance, and length-frequency composition of schoolmaster gonate squid, *Berryteuthis magister*, were studied during seven trawl surveys in the western Bering Sea between June and November 1993. Statolith age analysis was undertaken for 1,381 *B. magister* to estimate age, stock structure, and both growth and maturation rates. Three kinds of growth increments were revealed in *B. magister* statoliths. Daily periodicity of the second-order increments was confirmed by two independent, indirect methods. According to our data, *B. magister* live >1 yr; the oldest specimen was about 16 months old. *Berryteuthis magister* is a slow-growing and slow-maturing squid, and males exhibit slower growth and earlier maturation than do females. Growth in length was best described by a logistic curve, with a larger asymptotic parameter for females. In summer, concentrations of *B. magister* were low within the whole region, whereas in September–October squids aggregated into dense shoals over the continental slope of the Navarin–Olyutorsky region and Olyutorsky Bay. Stock structure of *B. magister* was complicated: each month, from 5 to 12 (usually 7–8) monthly classes of squid were encountered in the western Bering Sea. Three seasonal groups of *B. magister* occurred in the region: winter-, summer- and fall-hatched squids utilizing resources of the continental slope in different ways. A possible life cycle for the *B. magister* fall-hatched group includes a longevity of ca. 2 yr: 6 mo of embryonic development and 18 mo of postembryonic growth.

## Distribution, stock structure, and growth of the squid *Berryteuthis magister* (Berry, 1913) (Cephalopoda, Gonatidae) during summer and fall in the western Bering Sea

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The schoolmaster gonate squid, *Berryteuthis magister* (Berry, 1913), is an abundant near-bottom species occurring over the continental slopes in the North Pacific from southern Japan, the Sea of Okhotsk, and the Kurile Islands to the northwestern coast of the United States (Roper et al., 1984; Nesis, 1987). This species is one of the important fishery resources in the North Pacific. It is captured mainly by Russian trawlers around the Kurile Islands, in the Sea of Okhotsk, and in the western Bering Sea with an annual catch of 30,000–60,000 metric tons (t) (Fedorets, 1986a). In Japan, *B. magister* is taken seasonally by the coastal fishery and yields an annual catch of 5,000–9,000 t (Kasahara et al., 1978).

Some aspects of the distribution, reproductive biology, and growth of *B. magister* have been investigated in the Sea of Japan (Naito et al., 1977; Kasahara et al., 1978; Nazumi et al., 1979), where spawning

occurs from December to May (with a peak between February and March). With the use of length-frequency analysis, the life cycle of *B. magister* was estimated to be 2 years or more, and growth of both sexes was approximated with a logistic function (Yuuki and Kitazawa, 1986). Natsukari et al. (1993) used statolith ageing techniques for age and growth analysis of *B. magister* captured in Kitamiyamato and Rebun Banks and suggested a longevity of four years, with females attaining a larger size than males at any given age.

Patterns of vertical and spatial distribution of *B. magister* juveniles and adults were analyzed in the Sea of Okhotsk and waters of the Kurile Islands (Railko, 1983; Alexeev and Bizikov, 1986; Nesis, 1989). Preliminary data on age were obtained by comparing increment number between statoliths and gladii in five immature specimens with mantle lengths ranging from 220 to 250

mm. The age of these individuals was estimated to be less than one year (Arkhipkin and Bizikov, 1991). Feeding, shoal, and escaping behaviors have also been examined from manned submersibles (Alexeev et al., 1989).

The first studies on *B. magister* biology in the Bering Sea appeared in the seventies (Shevtsov, 1974; Fedorets, 1977, 1979). During the next decade, investigations were focused on distribution and stock dynamics (Fedorets, 1986a), feeding rhythms (Fedorets, 1986b; Kuznetsova and Fedorets, 1987), gametogenesis, fecundity, and spawning (Reznik, 1982; Fedorets and Kozlova, 1986). *B. magister* was common along the continental slope of the Bering Sea at depths varying from 100 to 1,500 m. In the western Bering Sea, and near the Commander and Aleutian Islands, dense seasonal aggregations formed at depths ranging from 300 to 500 m. According to Fedorets and Kozlova (1986), spawning occurred near the Commander Islands in winter and in the northwestern part of the Bering Sea in summer. Hatchlings were hypothesized to be transported by currents into the Bering Sea and Kurile Islands region. Total stock size in the Bering Sea was estimated to be about 350,000 t (Fedorets, 1986a).

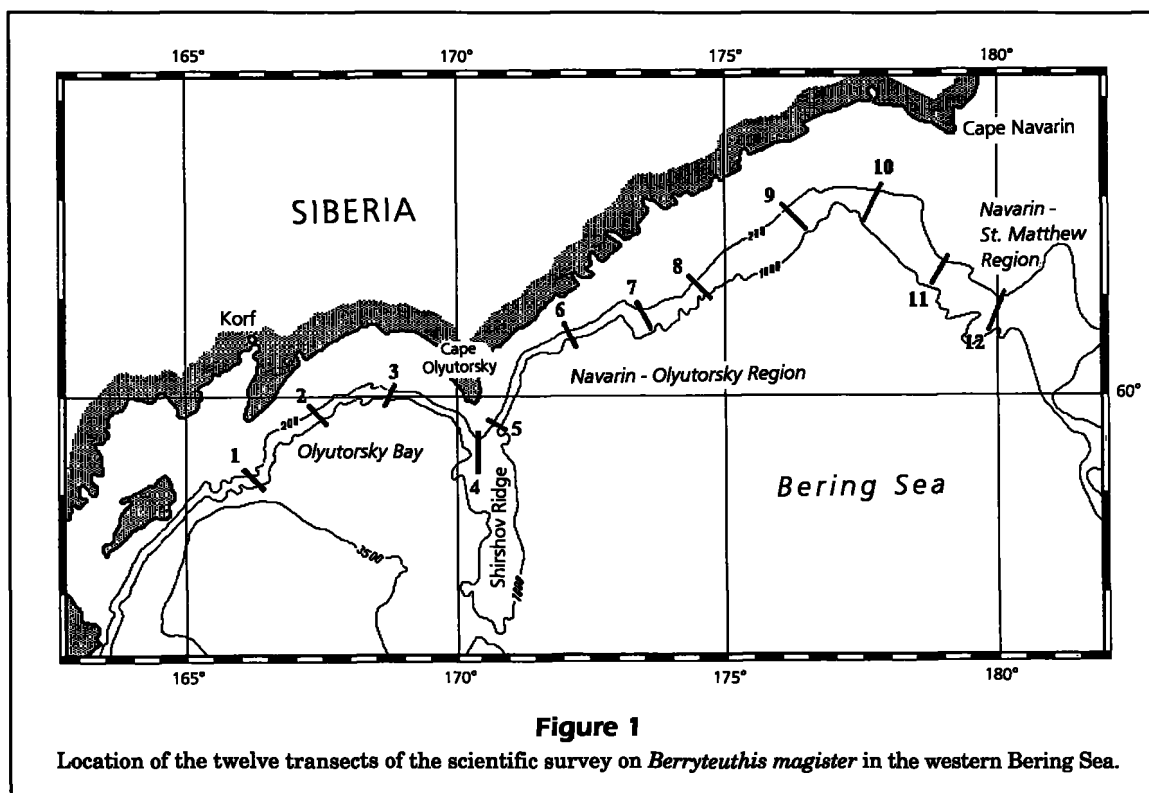
Research has been carried out on the presence of intraspecific groupings of *B. magister* in the Sea of Okhotsk (Nesis and Nezhlin, 1993). However, genetic

studies on protein variability have revealed a high polymorphism and heterozygosity without any significant differences within the species range (Katugin, 1991, 1993).

In contrast to a relatively good understanding of distribution, reproductive biology, and genetic variability, the growth and age-length dynamics of *B. magister* in the Bering Sea remain unknown. The present paper describes distribution, length frequency, stock-structure dynamics, and age and growth of *B. magister* in the western Bering Sea by using statolith and gladius ageing techniques.

## Materials and methods

Data were collected on *B. magister* during seven trawl surveys in the western Bering Sea (lat. 59°30'N–61°30'N; long. 166° 00'E–179°30'W) by three Japanese trawlers: *Tenyu-Maru N 57*, *Kaiyo-Maru N 28*, and *Kashima-Maru N 8* between June and November 1993. Each survey was carried out during the first 10–11 days of each month and consisted of 12 transects (Fig. 1). Additional surveys were performed in the second half of June and November. On each transect, three near-bottom trawls were made at depths of 170–250 m, 370–450 m, and 600–750 m. Trawls were conducted with the standard Japanese



pelagic trawl "Suketodara" with horizontal opening of 75 m, vertical opening of 20 m, and a 70-mm mesh size at the codend. The duration of each trawl was about one hour and the average speed of each trawl was 6.5–7.8 km·h<sup>-1</sup>.

### Length-frequency sampling

A total of 23,765 squids were analyzed during the expeditions, including 3,533 juveniles. A random sample of one hundred specimens was taken from each catch. If the number of squid in a given catch was less than 100, the entire squid catch was examined. Dorsal mantle length (ML) was measured to the nearest 1 mm and total body weight (BW) weighed to the nearest 1 g (during periods of calm sea only). Sex and maturity stage were identified according to the maturity scale for *Illex argentinus* (Nigmatullin, 1989). Evidence of mating and indices of stomach contents (fullness) were examined according to the methods of Zuev et al. (1985). The sex ratio was also determined. Because sex can be determined by eye only in squid >120 mm ML, all individuals <120 mm ML were considered juveniles and analyzed separately from males and females. Because juveniles were taken from the mesh of the trawl wings, we could not precisely estimate their abundance and occurrence.

For each sample, four length-frequency curves for each sex were constructed for the following ontogenetic periods: immature (maturity stages 1–2), maturing (maturity stages 3–4), mature (maturity stage 5), and spent (maturity stage 6). After preliminary analysis of the samples, length frequencies of all the catches taken within a given month were pooled together for each maturity period and for the three regions: Olyutorsky Bay, and both Navarin–Olyutorsky and Navarin–St. Matthew regions (Fig. 1).

### Age sampling

Every month from June to October, statoliths were removed from one hundred randomly sampled individuals of *B. magister* from one successful catch (>100 kg). In addition, statoliths were dissected from 50 juveniles and from specimens of uncommon sizes and maturity stages (i.e. large-size males and females and spent animals) that were not found in the sample but occasionally occurred in other catches within each month. Statoliths were sampled and analyzed separately in two regions: Olyutorsky Bay and the central part of the Navarin–Olyutorsky region. In June and October, statoliths were taken from two samples from the first and second halves of each month. A total of 1,453 statoliths were collected, washed in

distilled water, and stored in oil-paper envelopes in 96% ethanol.

In June and July, 87 gladii and pairs of statoliths were dissected from the same specimens for a comparison of the number of growth increments between ageing structures.

### Statolith ageing analysis

From a total of 1,453 statoliths, 740 were processed and read by two of the authors (AIA and VAB) aboard the *Tenyu-Maru N 57*; the rest were analyzed in the Laboratory of Commercial Invertebrates of AtlantNIRO by AIA. From the entire sample, 1,381 (95.1%) statoliths were successfully read. Statolith processing was rather time consuming because sizes (especially in adults) were unusually large: total statolith length (STL) ranged from 2.5 to 3.2 mm. Statolith terminology followed Clarke (1978) and Lipinski et al. (1991).

Statoliths were processed according to standard techniques (Arkhipkin and Murzov, 1985) with minor modifications. They were ground (on 600 grit) and polished (on 1,000 grit) wet waterproof sandpaper. Because the direction of the maximum growth within statoliths changed during ontogenesis, it was necessary to grind the convex side of the same statolith in two planes: one plane running through the lateral and dorsal domes and spur, and the other plane running through the spur and along the central axis of the rostrum. This method of grinding exposes the growth increments lying immediately below the wing. The ground statolith was not flat and thin as in Natsukari et al. (1993) but thickened in the region of the lower part of the lateral dome and the proximal part of the rostrum. This feature allowed all increments from the nucleus to the most distal part of the rostrum to be unambiguously resolved.

Ground statoliths were embedded in glycerin and covered with glass for immediate reading. Statoliths were read under a Biolam R14 light microscope with 450–500× magnification. Growth increments were counted from the nucleus to the distal part of the rostrum and from farther within the rostrum as described by Natsukari et al. (1993) by using the eyepiece (as described in Dawe and Natsukari, 1991). To avoid possible counting errors, each statolith was counted at least twice by two observers, and if the difference between readings was less than 5%, squid age was taken as the mean of these counts. Readings were made only after achievement of the maximum resolution of growth increments with fine-adjustment focusing. Because the periodicity of different types of growth increments was unknown for the northern populations of *B. magister*, their number was calculated separately for each type.

## Gladius ageing analysis

A total of 87 gladii were extracted from squid captured from the Navarin–Olyutorsky region during June and July. The gladii were processed according to the techniques elaborated by Bizikov (1991). Each gladius was dissected from the animal through the dorsal section of the mantle, then washed carefully with warm soapy water, labeled, and stored in 6% formaldehyde. The periodic laminae were counted in the cross sections of the inner shell layer of the gladius by using the same microscope (100–200×) as that used for statoliths. The sections were made at the area of greatest thickness of the gladius inner layer, near the ventral anterior margin of the conus. These sections were placed on slides with a drop of glycerine and covered with glass for viewing. In some intact gladii, periodic laminae on the dorsal plate (proostracum) were analyzed by using a zoom microscope under reflected light (32–56× magnification).

## Validation of the periodicity of increment formation within ageing structures

Two indirect methods were applied for validation of the periodicity of statoliths and gladii increment formation. The first involved comparison of increment number in both gladius and statoliths taken from the same specimen (Arkhipkin and Bizikov, 1991). The second method included a comparison of the difference between the mean number of statolith increments from the modal groups of two successive samples with the number of days elapsed between these samples (Uozumi and Ohara, 1993; Uozumi and Shiba, 1993). To analyze both relationships, a predictive regression model was applied (Ricker, 1973). The estimated values of slopes (SL) of both regressions were tested with the null hypothesis (SL=1) at the 0.05% level for SL by using the statistic  $t = (SL-1)/SD$ , where SD is a standard deviation of SL (Wesolowsky, 1976).

## Age and growth parameters

Unfortunately, we had no opportunity to validate directly the periodicity of growth increments within statoliths and gladii. However, after examination of increment number and microstructure within statoliths taken from the same specimen and after comparison of these with daily growth increments in the statoliths of validated species (*Loligo opalescens*, Hixon and Villoch, 1984; *Illex illecebrosus*, Dawe et al., 1985; *Alloteuthis subulata*, Lipinski, 1986; *Sepioteuthis lessoniana*, Jackson, 1990; *Todarodes pacificus*, Nakamura and Sakurai, 1990), we assumed that growth increments were deposited daily

(see the corresponding section in Results section). We considered the total number of increments beyond the “natal ring” (observed by Natsukari et al., 1993) to be the age of squid in days. Hatching dates were backcalculated. Month classes of hatching (further “month classes”) were defined by the pooling of squid into each month of hatching.

Length-at-age data were analyzed separately for both sexes and hatching months. Monthly age structure in a given region was defined by routine procedures of age-length key construction. For more precise construction of age-length keys, we determined the numbers of squid of each month class separately for each sex and maturity period (Table 1A). With these keys, month-class compositions in each month were estimated from the monthly length-frequency compositions (Table 1B). The similarity of age structures observed in different months was estimated by applying a coefficient of similarity (as %, 0% as absolute difference, and 100% as absolute resemblance) elaborated by Shorygin (1952) during studies of fish food spectra.

The relatively short period of investigation in this study did not permit the resolution of ontogenetic growth curves for each hatching month of squid. However, it was possible to construct a growth curve for the species by pooling the individual age-at-length data over various hatching months. Curves (logistic, Gompertz, and von Bertalanffy) were fitted to the age-at-length data by using the method of iterative nonlinear least squares. As a result, the values of *ML* were calculated by using the formula of the best fitted curve. Unfortunately, pitching and rolling of the vessel during frequently occurring storms prevented us from weighing precisely almost half of the specimens analyzed, especially small-size ones. For investigation of growth in weight, we constructed at first length-weight curves for both sexes, and then calculated age-weight curves. Daily growth rates in length or weight (DGR; mm or g per day) and instantaneous growth rates (*G*) were calculated after Ricker (1958) as

$$DGR = (M_2 - M_1)/T$$

and

$$G = (\ln M_2 - \ln M_1)/T,$$

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

## Results

### Distribution and abundance

*Berryteuthis magister* occurred in most trawl catches along the continental slope of the western Bering Sea

Table 1

An example of "raw" and calculated age-length key for *B. magister* females trawled in the Navarin–Olyutorsky region in August ( $n=87$ ;  $N=253$ ). Maturity state: imm = immature; ming = maturing; and mat = mature. FD = frequency distribution, as a percentage.

**A** Number of specimens observed with respect to the month class (raw age-length key)

ML interval (cm)	Maturity state	Month class (month of hatching)									Number of aged squid	FD of age sample
		Jan	Feb	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
13–14	imm	3	1							1	5	5.75
15–17	imm		1							1	2	2.30
18–20	ming										0	0
	imm							1	3	3	7	8.05
	ming									1	1	1.15
21–23	mat										0	0
	imm								8	2	10	11.49
	ming					1	3	2			6	6.90
	mat										0	0
24–26	spent					1					1	1.15
	imm								2		2	2.30
	ming				1	3	13	6			23	26.44
	mat				1	2		1			4	4.60
27–29	spent			1	3	2					6	6.90
	imm										0	0
	ming				1	3	4	2			10	11.49
	mat							1			1	1.15
30–32	spent							1		1	1	1.15
	ming					1					2	2.30
	mat					1	1				2	2.30
33–35	spent				1						1	1.15
	ming										0	0
	mat				1	2					3	3.45
	spent										0	0
Total		3	2	1	8	16	21	15	13	8	87	100
Percent		3.45	2.30	1.15	9.20	18.39	24.14	17.24	14.94	9.20	100	

(Fig. 2). Although spatial distribution varied greatly in different regions and seasons, vertical distribution showed the same general pattern throughout the entire period of study. During the day, squid occurred near bottom at depths ranging from 150 m to 800 m, with the greatest densities usually between 350 and 450 m. At night, *B. magister* was generally dispersed throughout the water column. Females always predominated over males, the sex ratio (males/females) varying from 0.6 to 0.8.

**Olyutorsky Bay** During June, July, and August, *B. magister* occurred in small numbers along the slope of Olyutorsky Bay and Shirshov Ridge with average catches  $<100 \text{ kg}\cdot\text{h}^{-1}$  at depths from 250 to 450 m. Local aggregations of mature squids (from 160 to 270  $\text{kg}\cdot\text{h}^{-1}$ ) were found in the western part of Olyutorsky Bay and south of Cape Olyutorsky. Dense concentrations appeared in the eastern part of the Bay and Shirshov Ridge in September, reaching the highest values (1,100–1,400  $\text{kg}\cdot\text{h}^{-1}$ ) in the first ten days of

October. Later, smaller numbers of squid were observed and by the second half of November had decreased to  $100 \text{ kg}\cdot\text{h}^{-1}$  or less.

**Navarin–Olyutorsky region** In June, density of *B. magister* shoals along the Navarin–Olyutorsky slope was low; average catches were around  $50 \text{ kg}\cdot\text{h}^{-1}$ . A few large catches (up to  $400 \text{ kg}\cdot\text{h}^{-1}$ ) were taken in the eastern part of the region between  $176^\circ\text{E}$  and  $177^\circ\text{E}$ . From July to September, numbers of squids increased steadily and catches averaged  $700\text{--}800 \text{ kg}\cdot\text{h}^{-1}$  by the end of September. The most dense aggregations ( $1,000$  to  $1,500 \text{ kg}\cdot\text{h}^{-1}$ ) were captured at depths of 350–450 m between  $172^\circ\text{E}$  and  $174^\circ\text{E}$  in September and October. By the second half of November, catches of *B. magister* decreased rapidly to  $90\text{--}100 \text{ kg}\cdot\text{h}^{-1}$ .

**Navarin–St. Matthew region** From June to August, catches of *B. magister* were very low ( $<50 \text{ kg}\cdot\text{h}^{-1}$ ). Catches increased steadily during September and

Table 1 (continued)

B Calculated month-class-length key												
ML interval (cm)	Maturity state	Month class (month of hatching)								Number of squid	FD of total sample	
		Jan	Feb	Jun	Jul	Aug	Sep	Oct	Nov			Dec
13-14	imm	0.47	0.16							0.16	2	0.79
15-17	imm		2.37							2.37	12	4.74
	ming										0	0
18-20	imm							1.30	3.90	3.90	23	9.04
	ming									0.40	1	0.4
	mat										0	0
21-23	imm								6.32	1.58	20	7.91
	ming					0.99	2.96	1.98			15	5.93
	mat										5	1.98
	spent					0.79					2	0.79
24-26	imm								0.79		2	0.79
	ming				1.50	4.40	19.44	8.97			87	34.39
	mat				3.06	6.13		3.06			31	12.25
	spent			0.40	1.19	0.79					6	2.37
27-29	imm										0	0
	ming				1.03	3.08	4.11	2.06			26	10.28
	mat							4.74			12	4.74
	spent							0.40			1	0.4
30-32	ming					0.40		0.40			2	0.79
	mat					0.40	0.40				2	0.79
	spent				0.40						1	0.4
33-35	ming										0	0
	mat				0.40	0.79					3	1.19
	spent										0	0
Total											253	100
Percentages of month classes in total sample		0.47	2.53	0.40	7.56	17.84	26.91	22.90	11.01	8.40		

reached 800–900 kg·h<sup>-1</sup> in the first half of October. However, these aggregations quickly disappeared by the middle of November.

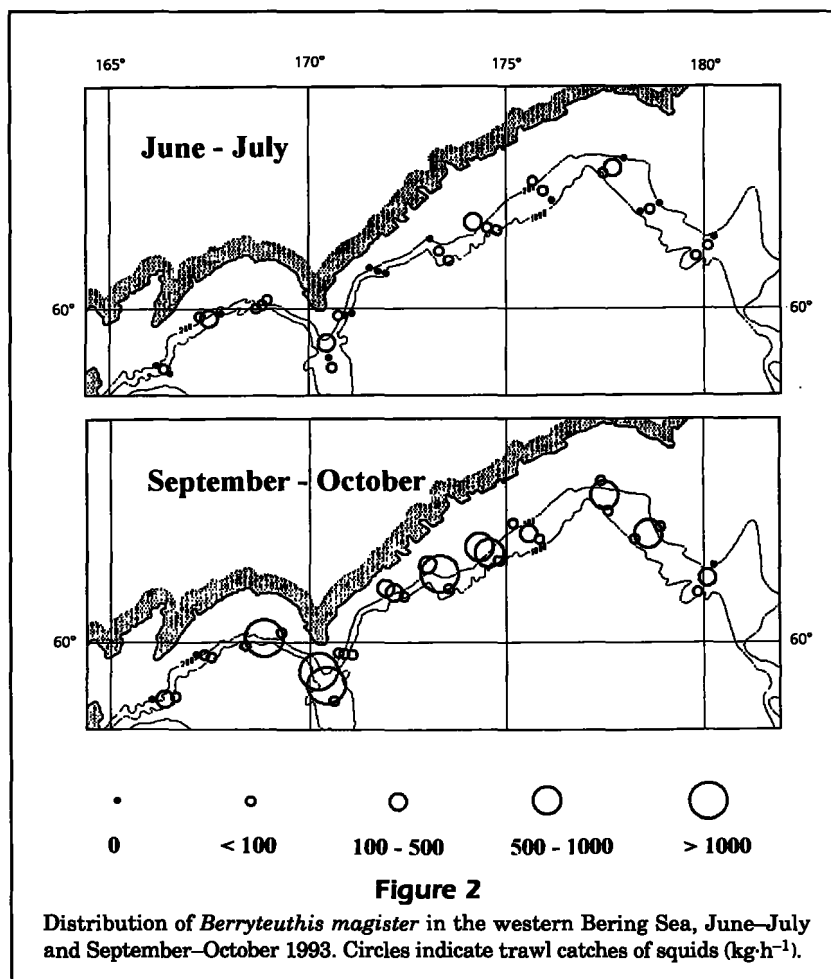
### Length-frequency composition

**Olyutorsky Bay** In Olyutorsky Bay (Fig. 3), proportions of immature and maturing males gradually decreased from June to October, then expanded in November. Among males, mature males always predominated in catches. Their numbers increased steadily from June to October, then decreased slightly in November. The size range of mature males was wide (170–270 mm) and unimodal (210 mm), remaining invariable throughout the period of study. Spent males were rare; greatest numbers were observed in June (2–3%) and in November (2%).

Immature females were not abundant in June, very abundant in July (46%), then successively diminished to 11% in October and November. During summer, length distribution of immature females was bimo-

dal; their modal sizes increased slightly from 190–200 mm and 220–230 mm in June to 200–210 mm and 230–240 mm in August. In fall, when the number of immature females was low, their length composition did not reveal well-defined modes. The proportion of maturing females increased steadily from June to September and decreased rapidly in October–November. Their length composition was unimodal, with modal lengths slightly increasing from June (230–240 mm) to September (240–260 mm).

Mature females were abundant in June. From July to September, their numbers diminished, then increased again in October. Length composition of mature females was always unimodal and wide (200–330 mm); their modal lengths remained constant between June and August (230–250 mm), then increased slightly in September–November (250–270 mm). Evidence of mating was observed in mature females as one or two bundles of spermatophores attached to the inner mantle surface near the gills. The number of mature females with evidence of mating grew from



June (75%) to July–August (90%), then decreased abruptly in October (37%). Spent females appeared in July (1%). In August–October, their numbers were low, except for a few catches along the Shirshov Ridge. Spent females were most abundant in November (11–12%).

Juveniles were seldom caught from July to October. Their size range was wide (20–120 mm). Juvenile length composition was bimodal in summer and without well-expressed modes in fall.

**Navarin–Olyutorsky region** In the Navarin–Olyutorsky region (Fig. 4), proportions of immature and maturing males gradually decreased from June to August. During September and October, both groups almost vanished from catches (<2% each) and appeared again in November. Length composition of immature males was roughly unimodal (160–170 mm). Mantle length of the largest immature males never exceeded 200 mm. Length composition of maturing males was unimodal and wide (150–240 mm), with modes shifting slightly from June (170–180 mm) to October (190–200 mm).

Among males, mature animals always predominated in catches, with the greatest number in September and October (95%). The size range of mature males was wide (170–290 mm) and did not vary considerably from June to November. The size composition was distinctly unimodal (modal length was 210 mm during the entire period of study). The number of spent males was extremely low from June to October and increased slightly in November (3%). Their sizes always coincided with modal lengths of mature males.

Numbers of immature females decreased successively from June to September. In October, their proportion remained low, then expanded slightly in November. The size range of immature females was always wide, with largest individuals of about 280 mm ML. Length composition had two modes in June (180–190 mm and 220–230 mm), and three in July (130 mm; 190–200 mm; and 240 mm). In August, only one very broad mode was traced among this group (190–240 mm). From September to November, length composition of immature females had no clear modes.

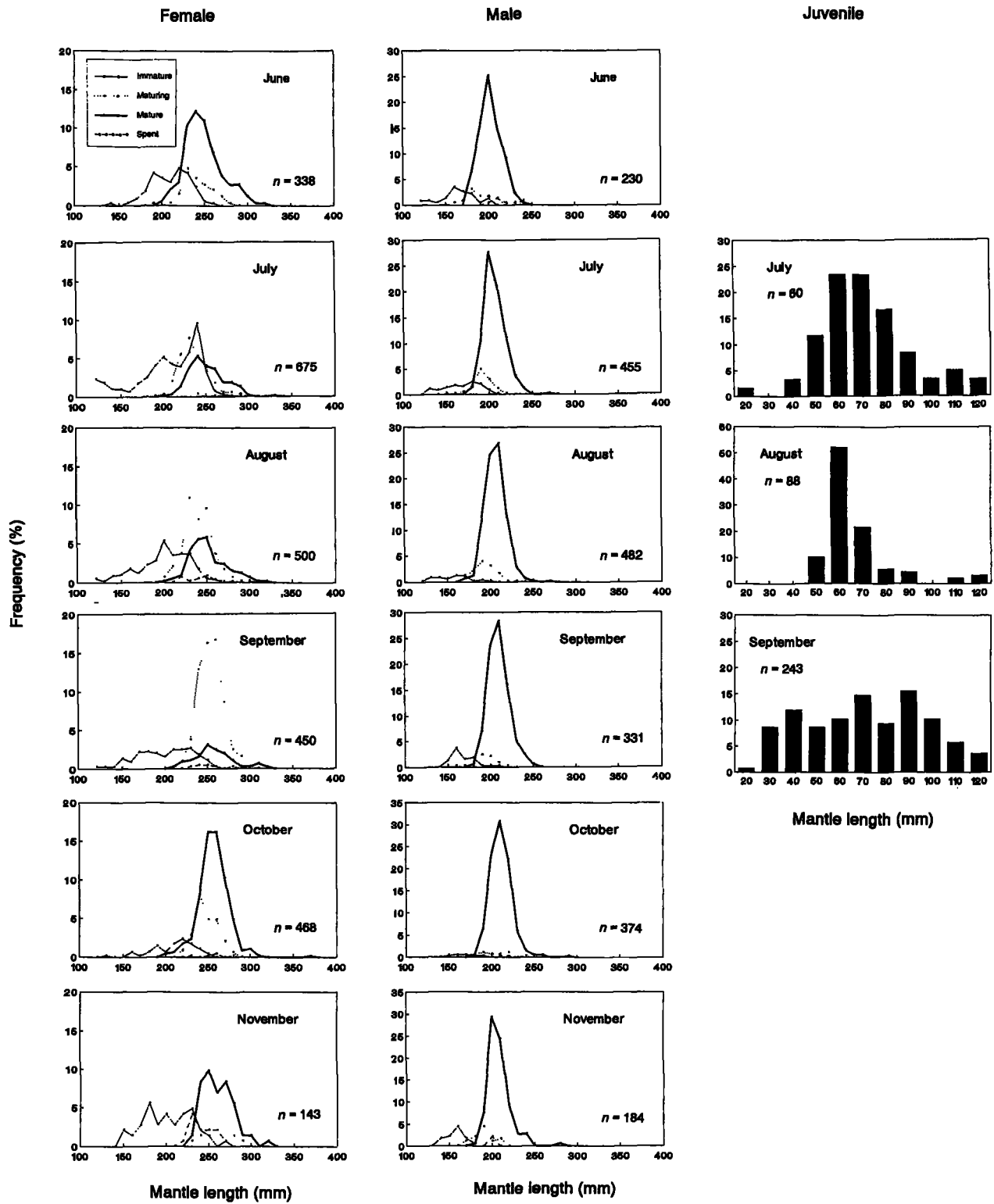
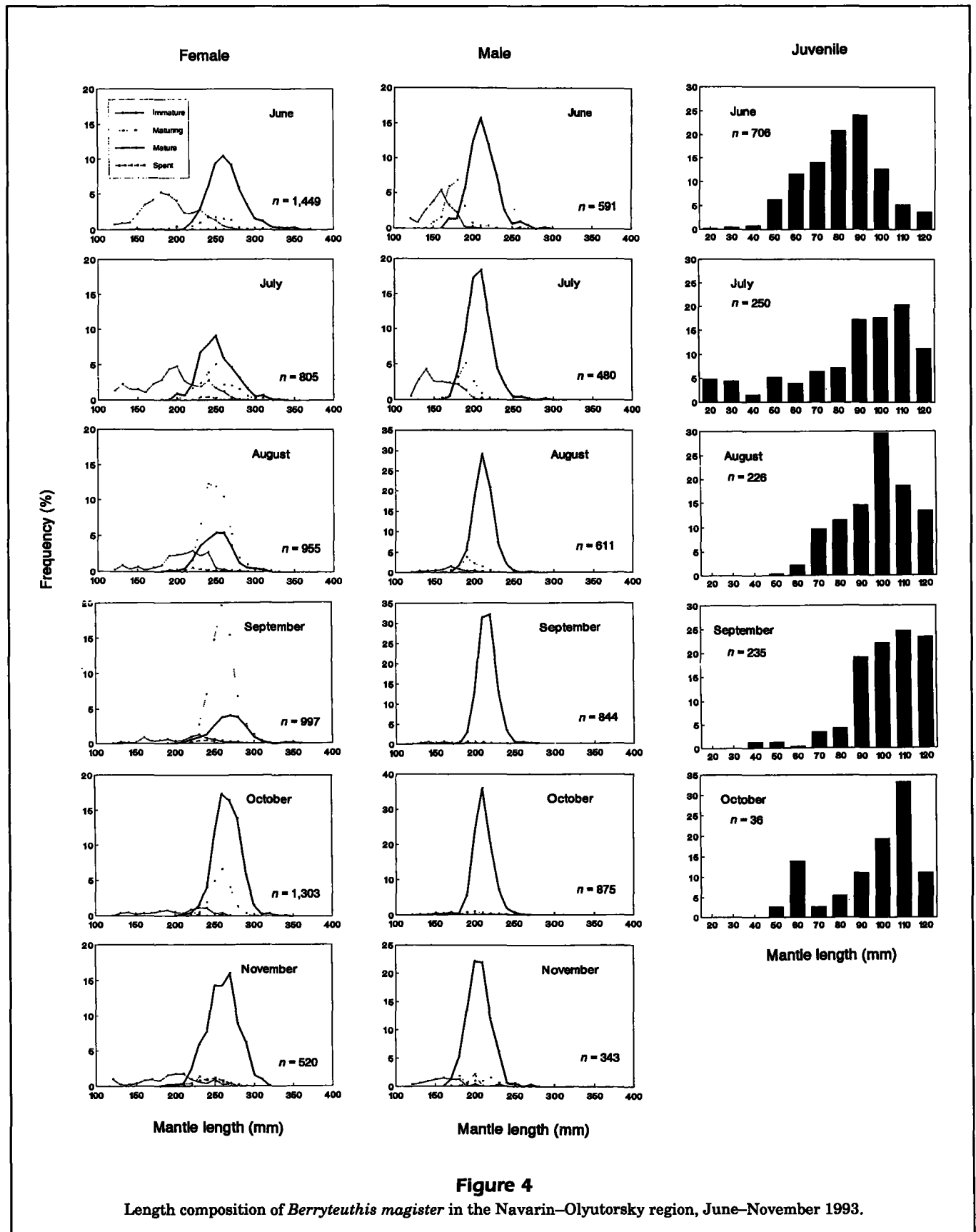


Figure 3

Length composition of *Berryteuthis magister* in the Olyutorsky Bay, June–November 1993.





The proportion of maturing females increased during the summer; this group predominated in catches (70%) in August–September. In October, maturing females decreased rapidly in numbers and almost disappeared in November. Their size range gradually narrowed from 170–320 mm in June to 210–280 mm in November. The length composition of maturing females was unimodal. Their modal classes remained constant (240–250 mm) from June to August, then increased slightly to 260 mm in September–October.

Mature females were predominant among females in June (53%). Subsequently their numbers decreased constantly until September (20%), then increased abruptly in October–November (70%). Length composition of mature females was always unimodal and wide (180–370 mm). Their modal lengths did not change from June to August (250–260 mm), but increased slightly in September–November (260–270 mm). The proportion of mature females that had mated was very high during June–August (86–90%), then diminished considerably by the beginning of October (34%). The numbers of spent females were low from June to September (<2%). In October, they almost vanished from catches, appearing again in November (5%). Their size range was wide (220–330 mm) with an indistinct mode at 240–250 mm.

Juvenile abundance was greatest in June–July and diminished successively until November. The length composition for this group varied greatly throughout the period of study, with one distinct modal size in June (80–90 mm), two in July (30 mm and 70 mm), one in August and September (100 mm and 110 mm, respectively), and two in October (60 mm and 119 mm).

**Navarin–St. Matthew region** In the Navarin–St. Matthew region (Fig. 5), immature and maturing males were most abundant in June (22% and 44%, respectively). They decreased progressively in number from July to September and almost disappeared in October (about 3% each). The largest immature specimens were 190–200 mm ML. Their size composition was unimodal (160–170 mm) and constant throughout the study. The size range of maturing males was narrow (150–220 mm). Their length distribution was unimodal, the modes shifting slightly from 170–180 mm in June–July to 190–200 mm in September–October.

The percentage of mature males steadily increased from June (35%) to September (60%). In October, almost all males were mature (92%). The size range of mature males was wide in June–July (160–290 mm) and narrowed slightly in October (170–260 mm).

Their length composition was unimodal (200–210 mm) throughout the study. Spent males appeared in August and represented about 4% of all males in September.

Immature females predominated in June–July (70–75%), then decreased abruptly in August (10%) and remained at this level until October. Size of the largest immature females diminished from 280 mm in June to 250 mm in October. Length composition was distinctly unimodal, the modes increasing from June (180–190 mm) to October (220–230 mm). The percentage of maturing females expanded from June (12%) to September (38%), but in October this group almost disappeared. Mantle length of maturing females ranged from 160 mm to 330 mm. Their length composition was unimodal (250–260 mm).

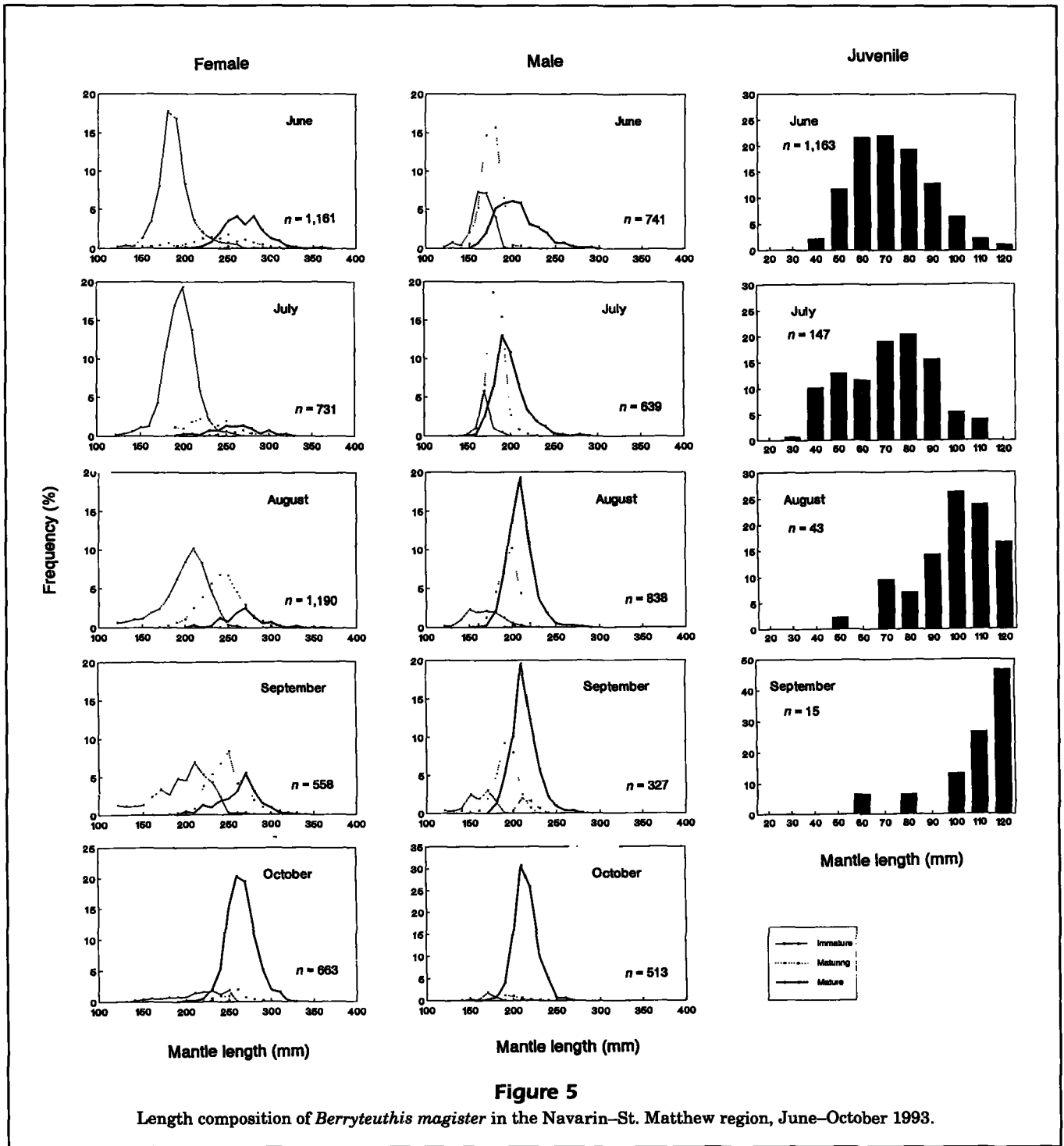
Numbers of mature females decreased from June (23%) to July (8%), later increased gradually until October (83%). Mantle-length range for mature females was wide in June (200–370 mm) and slightly narrower in October (200–320 mm). Length distribution was roughly unimodal at 260–270 mm. The proportion of mature females that had mated was high in summer (70–80%), then decreased abruptly in September (30–40%). A few spent females were encountered in this region, with mantle lengths largest in June (250–290 mm) and smallest in October (200–250 mm).

Juveniles were very abundant in June. In summer, they gradually decreased in numbers and almost disappeared by October. The minimum length of juveniles increased from 20 mm in June–July to 50–60 mm in September. Their length composition was unimodal; modal lengths increased from June (60–70 mm) to September (110–120 mm).

### Gladius microstructure

The gladius of *B. magister* exhibits the typical oegopsid plane in structure (Arkhipkin and Bizikov, 1991; Bizikov, 1991) and is composed of three layers: the middle layer, forming the rigid chitinous frame of the gladius; the inner layer, filling the conus inside and forming a thick cartilaginous layer on the ventral surface in the posterior part of the gladius; and the outer layer, which is reduced to a film-like pellicle covering the conus.

**Microstructure of the inner layer** A cross section of the anterior part of the conus has the shape of a broad isosceles triangle, the inner layer filling the entire space between the dorsal and lateral walls of the conus (Fig. 6A). Regular laminae were observed on sections within the inner layer. In contrast to statoliths, no distinct growth zones were visible on the

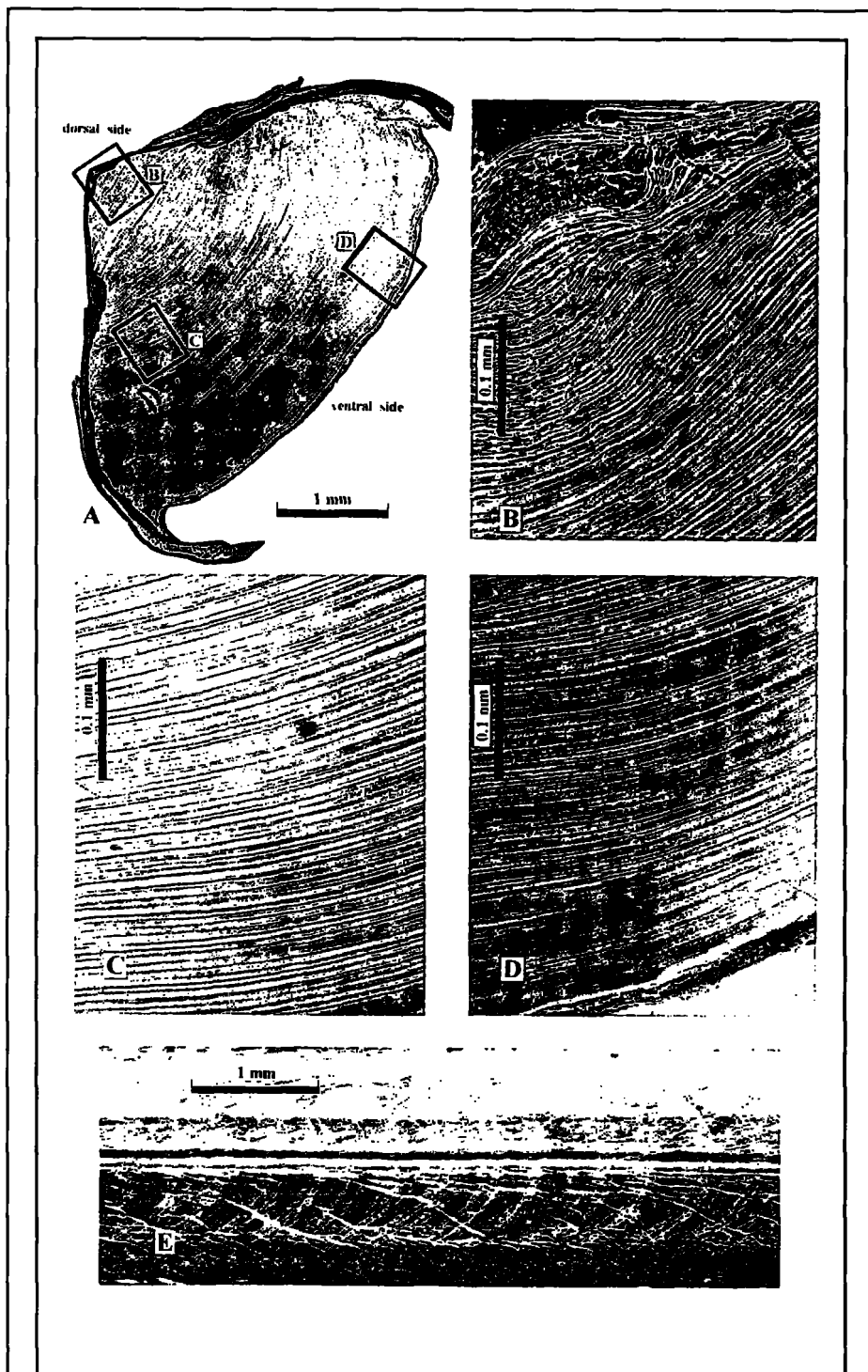


**Figure 5**

Length composition of *Beryteuthis magister* in the Navarin–St. Matthew region, June–October 1993.

sections. Laminae were rather quite uniform from the dorsal apex to the broad ventral side. Each lamina consisted of a broad translucent layer and a narrow dark layer. Counting of laminae commenced from the border between the middle and the inner shell layers in the dorsal apex of the section. The width of

laminae varied greatly along the section. The first 35–45 laminae in the dorsal angle of the section usually were narrow: (ca. 3.0–4.0  $\mu\text{m}$ , Fig. 6B). The middle part of the sections was formed by wide, uniform laminae (ca. 7–9  $\mu\text{m}$ , Fig. 6C), and the last 20–30 peripheral laminae narrowed to 4–5  $\mu\text{m}$  (Fig. 6D).



**Figure 6**

Microstructure of the gladius of *Berryteuthis magister* (light micrographs). (A) General view of a transverse cross section through the anterior part of the conus (mature male, ML 242 mm); (B–D) magnified views of the areas outlined by rectangles B–D in panel A; (E) increments of the middle layer visible on the dorsal surface of the gladius proostracum in reflected light (immature female, ML 273 mm; micrograph taken at 190 mm from the posterior end of the gladius).

**Microstructure of the middle layer** Laminae were visible as faint microstructural ridges on the dorsal surface of the proostracum (Fig. 6E). Each lamina consisted of a broad growth layer with a rather smooth surface confined by a narrow layer with a convoluted surface. Average width of laminae varied (depending on squid size) from 0.4–0.5 mm at 50 mm ML to 0.7–0.9 mm at 250–300 mm ML. In most specimens the laminae were best resolved in the middle part of the gladius. The general illegibility of laminae in the proostracum made it impossible to calculate individual growth rates with this gladius structure.

### Statolith microstructure

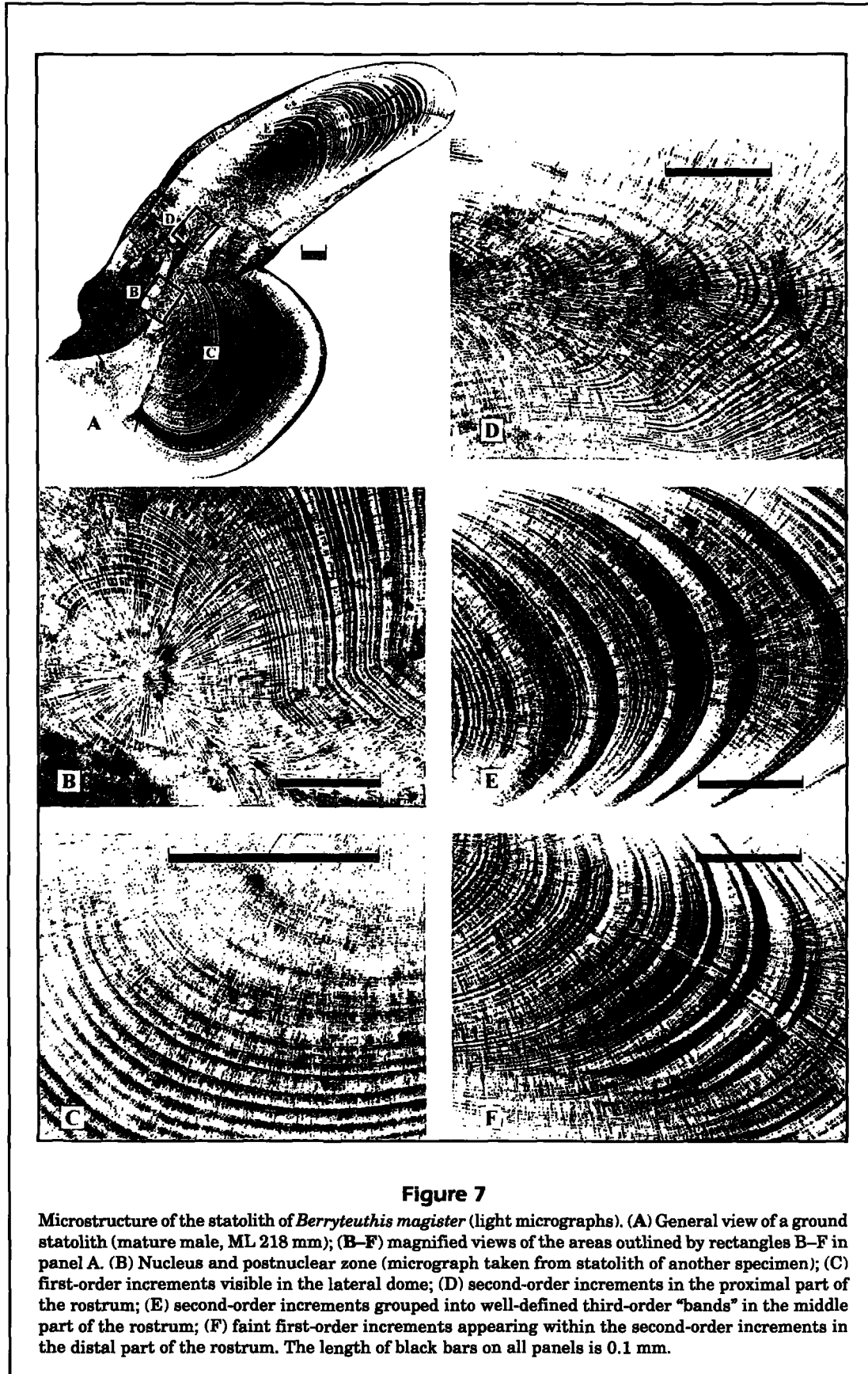
Growth increments were observed in all statolith preparations. The nucleus was oval-shaped and had a maximum diameter of 40–45  $\mu\text{m}$  along the rostrum axis (Fig. 7). The postnuclear zone lay beyond the nucleus; its color resembled that of the dark and peripheral zones. Approximately 10–12 narrow and rather uniform increments were observed within the postnuclear zone, each with a maximum width of 4.3–6.5  $\mu\text{m}$ . Maximum radius of the postnuclear zone was 65–75  $\mu\text{m}$ . The postnuclear zone was separated from the dark zone by the first prominent growth increment which was assumed (after Natsukari et al., 1993) to be the “natal ring.” Within the dark zone and sometimes in the peripheral zone, three types of growth increments were revealed. The first-order growth increments occurred mainly within the inner part of the dark zone. They were very narrow (ca. 1–1.2  $\mu\text{m}$ ) and faint, corresponding to the “fine rings” of Natsukari et al. (1993). However, they could not be seen in all statolith preparations, especially within the outer part of the dark zone and in the peripheral zone. The second-order growth increments (corresponding to the “heavy rings” of Natsukari et al., 1993) were prominent and seen both in the dark and peripheral zones. Their width varied from 4.7–7.1  $\mu\text{m}$  in the inner portion of the dark zone in the direction of the lateral dome to 9.5–12.2  $\mu\text{m}$  in the proximal portion of the rostrum, from 3.5 to 4.3  $\mu\text{m}$  in the midpart of the rostrum, and from 4.7 to 5.4  $\mu\text{m}$  in the distal portion of the rostrum. Usually 4–6 first-order growth increments were observed within each second-order increment in the inner portion of the dark zone, and 3 or 4 increments within the peripheral zone (if they were present). In both the middle and distal portion of the rostrum, second-order increments were grouped within third-order increments: 4–7 second-order growth increments in each third-order increment. These third-order growth increments were not noted in Natsukari et al. (1993).

### Validation of statolith growth increments

The presence of three different types of growth increments within statoliths prevented us from assuming that any of them were deposited daily. Therefore, we attempted to validate the periodicity of growth-increment deposition on the basis of two independent and indirect methods.

**Comparison of growth increment numbers in statoliths and gladii** We investigated statoliths and gladii within the entire size range of *B. magister* sampled from early juveniles (35–40 mm ML) to large mature adults (280–330 mm ML). The total number of laminae within the inner layer of the gladius corresponded well with the total number of second-order growth increments within the statoliths (Fig. 8A). The estimated value of the slope was close to 1 (Table 2), which indicates that growth increments in statoliths and laminae within the inner layer of gladii were laid down synchronously. The results of increment validation from the first method were checked by the following second method.

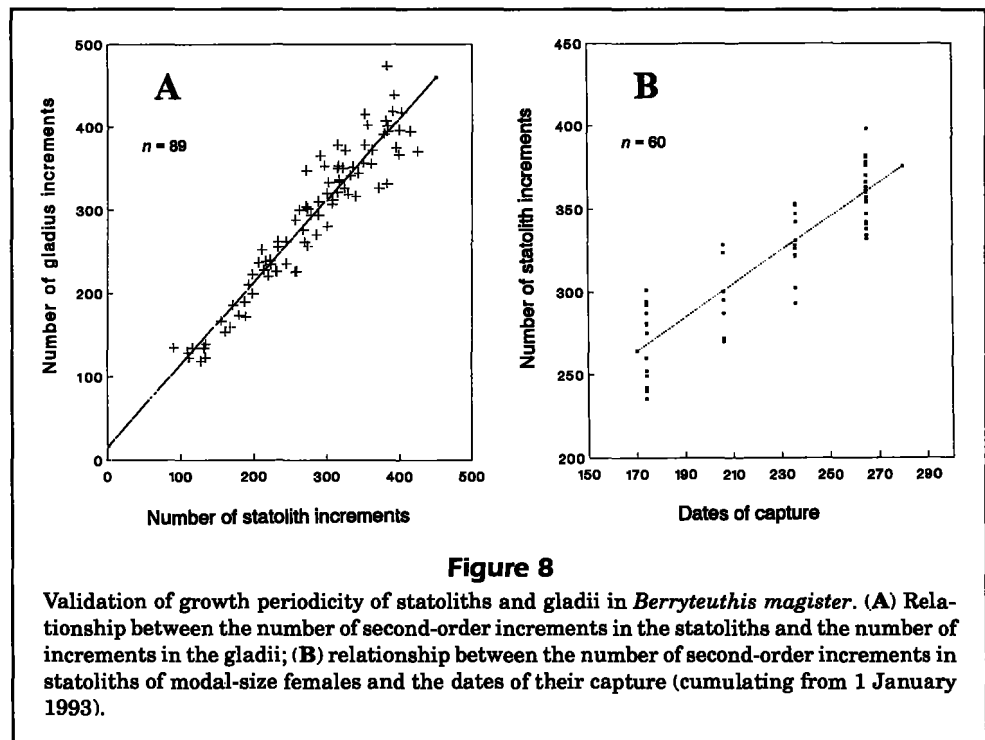
**Growth-increment analysis of successive modal classes** The method of comparison of difference between mean ages of successive modes with elapsed days is relevant when 1) good resolution of the modes is possible, and 2) these modes represent the same cohort of squid, without substantial emigration and immigration (Caddy, 1991). It is known that sexual maturation affects the growth of both sexes and that during maturation squid either slow or cease somatic growth (Forsythe and van Heukelem, 1987). Hence, data on *B. magister* males were inappropriate for our purpose because most of them were mature during the period of our study (Figs. 3 and 4) and, therefore, a mode of male length composition might consist of several cohorts. Length-frequency compositions of females in Olyutorsky Bay were rather complex, especially during the summer (Fig. 3), and thus we were prevented from choosing progressive modal classes. Unfortunately, we had no statoliths from well-distinguished modal classes of females in the Navarin–St. Matthew region (Fig. 5). However, in the Navarin–Olyutorsky region, a clearly distinguishable modal group of females (immature in June–July, gradually maturing in August–September) was traced within the catches from June to September. The modal sizes of these females increased progressively from 180–190 mm in June to 250–270 mm in September, suggesting that these females belonged to the same cohort (Fig. 4). This group of females was analyzed from four successive monthly samples taken from June to September.



Comparison of the difference between the average number of second-order statolith growth increments of females representing the modal size classes in two successive samples with the number of days elapsed between the samples showed that their values were very close (Table 3). This provided further confirmation of daily formation of each second-order increment. The relationship between the number of second-order growth increments of modal-size females and their date of capture was approximated well by linear regression (Fig. 8B; Table 2). The estimated slope value (1.011) was very close to 1, further suggesting that a second-order increment may correspond to one day.

### Age structure

Minimum age (40 and 47 days) was observed in two juveniles of 26 and 24 mm ML, respectively, caught in the Navarin–Olyutorsky region in July. The oldest male (mature, 295 mm ML) that was aged was 473 days. The two oldest females (276 and 369 mm ML) were also mature and were 479 days old. All these animals were captured in June in the eastern part of the Navarin–Olyutorsky region. During summer and fall, the stock structure of *B. magister* was rather complex. Each month, both in Olyutorsky Bay and the Navarin–Olyutorsky region, we captured squid of 5–12 (usually 7–8) month classes (Figs. 9 and 10).



**Figure 8**

Validation of growth periodicity of statoliths and gladii in *Beryteuthis magister*. (A) Relationship between the number of second-order increments in the statoliths and the number of increments in the gladii; (B) relationship between the number of second-order increments in statoliths of modal-size females and the dates of their capture (cumulating from 1 January 1993).

**Olyutorsky Bay** In Olyutorsky Bay (Fig. 9), May–July hatched males (age: 310–390 d) and females (age: 325–385 d) were the most abundant mature animals in June. Immature females (age: 300–320 d) of 180–210 mm ML were hatched during July, August (mainly), and September and were not abundant. Immature males of 150–210 mm ML were hatched in August and September.

In August, the stock structure of *B. magister* was considerably different from that observed in June (Table 4). Mature June- and July-hatched squids almost disappeared from catches. Immature and maturing August- and September-hatched squid of 210–270 mm ML (age: 320–350 d) prevailed among females, whereas among males the most abundant were August–October hatched mature individuals of 180–240 mm ML (age: 300–350 d). Small maturing

**Table 2**

Parameters of the linear function  $Y = a + bX$ , their standard deviations in parentheses,  $r$ -squares,  $t$ -statistics, and null hypothesis tests ( $b = 1$  at  $\alpha = 0.05$ ) for two relationships between 1) the number of second-order increments in the statoliths ( $X$ ) and the number of laminae in gladii ( $Y$ ) and 2) the number of the second-order increments in statoliths of modal-size females and the dates of their capture (cumulating from 1 January 1993).

Relationship	$n$	$a$	$r^2$	$b$	$t$ -statistic	Results of $H_0$ -test
1	88	13.90 (2.887)	0.8959	0.9949 (0.03655)	0.1396	do not reject
2	60	92.38 (19.94)	0.7904	1.0116 (0.0684)	0.1688	do not reject

males of 150–190 mm ML represented the November month class.

During September, fall-hatched squid still predominated in catches. There were twice as many October-hatched females in September than in August. September- and October-hatched maturing females of 240–270 mm ML (age: 340–370 d) occurred in great numbers. Immature December–January hatched females and males of 150–210 mm ML composed up to 15% of the total catches. Mature males of 210–240 mm belonged mainly to September–October hatched squid. Juveniles of 20–40 mm ML were June-hatched, whereas larger ones (60–120 mm ML) belonged to March–May month classes.

**Navarin–Olyutorsky region** Age structure of *B. magister* in the Navarin–Olyutorsky region (Fig. 10) in June was somewhat different from that in Olyutorsky Bay (Table 4). During the first half of

June, 9 month classes for females and only 5 month classes for males were observed. One-third of females (250–360 mm ML, 380–460 d) had mated and belonged to February–May month classes. The majority of the catches were represented by summer-hatched females (maturing specimens of 210–240 mm ML, 300–320 d) and mature specimens (240–340 mm ML, 330–370 d). Among males, summer-hatched individuals were most abundant (220–250 mm ML, 320–340 d). Immature males, and females (160–190 mm ML, 260–280 d) belonged to the September month class. Juveniles caught in considerable numbers were from late fall (90–120 mm ML), winter (40–80 mm ML), and spring (26–37 mm ML) hatching. In the second half of June, maturing and mature squids from the summer hatch still predominated for catches of both males and females. However, the proportion of fall-hatched squid approximately doubled.

**Table 3**

Results of growth-increment validation in *B. magister* statoliths, obtained by the method of comparison of difference between average numbers of the second-order increments (mean age in d) of two successive modes of females with the number of days elapsed between the samples.

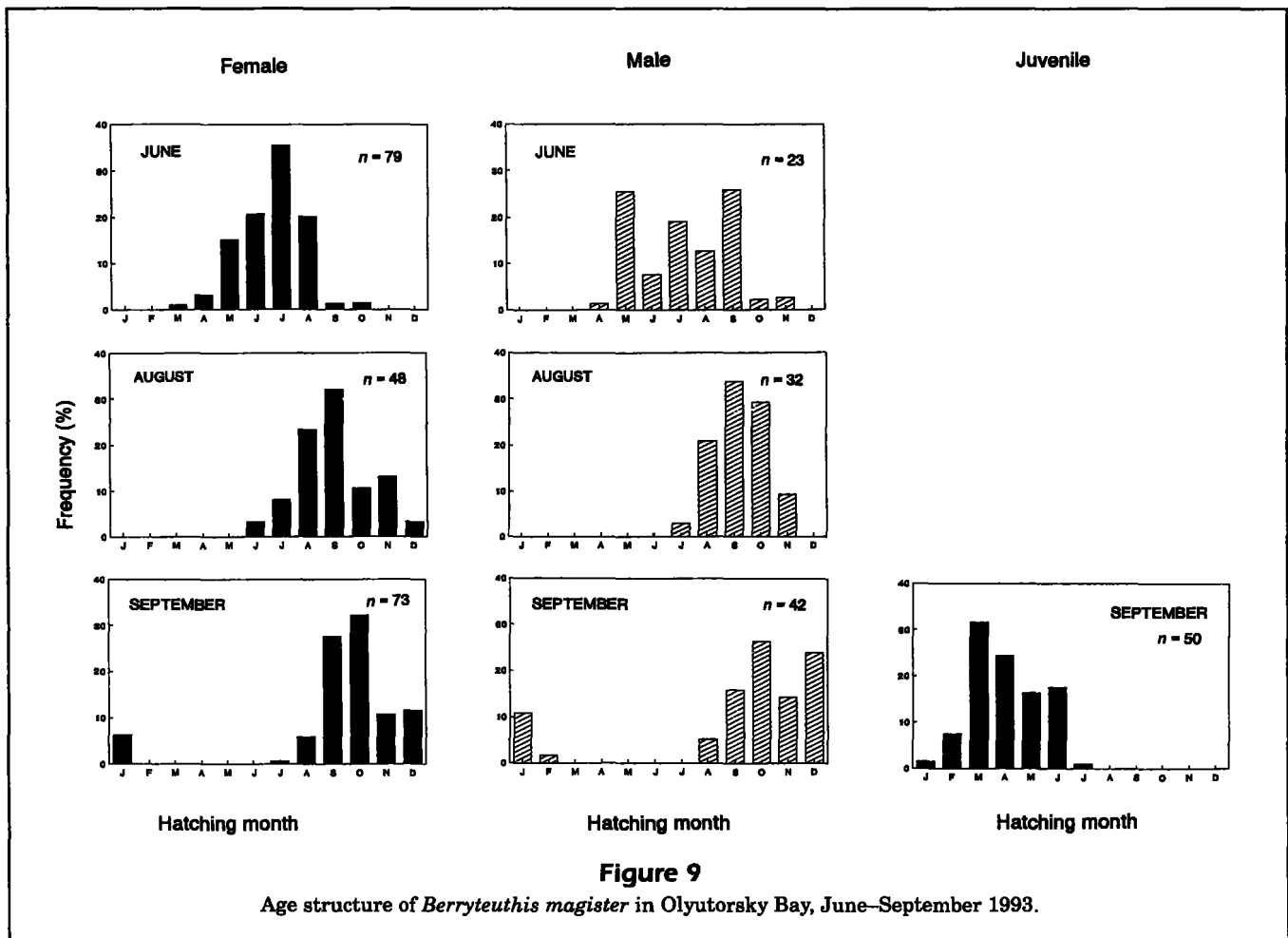
Sample no. (i)	Sampling date (T)	Modal ML (mm)	Mean age, d (A)	SD of mean age	Number of squid in sample	Elapsed days $T_{i+1} - T_i$	Differences between means $A_{i+1} - A_i$
1	23 June	170–190	265.3	22.8	13	—	—
2	25 Jul	230–260	296.4	21.1	6	32	31.1
3	24 Aug	240–260	330.8	18.9	22	30	34.4
4	22 Sep	250–270	361.0	17.1	24	29	30.2

**Table 4**

Coefficients of similarity (CS, according to Shorygin, 1952) of *B. magister* age structures in Olyutorsky Bay (O) and the Navarin–Olyutorsky region (N) in different months. (1) and (2) = first and second halves of a given month, respectively. Above right — CS's of age structures of males; below left — CS's of age structures of females.

			A	B	C	D	E	F	G	H	I	J
O	Jun	A	100	45.7	26	68.7	55.4	37	35.9	31.7	23.2	4.9
O	Aug	B	34.9	100	56.8	33.2	54.9	71.5	56.2	65.4	56.8	34.3
O	Sep	C	9.4	59	100	21.5	36.5	74.7	72.8	68.8	67.2	66.1
N	Jun/1	D	76	42.2	15.1	100	55.2	32.1	28.3	19.4	18.3	0.4
N	Jun/2	E	64.5	54.4	41.7	63.9	100	47.5	41.3	32.1	34.2	19.3
N	Jul	F	27.3	73.9	74.5	34.2	50.5	100	81	72.9	72.9	62.7
N	Aug	G	27.7	77.2	76.9	36	54.3	86.9	100	68.1	61.9	67.5
N	Sep	H	11.8	56	74.8	19.3	44.1	63.9	66.2	100	79.7	58.3
N	Oct/1	I	7.1	43.5	66.7	15.5	33.3	63.3	57.2	55.2	100	52
N	Oct/2	J	2.1	34.1	58.4	9.8	22.2	59.6	51.4	45.6	72	100





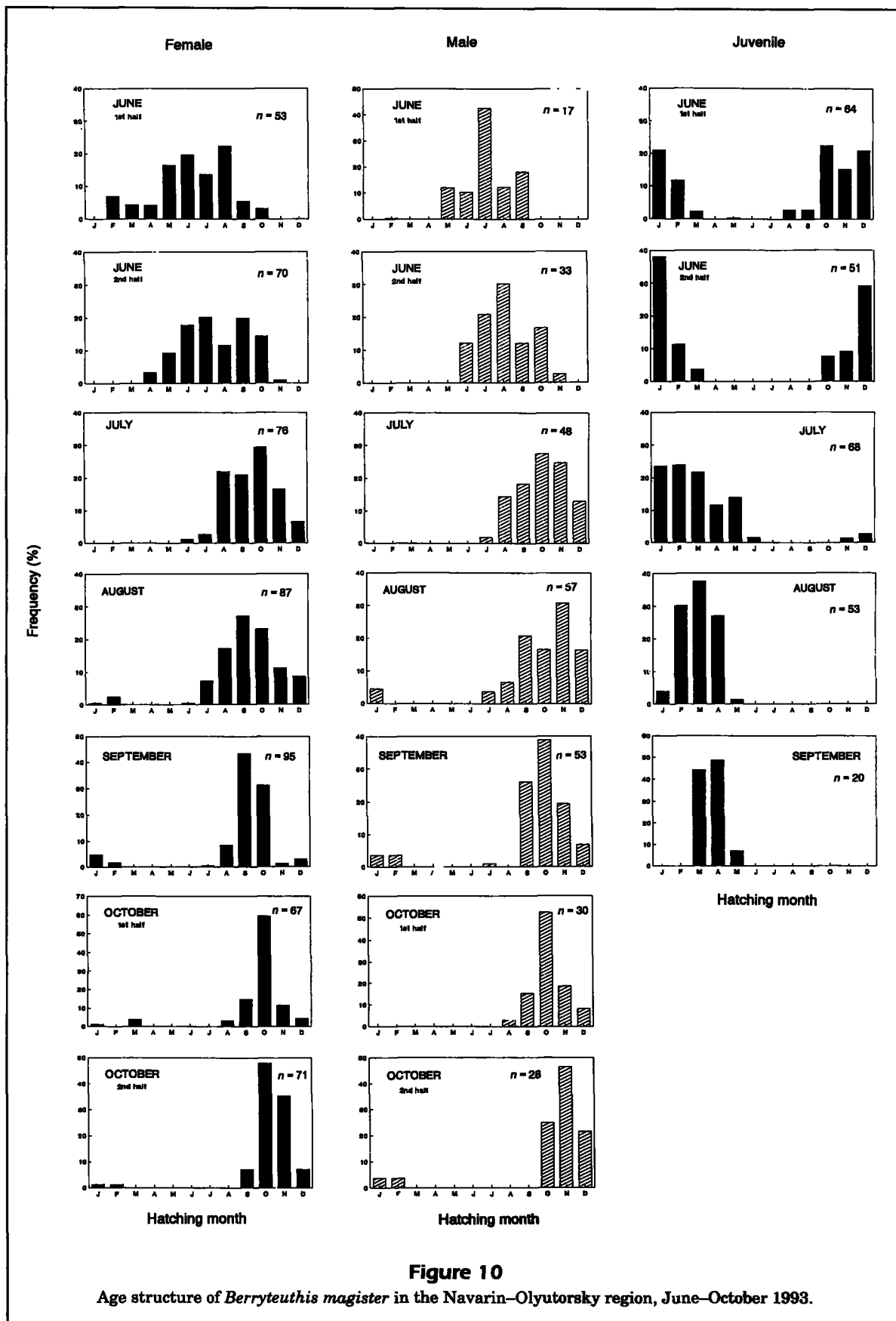
In July, the age composition of *B. magister* changed considerably compared with that for June (Table 4). Among large mature squid (males of 210–240 mm ML, females of 240–300 mm ML), the most abundant group belonged to the August month class (age: 320–340 d), whereas the May and June month classes almost vanished. September- and October-hatched females, which were immature in June, began maturing and a great majority of them attained maturity stage 3. Immature squid of 150–210 mm ML were represented by October and November month classes. Along with grown winter-hatched juveniles (up to 80–120 mm ML) were small juveniles (30–60 mm ML) of April and May month classes.

In August, age composition remained almost the same as that in July (Table 4). Maturing August–October females of 240–300 mm ML and mature September–October males were predominant. Spent females belonged to the summer hatch (age 360–410 d). Immature *B. magister* of 180–240 mm ML were of November and December hatching months. A proportion of January- and May-hatched juveniles de-

creased, and March- and April-hatched individuals increased.

In September, mature and spent summer-hatched squid almost disappeared from the region. As in August, fall-hatched squids (mainly September and October month classes) predominated, particularly maturing females (230–280 mm ML, 330–370 d) and mature males (210–240 mm ML, 325–380 d). Immature females and immature, maturing, and mature males of 150–210 mm ML were from November–January month classes. Juveniles (70–120 mm ML) belonged to the spring hatch (March and April).

September- and October-hatched females at maturity stages 4 and 5 (240–290 mm ML, 330–390 d) predominated in catches during the first half of October, but, in contrast with September catches, the proportion of mature females increased sharply. The proportion of September-hatched males decreased, but the October-hatched ones increased. All these males were mature (200–235 mm ML, 340–385 d). Immature females of 130–140 mm ML belonged to the March class. In the second half of October, the



**Figure 10**

Age structure of *Berryteuthis magister* in the Navarin–Olyutorsky region, June–October 1993.

number of November-hatched squid increased three times for females and twice for males. Almost all fall-hatched females (240–290 mm ML, 350–380 d) were mature and had already mated. Fall-hatched males were 205–238 mm ML (352–385 d).

Analysis of coefficients of similarity (CS) (Table 4) revealed considerable differences in stock structures of *B. magister* observed in different months in Olyutorsky Bay. However, high values of CS (more than 70%) were noted (in both sexes) between the samples taken in June from Olyutorsky Bay (OB) and from the Navarin–Olyutorsky region (NOR); between OB in August and NOR in July; and between OB in September and NOR in July, October, and September. The CS's between the samples taken in different months within the NOR were generally low. However, there was a high resemblance of the stock structure for both sexes between July and August: for females between the first and the second half of October and for males between September and the first half of October. Samples taken in July and Sep-

tember to the first half of October also showed a high CS in males (Table 4).

### Growth and maturation

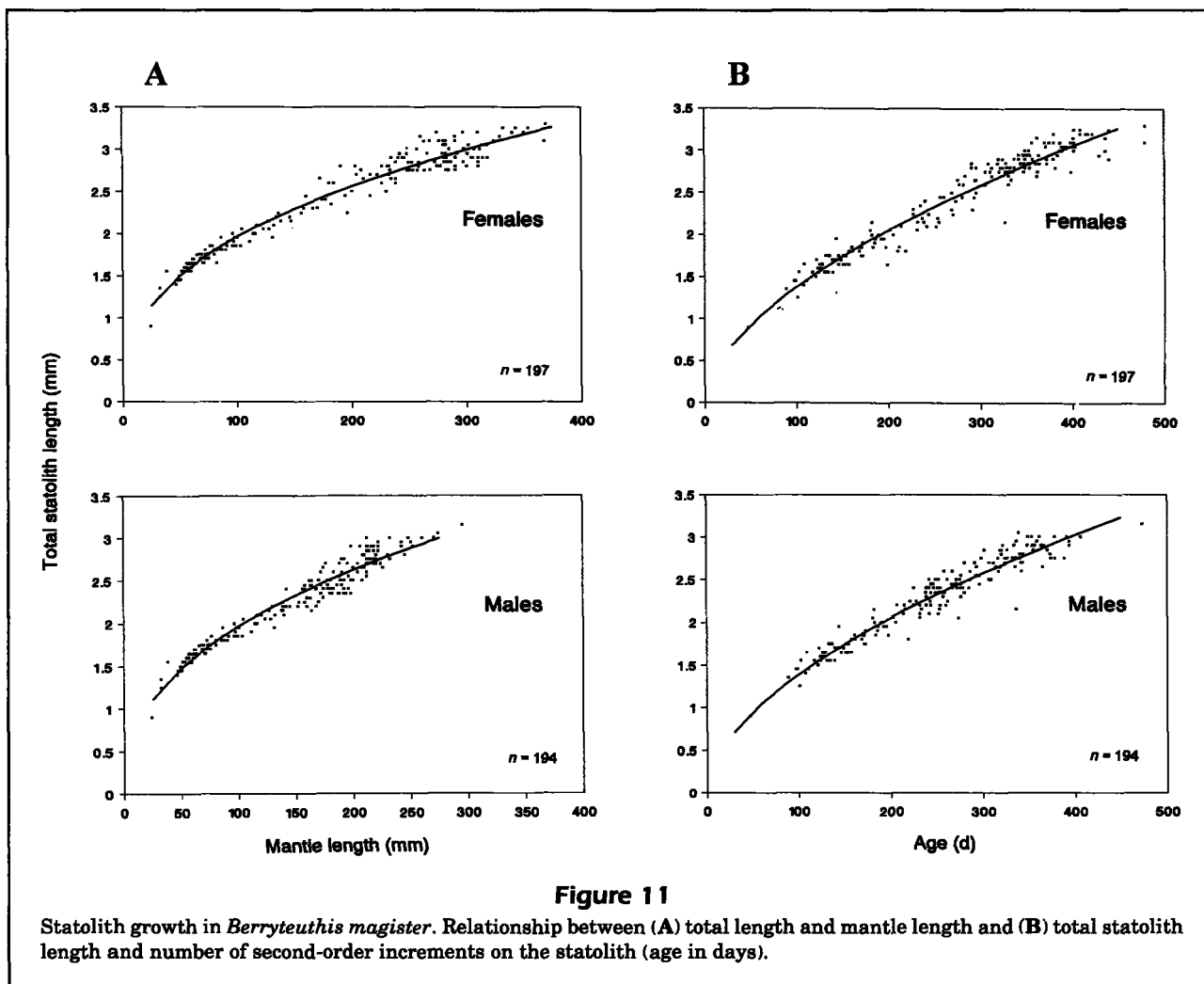
**Statolith growth** Statoliths of early juveniles (24–32 mm ML) were unusually large; their total length (STL) ranged from 0.9 to 1.35 mm (3.8–4.2% ML, respectively). During ontogenesis, they grew rather slowly and by age 450–470 d increased 2.5–3 times in length. In both sexes, statolith growth was best fitted by a power function and did not reveal sexual dimorphism (Fig. 11, A and B). Allometric growth of the total statolith length (STL) versus mantle length (ML) was negative with a high value of allometric coefficient ( $>0.38$ ) (Fig. 11, C and D; Table 5). STL allometric growth rates were higher in males than in females, resulting in larger sizes for male statoliths among the same-size animals.

**Squid growth** Length-at age data assigned for each hatching month demonstrated that *B. magister* be-

**Table 5**

Parameters of the power function  $Y = aX^b$  and logistic growth function  $Y_t = K/(1 + ((K - Y_0)/Y_0) \exp(-rt))$ , their asymptotic standard errors and r-squares of different relationships of *B. magister*. STL = total statolith length (mm); ML = mantle length (mm); Age = age (d); BW = body weight (g).

Parameter	Estimate	Asymptotic standard error	R <sup>2</sup>
<b>Allometric growth curve: STL versus ML</b>			
Females			
<i>a</i>	0.3330	0.009229	0.938
<i>b</i>	0.3851	0.005190	
Males			
<i>a</i>	0.2929	0.009551	0.943
<i>b</i>	0.4144	0.006487	
<b>Power growth curve: STL versus Age</b>			
Females			
<i>a</i>	0.09859	0.004572	0.931
<i>b</i>	0.5732	0.008117	
Males			
<i>a</i>	0.1061	0.005687	0.930
<i>b</i>	0.5591	0.008664	
<b>Power curve: BW versus ML</b>			
<i>a</i>	0.0001765	0.00003462	0.907
<i>b</i>	2.6743	0.5214	
<b>Logistic growth curve: ML versus Age</b>			
Females			
<i>r</i>	0.01266	0.0007469	0.919
<i>K</i>	343.8	11.29	
<i>Y</i> <sub>0</sub>	13.25	1.936	
Males			
<i>r</i>	0.01358	0.0006863	0.946
<i>K</i>	271.4	6.242	
<i>Y</i> <sub>0</sub>	12.98	1.502	



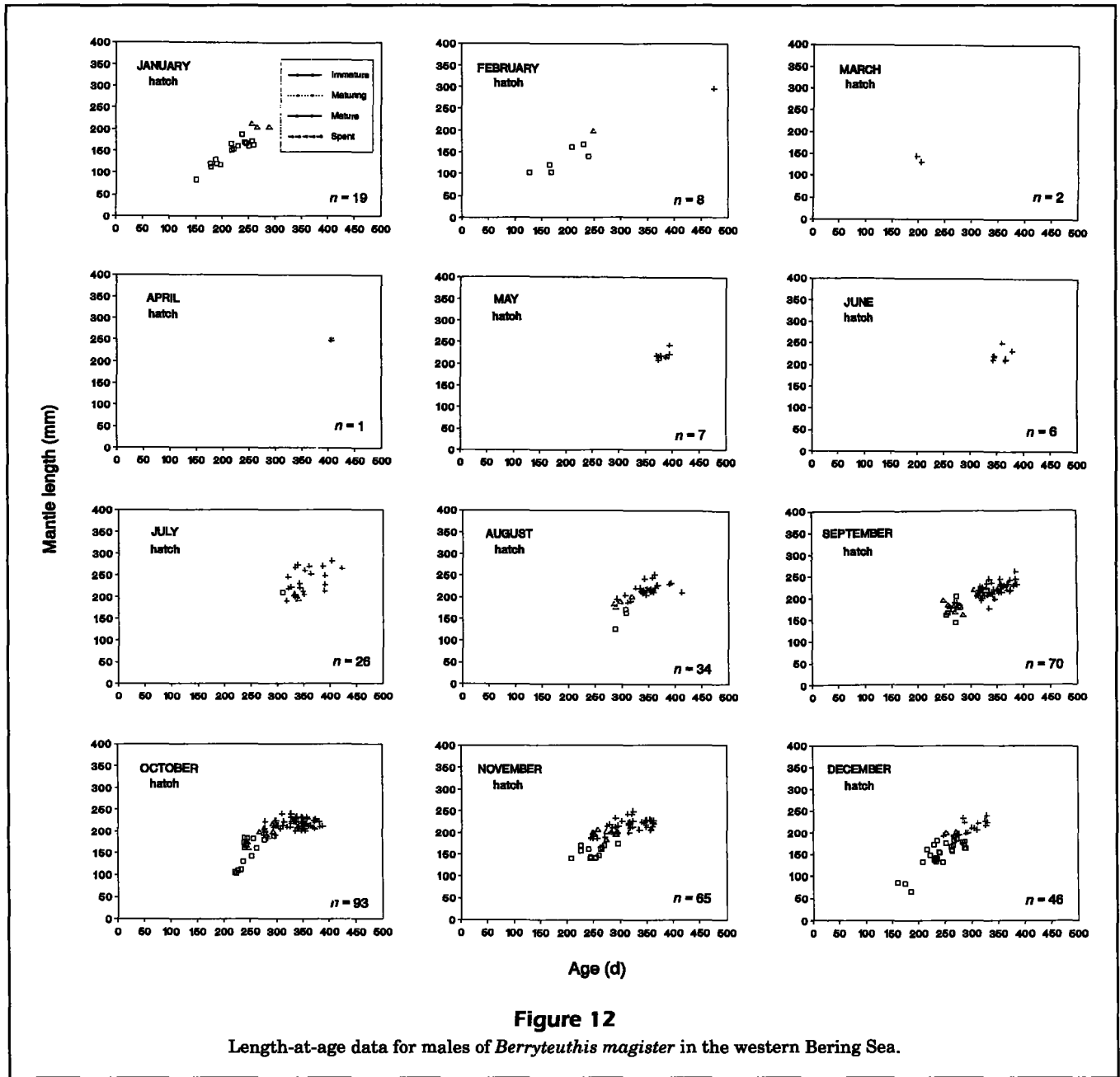
longed to different month classes, differed in size, and represented different sections of the group growth curves. There were only a few data on spring-hatched *B. magister*, especially for males (Figs. 12 and 13). This prevented the comparison of growth rates of the same-age squids from, for example, winter- and summer-hatched animals.

The growth curve of mantle length versus age was best fitted with a logistic growth curve (Table 5). Males and females grew at the same growth rate until 210–240 d (Fig. 14, A and B). Thereafter, males grew more slowly than females and at age 390 d their mean ML was approximately 50 mm less than that of females.

The relationship of mantle length to body length did not show any pattern of sexual dimorphism (Fig. 14C). The power coefficient was less than 3 (2.62), demonstrating the relative slenderness of the body of large-size squid. According to calculated weight growth curves, females began to exceed males in body

weight later than in mantle length (at age 270 d) (Fig. 14D).

*Berryteuthis magister* is a rather slow-growing squid. Daily growth rates (DGR) in ML were low in juveniles (0.27–0.35 mm·d<sup>-1</sup>), reached their maximum values in males at ages 180–210 d (ca. 0.9 mm·d<sup>-1</sup>) and in females at ages 210–270 d (1.05–1.08 mm·d<sup>-1</sup>), then gradually decreased to juvenile levels for females and fell even lower for males (Fig. 14E). Juvenile DGR in BW were very low (0.02–0.06 g·d<sup>-1</sup>). However, they quickly increased with age and attained maximum values at older ages in both males and females, 270–300 d and 300–330 d, respectively (Fig. 14F). The instantaneous rate of growth (G) in ML was maximum in early juveniles (0.0118–0.0124), then gradually decreased to the age of 420 days, in males to a greater extent than in females (0.0007 and 0.0012, respectively). Calculated values of G in BW were similar to the trend in ML (Fig. 14, G and H).

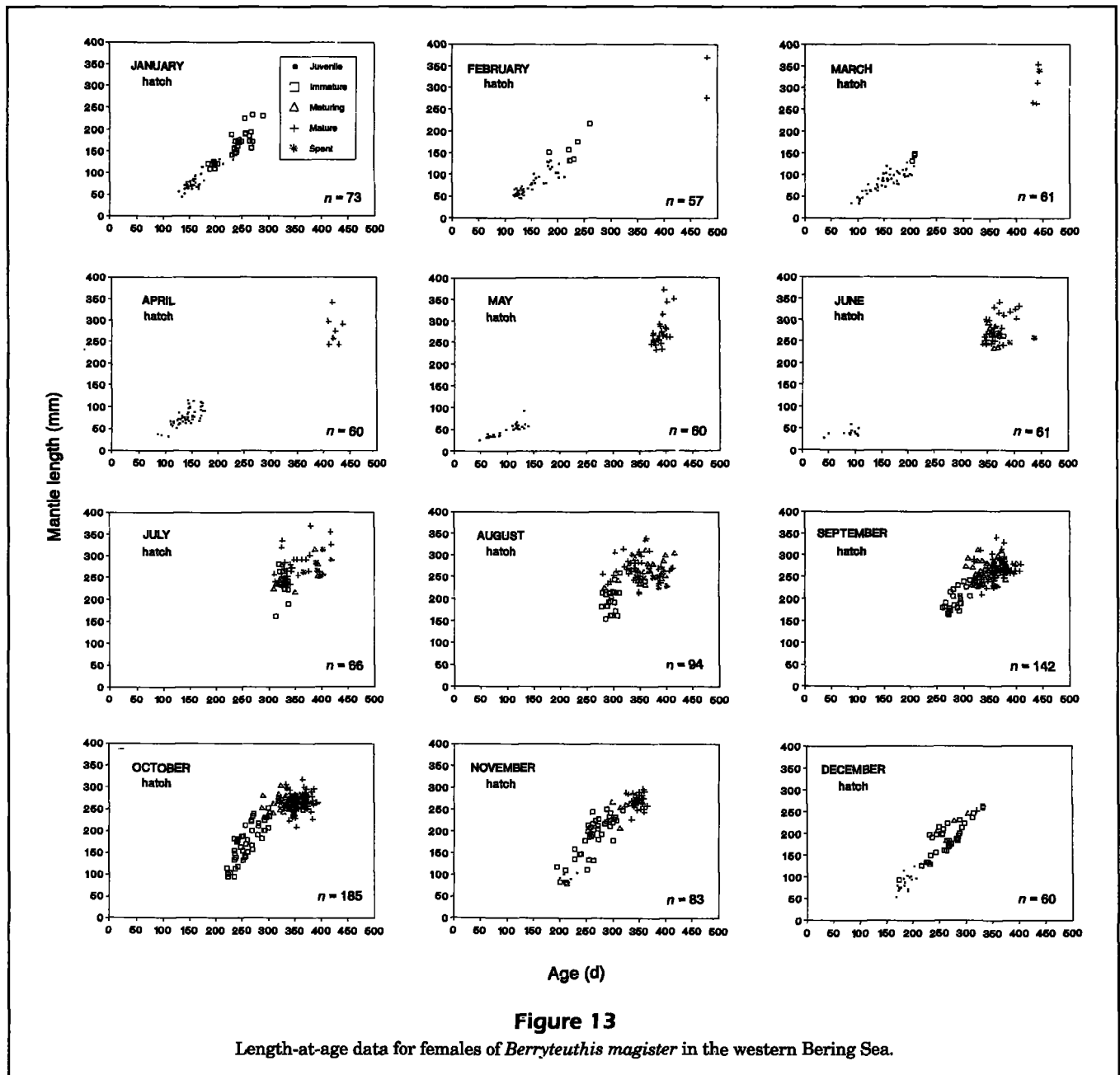


**Figure 12**  
Length-at-age data for males of *Beryteuthis magister* in the western Bering Sea.

**Maturation with growth** Males and females of various month classes matured at different sizes and ages (Figs. 12 and 13). In our samples, juveniles were mainly from a winter-hatched group, mature specimens at different substages of maturity stage 5 were from a summer-hatched group, and squid of various stages of maturation and maturity were from a fall-hatched group. Thus, it was reasonable to analyze group rates of *B. magister* maturation by using the data on both sexes from the fall-hatched group and females from the summer-hatched group (because all

summer-hatched males were already mature during the period studied).

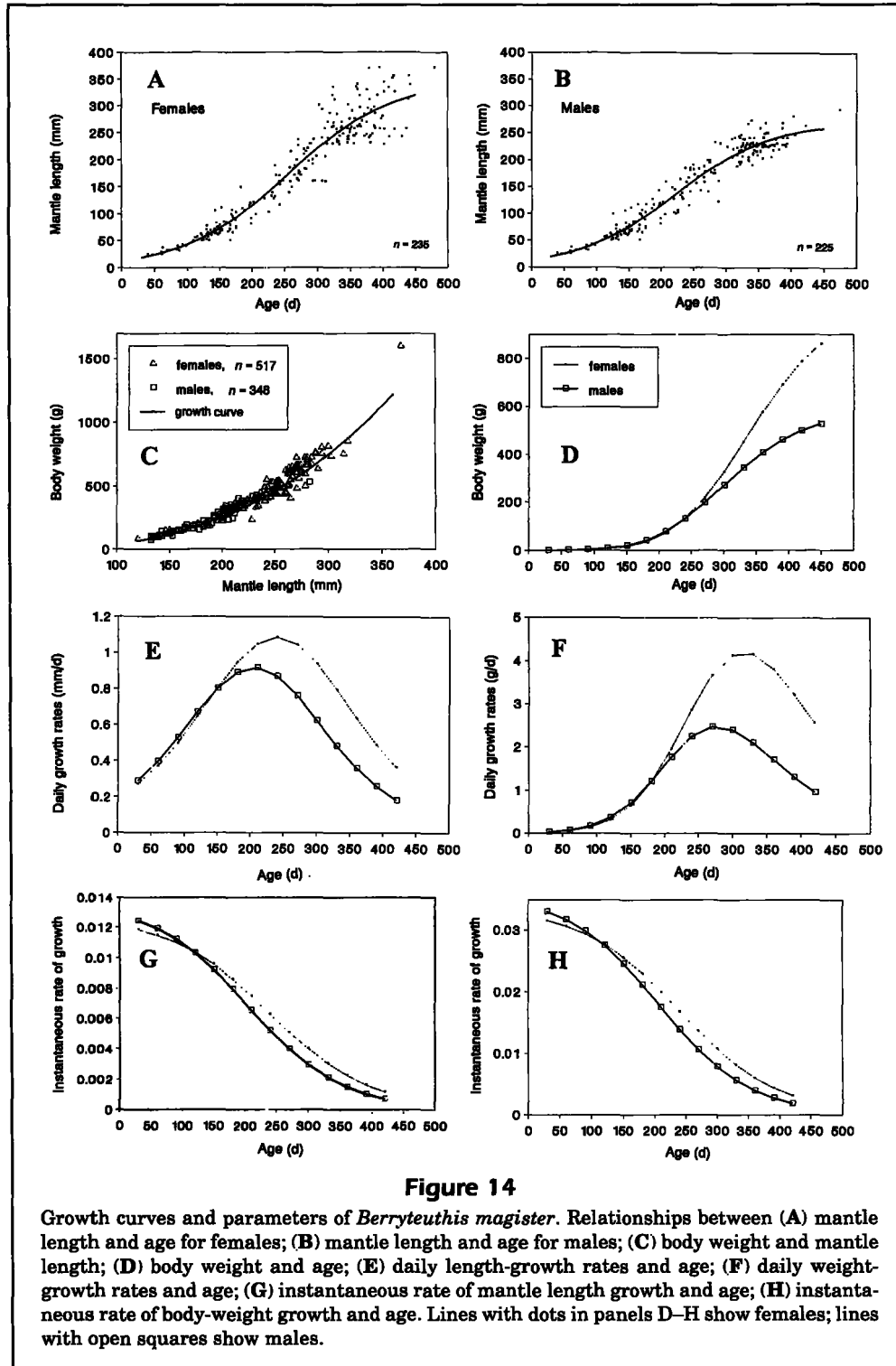
Ages at various maturity stages (maturity rates) differed between the sexes (Fig. 15). Males began maturing earlier than females. All males were at maturity stage 1 at 210 days. However, at 240 days almost half of them reached maturity stage 2 (a few specimens already being mature). By 300 d, the proportion of immature and maturing males (maturity stages 3 and 4) was greatly reduced, with most of the males already mature. At ages older than 310 d,



there were only mature and occasionally spent specimens (we caught only two spent fall-hatched males at 330 and 340 d). All males at 370–380 d were mature and showed many spermatophores in the Needham sac and no apparent gonad degeneration. An extensive transition of males into the spawning and spent conditions (maturity stage 6) would have to occur far later than age 380 d.

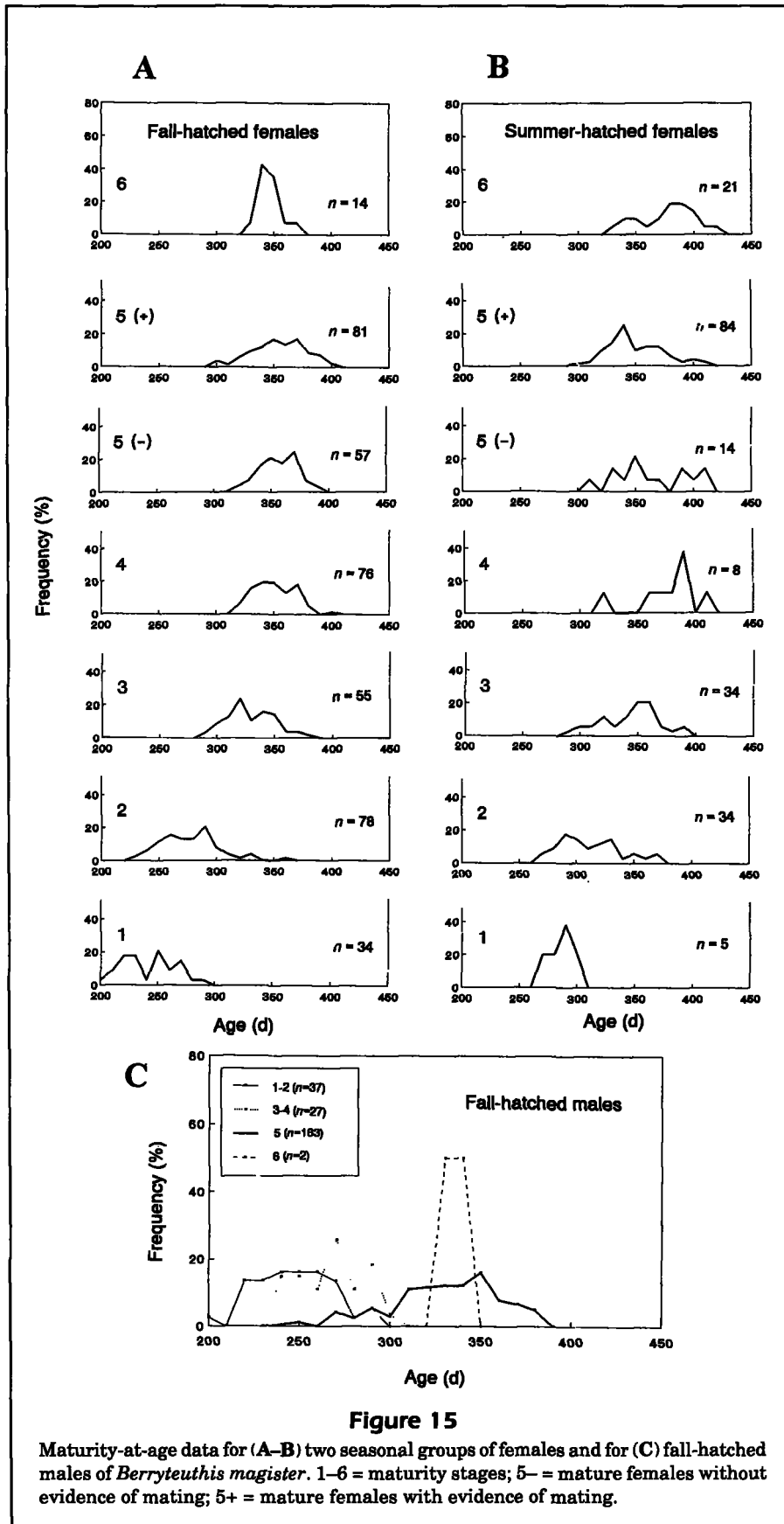
Between 210 and 280 d, all fall-hatched females were immature, with an increasing proportion of females at maturity stage 2. Females started maturing (maturity stage 3) at 290 d. At 330 d, there were

still some immature animals, but most of the females were maturing (maturity stages 3 and 4). At this age, there were already a small number of mature and even four spent females. The proportion of females at maturity stage 3 decreased from 330 d to 360 d, and disappeared at 390 d. Between 330 and 390 d, the proportion of females at maturity stage 4 remained approximately constant, whereas mature females gradually increased. Mature females began mating between 300 and 320 d, most of them mating by 350–370 d. There was evidence for both early and late-maturing females, with the bimodal distribution



obvious at all maturity stages except for spent-stage animals. The difference between these modes was 30–40 d. Like the fall-hatched males, almost all fall-hatched mature females were in good condition, with-

out any pattern of reduction of the gonad, liver, and mantle. Early maturing and late-maturing groups were observed also among summer-hatched females, with a bimodal distribution for spent females (Fig. 15).



**Figure 15**

Maturity-at-age data for (A-B) two seasonal groups of females and for (C) fall-hatched males of *Berryteuthis magister*. 1-6 = maturity stages; 5- = mature females without evidence of mating; 5+ = mature females with evidence of mating.



## Discussion

### Statolith and gladius microstructure with validation of growth increments

Statoliths of all previously investigated species usually had one or two kinds of growth increments, usually referred to as first- and second-order growth increments. Growth increments of only one kind occur in ommastrephids: *Illex illecebrosus* (Dawe et al., 1985), *Illex argentinus* (Rodhouse and Hatfield, 1990; Arkhipkin, 1993), and *Nototodarus sloanii* (Uozumi and Ohara, 1993). Growth increments of two types were found mainly in loliginids: *Loligo opalescens* (Spratt, 1978), *Photololigo edulis* (Natsukari et al., 1988), and *Loligo vulgaris* (Natsukari and Komine, 1992); and in gonatids: *Gonatus fabricii* (Kristensen, 1980). The first-order growth increments or “rings” in loliginids and gonatids and the growth increments in ommastrephids have been validated as daily increments, whereas an interpretation of the second-order growth increments has not been consistent in different studies. Some authors (Spratt, 1978; Kristensen, 1980) have assumed them to be of fortnightly or monthly origin; others have not been able to find any definite pattern in their deposition and have treated them like first-order increments (Natsukari et al., 1988; Natsukari and Komine, 1992). In this investigation, it was revealed that unlike statoliths of loliginids and ommastrephids, ground statoliths of *B. magister* exhibit three kinds of growth increments: namely, of the first, second, and third orders. Previously, Natsukari et al. (1993) noted only two kinds of growth increments in *B. magister* statoliths. We revealed that the “second-order growth increments” were grouped into distinct “bands” of the third order, very similar in structure and appearance to loliginid “second-order bands.”

Natsukari et al. (1993) hypothesized that the first-order growth increments (“fine low contrast rings”) in *B. magister* were deposited daily. However, the authors did not validate the periodicity of “fine rings” directly. Their suggestion that there were two different modes of year classes for *B. magister* encountered in the southwestern part of the Sea of Japan, as assumed earlier (Yuuki and Kitazawa, 1986), seemed to be rather speculative without some direct verification (e.g. by statolith ageing techniques).

Squid, like fishes, have physiological processes that are related to diel rhythms (Campana and Neilson, 1985) reflected in periodical changes in metabolic processes and resulting in different rates of deposition onto various hard structures (e.g. gladius and statolith). We found that within the inner layer of the gladius there were regular well-defined laminae

that were not grouped into any other growth zones or bands. The similarity in the number of growth increments observed within the gladius with the number of “second-order growth increments” in statoliths corresponded to the same internal rhythm in the squid organism. Previous research on gladii (e.g. *Sthenoteuthis oualaniensis* [Arkhipkin and Bizikov, 1991]) has suggested that this kind of internal rhythm is diel, and therefore we consider the “second-order growth increments” of *B. magister* statoliths as deposited daily. However, this method could not be applied to some cold-water species (e.g. *Moroteuthis ingens* [Arkhipkin and Bizikov, 1991]); therefore it had to be confirmed by another independent validation method. As in the studies by Uozumi and Ohara (1993) and Uozumi and Shiba (1993), we compared differences between mean ages of successive well-defined modes of frequency compositions with elapsed days between samples and found a good correspondence between them. Therefore, the nature of the “second-order growth increments” within *B. magister* statoliths and consequently that of increments within the inner layer of their gladii were confirmed. The statolith ageing technique, however, was found to be more effective because its actual productivity (about 120 ground statoliths per week by one skilled technician) was far higher than that of the gladius technique (40–50 cross sections, respectively). Thus, statoliths were more efficient tools in investigations of age, growth, and stock dynamics of *B. magister*.

It is noteworthy that the “second-order” growth increments observed in *B. magister* statoliths (“heavy rings” of Natsukari et al., 1993) correspond to the first-order daily increments of other squid species, whereas the distinct “third-order” bands that we found in *B. magister* statoliths correspond to the second-order bands of loliginids and other gonatids. “Fine rings” or “first-order increments” revealed in *B. magister* statoliths obviously were of a subdaily nature like those observed earlier in *Sepioteuthis lessoniana* (Jackson, 1990) and in other fish species (Campana and Neilson, 1985).

The starting point for increment counts remains unclear. In ommastrephids, growth increments are deposited after hatching (Balch et al., 1988), whereas loliginid hatchlings have a few dozen growth increments within their statoliths at hatching, with a prominent check occurring outside the nucleus (Natsukari et al., 1988). Statolith size at hatching for *B. magister* is unknown, therefore we assumed (after Natsukari et al., 1993) that the first prominent check lying outside the nucleus was the “natal” ring. If this assumption turns out to be incorrect, and the nucleus in *B. magister* appears at hatching as in

ommastrephids, then the actual age of squids in this study should be corrected by adding the number of increments between the nucleus and "natal" ring (10–12 rings). However, in relation to the longevity of *B. magister*, this bias appears negligible.

### Seasonal dynamics in distribution, length-frequency composition, and stock structure

We found three main seasonal groups of *B. magister* in the western Bering Sea: winter-hatched, summer-hatched, and fall-hatched groups. Winter-hatched squids were caught in great numbers during the summer as juveniles ranging from 40 to 100 mm ML. From June to September, these squids increased in size over the slope of the Navarin–Olyutorsky region, growing up to 110–150 mm ML. Later these squids disappeared from catches.

The summer-hatched group predominated catches in Olyutorsky Bay and the Navarin–Olyutorsky region from June to August. About 80% of females and 85% of males from this group were mature in June; their modal length was 250–260 mm and 200–210 mm, respectively. Spawning for this group began in June and was encountered along the slope (400–600 m) between 165°E and 177°E. The average age of spawning squid in June was 330–370 d for females and 320–340 d for males. Spawning intensified in August and finished by the middle of September. Summer spawning of *B. magister* in the western Bering Sea was identified by the pronounced predominance of mature males and mature females that had mated and by relatively large numbers of spent squid in August. Average age of spent males and females was 11–12 months. Aggregations of summer-hatched squid were not dense; catches on their spawning shoals never exceeded 300–400 kg·h<sup>-1</sup>. By October these squid vanished from catches.

Squid of the fall-hatched group occurred in the western Bering Sea during the entire period of study, representing the bulk of catches from August until November. In June, these squid were immature (maturity stages 1–2) and of modal size 170–180 mm ML and were not abundant in catches (ca. 20% of total catch) in all three regions. The abundance of fall-hatched squid increased in the Navarin–Olyutorsky region during summer, apparently because of their continuing immigration along the slope from the eastern Bering Sea shelf. Several factors indicated the presence of a westward migration. First, fall-hatched juveniles appeared in Olyutorsky Bay only in July, whereas in the Navarin–Olyutorsky region they occurred from June onwards. Second, size-frequency composition of squid in the Navarin–St. Matthew region was rather stable from June to September;

juveniles and immature squid predominated in catches. The latter observation, together with the observed growth of squid, strongly indicated that this region was transient for shoals of juveniles and immature adults migrating from the east to the Navarin–Olyutorsky region.

Growth and maturation of the fall-hatched squid were observed on the slope of the Navarin–Olyutorsky region and within Olyutorsky Bay from June to August. By September, 90% of the fall-hatched males achieved full maturity at modal length 200–210 mm, whereas a majority of females (about 60%) were still maturing (stage 3), attaining 250–260 mm ML. Maturation of the fall-hatched females began in October at modal length 270 mm ML. By November, about 75% of females were mature and ca. 70% of them had mated. Maturation of the fall-hatched squid in September–October was accompanied by their aggregation into dense shoals at depths ranging from 350 to 450 m along the slope of the Navarin–Olyutorsky region and in Olyutorsky Bay with average catches >1 t·h<sup>-1</sup>. Thus, fall-hatched squid represented the bulk of *B. magister* stock in the western Bering Sea, with the highest fishery potential of all seasonal groups.

The population of fall-hatched squid in the Navarin–Olyutorsky region successively changed in structure during September and October. This shift demonstrated the ongoing emigration of mature squid from the Navarin–Olyutorsky region. Squid possibly moved in a southwest direction along the slope during October–November. Dense shoals of *B. magister* disappeared, first in the Navarin–Olyutorsky region, and only later in Olyutorsky Bay.

During summer and fall, seasonal groups of *B. magister* used the continental slope of the western Bering Sea in somewhat different ways. Summer-hatched squid used the slope during June–August as spawning grounds, mainly at depths of 350–450 m. For the fall-hatched squid, the slope was a feeding ground and, at least for a number of them, a spawning ground. During summer, the fall-hatched squid increased in size rapidly at depths of 350–500 m. In September–October, they formed dense aggregations and after spawning, rather quickly disappeared from the region. As for the winter-hatched group, its migratory behavior remained unclear, and we cannot say whether or not this group used the slope as a feeding ground only or as a spawning area as well. With respect to spawning seasons of different groups, it is obvious that the time lag between summer spawning and fall spawning is much greater than that between fall- and winter-spawning groups. Unfortunately, we do not have enough data on the winter season, and it is possible that there are not three

but two seasonal spawning groups: summer-spawning and fall-winter spawning, the latter with two spawning peaks, during fall and winter. It is interesting that Natsukari et al. (1993) found the same two spawning peaks (summer and fall-winter), although of different intensity, for *B. magister* occurring in the Rebun Bank (Sea of Japan) and Kitamiyamato Bank (Sea of Okhotsk).

### Age, growth, maturation, and possible life cycle

Until now, investigations of squid life cycles by any direct method have shown that tropical species are characterized mainly by a half-year life cycle (small- and medium-size loliginids [Jackson and Choat, 1992]) and a one-year life cycle (medium-size and large ommastrephids [Arkhipkin and Bizikov, 1991; Arkhipkin and Mikheev, 1992]), whereas subtropical and temperate species generally have a one-year life cycle (Natsukari et al., 1988; Arkhipkin, 1990; Natsukari and Komine, 1992). The maximum age of cold-water subarctic, Arctic, and Antarctic species has not been determined directly yet. However, studies of length-composition dynamics through various years as well as growth data obtained from the hard structures of squid have suggested that cold-water species may live two years or more (i.e. *B. magister* [Fedorets, 1986a]; *Kondakovia longimana* [Bizikov, 1991; Jarre et al., 1991]; *Martialia hyadesi* [Rodhouse, 1991]). Natsukari et al. (1993) suggested that *B. magister* live four years, but we have produced different estimates which reflect different criteria for increment counting.

According to our data, *B. magister* in waters of the western Bering Sea live more than one year, with the oldest specimens about 16 months old, and the bulk of fall-hatched squid 13–14 months old and far from being in a spent condition. However, summer-hatched squid matured earlier, with the majority of spent animals being 12–14 months old.

*Beryteuthis magister* is a nektonic species resembling active oceanic ommastrephids in body shape and muscle strength (Nesis, 1985). It showed the same growth and maturation features as many middle- and large-size ommastrephids, namely 1) an earlier decrease in growth rates for males, which results in smaller sizes at maturation for males in comparison with females of the same age; 2) maximum daily growth rates in the middle of ontogenesis with a gradual decrease by the end of life; 3) a constant reduction of instantaneous growth rates from maximum values in early juveniles to minimum values in mature specimens; 4) the achievement of maximum DGR in body weight at older ages than those attained for maximum DGR in ML; 5) a wide length-weight range for

squid of the same age; and 6) the presence of early and late-maturing animals within the same seasonal group of females. As expected, cold-water *B. magister* grew and matured slower than large species of ommastrephids, had a smaller body size, and lived longer.

Growth curves of seasonal groups of squid would probably differ, as has been shown before for ommastrephid (Arkhipkin, 1990; Uozumi and Ohara, 1993) and loliginid squid (Natsukari et al., 1988; Jackson and Choat, 1992). This was confirmed indirectly for *B. magister* in comparing the smaller sizes of mature summer-hatched females (250–260 mm ML) with mature fall-hatched females (270–280 mm ML).

Taking into account our data with those of several previous studies (Fedorets, 1986a; Okiyama, 1993), we were able to suggest an approximate scheme for the life cycle of *B. magister* in the Bering sea for the most fully investigated, abundant fall-hatched group. The direction of ontogenetic migrations of *B. magister* is expected to coincide with the general scheme of water circulation in the Bering Sea (Hughes et al., 1974; Favorite et al., 1976; Shuntov et al., 1993). In the deepwater southern part of the Bering Sea there are three main counterclockwise circulations: that which lies westward from Shirshov Ridge, that between Shirshov and Bowers Ridges, and that between Bowers Ridge and the shelf of Bristol Bay. There are many lesser circulations (Shuntov et al., 1993). Immature fall-hatched squid (180–200 mm ML) in early summer appeared in the Navarin–St. Matthew region and began migrating southwestward along the continental slope of the Navarin–Olyutorsky region. During summer, these squid fed actively over the slope and grew quickly. In August–September, maturing females attained 260–270 mm ML. In October, the majority of them were mature and, by the end of the month, had mated. In November they vanished, first from the Navarin–Olyutorsky region and later from Olyutorsky Bay. One group of these squid spawns and dies in the two regions just mentioned. Another group of these squid, however, may migrate actively in a southwest direction onto the slope of the Commander Islands. There are two possible migration routes from the main feeding grounds in the Navarin–Olyutorsky region to the area around the Commander Islands: 1) along the slopes of Olyutorsky Bay and North Kamchatka (total distance about 1,800 km); and 2) south of Cape Olyutorsky along the Shirshov Ridge (ca. 1,000 km). Both routes include sections with great depths (>1,500 m); the first route having an approximately 100-km section and the second route an approximately 500-km section. It is known that not only immature squid but even mature males and maturing females of *B. magister* may occur in pelagic wa-

ters (Fedorets and Kozlova, 1988; Shevtsov, 1990). However, because *B. magister* adults occur mainly at and over the slope, the first route seems more likely. Taking into account the similarity of body shape of *B. magister* and *I. argentinus*, as well as the depths and water temperatures of their spawning migrations, we assume that migratory swimming rates of *B. magister* may resemble those of *I. argentinus*: 0.46 of absolute length (including mantle length, length of head and arms, AL) per sec (Arkhipkin, 1993). As the modal AL values in *B. magister* are 350–390 mm for mature males and 440–490 mm for mature females (our data), their average migratory rates may be estimated as 0.1–0.18 m·sec<sup>-1</sup> and 0.20–0.23 m·sec<sup>-1</sup>, respectively. At this speed *B. magister* females may reach spawning grounds near the Commander Islands in 66–73 days and males in 80–92 days. But, in fact, *B. magister* cannot migrate at this speed, because its mantle is more watery and less muscular than that of ommastrephids: the protein content of *B. magister* mantle muscles is 13.5% compared with 20% which is typical for ommastrephids (Shevtsov and Dolbnina, 1975). Nevertheless, the data of Fedorets (1986a), who found dense aggregations of *B. magister* near the Commander Islands in November–January, support our suggestion of a squid migration to the Commander Islands. During this period, aggregations of *B. magister* near the Commander Islands consisted entirely of mature males and females of quite constant sizes (210–220 mm and 270–280 mm ML, respectively). However, these aggregations were observed at depths of 150–250 m, whereas *B. magister* migrates to much greater depths to spawn (1,000–1,100 m [Okuyama, 1993]). Thus, it is possible that mature squid of the fall-hatched group spawned one-two months later (in January–March) at mean ages around 18 months. It is hardly possible that *B. magister* from the western Bering Sea should reach even the Near Islands, the westernmost of the Aleutian Islands, because the northward current in the deep and wide Near Strait is very strong and may cross the squid migratory route. Kovalev (1990) has shown by the substrate-specific properties of cholinesterases that squid from the Pribilof–Alaska region (eastern Bering Sea) are different from those of the Navarin–Olyutorsky region, suggesting some degree of genetic isolation.

To estimate the total longevity of cold-water squid, it is important to consider the duration of their embryonic phase. Recently, Laptikhovskiy (1991) modeled longevity of the embryonic phase in squid by using two independent variables: water temperature and average egg diameter. Taking into account the large egg size of *B. magister* (3.5 mm [Fedorets and Kozlova, 1986]; our data) and the extremely cold water over its

spawning grounds (1.5–2.5°C [Fedorets, 1986a]), we believe the duration of the embryonic phase for *B. magister* could be from 4 to 6 months. This estimation corresponds well with data of von Boletzky (1994), who considered the duration of embryonic development in decapods as ranging from 6 to 12 months at water temperature 2–5°C. Thus, the life cycle of the fall-hatched group of *B. magister* could last about two years (6 months of embryonic phase and 18 months of postembryonic development). The life cycles of other seasonal groups require further investigations.

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