Intrapopulation structure of winter-spawned Argentine shortfin squid, *Illex argentinus* (Cephalopoda, Ommastrephidae), during its feeding period over the Patagonian Shelf

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Abstract.–Stock structure dynamics of the important commercial squid *Illex argentinus* were studied by using biological data from about 25 thousand squid caught January–April 1991 by Russian trawlers in three fishery regions: 51–52°S; 47–49°S within the exclusive economic zone of Argentina (EEZA); and 45–47°S outside the EEZA. A total of 2664 statoliths were read to prepare age-length keys for each 10-day interval of the period studied. It was found that between January and April, the Patagonian shelf south of 45°S was a feeding ground of two intraspecific groups of winter-hatched *I. argentinus*: a shelf group that matured at medium sizes (ShG) and a slope group that matured at large sizes (SlG). After massive immigration of *I. argentinus* from the north in January–February into the two fishery regions within 45–49°S, the stock structure remained rather stable until April, composed predominantly of June- and July-hatched squid. Squid grow and mature rapidly, and males mature at younger ages (from one to two months) than do females. During feeding, some redistribution of the stock was observed: maturing and mature SlG squid (mainly females) tended to shift from the shelf (130–150 m depth) in a northeast direction and concentrate over the shelf edge (160–170 m depth). In April, mature SlG squid began to shift to the continental slope around 45–47°S and migrated to depths >600 m where they then mixed with schools of SlG squid that had fed in the region 51–52°S and that were already migrating northwards along the slope. ShG squid remained on the shelf and made their prespawning northward migrations along the shelf edge.

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The Argentine shortfin squid, *Illex argentinus* (de Castellanos, 1960), is a common neritic species occurring in waters off Brazil, Uruguay, Argentina, and the Falkland Islands in the Southwest Atlantic (Nesis, 1987). This squid is an important world fishery resource. According to the FAO (1997), since 1978, its total annual catch has varied from 180 to 250 thousand metric tons (t), achieving 300–330 thousand tons in 1993–95. However, actual total annual catch of *I. argentinus* could reach up to 700 thousand tons (Uozumi and Shiba, 1993). *Illex argentinus* is captured by the international fleet consisting of both jigging light vessels (mainly from Asian countries) and trawlers (mostly from European countries: Poland, Spain, and Russia (former USSR) in two fishery regions off the Argentine Exclusive Economic Zone (EEZA): at 42°S and 45–47°S. In the 1970s and 1990s, *I. argentinus* was also caught in considerable numbers within the EEZA and Falkland Islands Interim Conservation Zone (FICZ) (Csirke, 1987; FAO, 1997). Such an extensive fishery has induced detailed studies of different biological aspects of *I. argentinus* in order to monitor and forecast its stock structure dynamics.

Originally, *I. argentinus* was considered to be a single stock (Sato and Hatanaka, 1983; Csirke, 1987). Then it was found that the species consisted of two populations differing both by season and place of their spawning: an abundant winter-spawning population (more than 95% of the total stock) and a small summer-spawning population (Hatanaka et al., 1985; Hatanaka, 1988). Brunetti (1988) divided winter-spawning squid into two stocks: the bonaerensis north Patagonian stock (BNPS) and the south Patagonian stock (SPS), differing both by feeding grounds and size of adults (medium and large, respectively). On the basis of occurrence of mature females in different seasons, Nigmatullin (1989a) revealed that *I. argentinus* spawn throughout the year, and proposed to subdivide the total stock into four seasonal spawning groups. Although Tsygankov (1987) found qualitative differences in three loci of esterases extracted from the buccal muscles of various intrapopulational groups of *I. argentinus*, the taxonomic status of these groups, however, still remained unclear. Analysis of dynamics in length-frequency compositions showed that completion of the life cycle of *I. argentinus* populations took one year (Hatanaka et al., 1985; Hatanaka, 1986) and this length of time was then confirmed by statolith aging investigations (Arkhipkin, 1990; Rodhouse and Hatfield, 1990).

The life cycle of the most abundant winter-spawned group can be subdivided into five stages: a postlarval period that takes place in waters off Brazil and Uruguay in August–September (Leta, 1987; Santos and Haimovici, 1997); a juvenile period that takes place in shelf and oceanic waters off Uruguay and Argentina in September–December (Brunetti, 1988; Parfeniuk et al., 1992); a feeding period that takes place on the Patagonian and Falkland Islands shelves in January–April (Brunetti, 1988; Hatanaka, 1988); a prespawning period that takes place on the shelf edge and slope off Argentina and Uruguay in May–July (Hatanaka, 1986, 1988; Arkhipkin, 1993); and a spawning period that takes place in shelf and slope waters off northern Argentina, Uruguay, and Brazil in July–August (Brunetti, 1988; Santos and Haimovici, 1997). Squid aggregate and are fished mainly during their feeding period on the shelf, as well as during their prespawning period on the shelf edge and slope (Nigmatullin, 1989b).

Stock structure dynamics of *I. argentinus* during their feeding period on the Patagonian Shelf were studied both in the fishery region of 45–47°S outside the EEZA and within the FICZ by using data obtained from Japanese jigging vessels (Rodhouse and Hatfield, 1990; Uozumi and Shiba, 1993). It was found that the age composition of *I. argentinus* catches changed between January and April owing to the gradual migrations of feeding schools of these squid. Earlier hatched squid immigrated to and emigrated from the fishery region earlier than later hatched groups (Uozumi and Shiba, 1993). Squid of the former group had slower growth rates than those of the latter group (Rodhouse and Hatfield, 1990). Data from trawling vessels showed that, during the prespawning period, winter-spawned *I. argentinus* made active northward migrations from the southern Patagonian Shelf along the continental slope of Argentina. Squid migrated in waves of abundance, consisting of 2–4 successive monthly generations. Males moved 2–3 weeks earlier than females of the same monthly group (Arkhipkin, 1993).

An analysis of length-frequency distributions of *I. argentinus* showed that the jigging fishery had a higher selectivity for squid than did the trawl fishery (Koronkiewicz, 1995), and therefore data from the trawl fishery reflected the natural population distribution far better than those from the jigging fishery. In the present report I examined the stock structure dynamics of *I. argentinus* during the January–April feeding period, using both data from two research vessels and two commercial trawlers (both fishing within the fishery) and statolith aging techniques, and comparing these stock structure data with those obtained by the Japanese jigging fishery both within and outside the EEZA. Together with the data obtained during the prespawning period (April–June) (Arkhipkin, 1993), the results of the present study make it possible to reconstruct the full picture of the stock structure dynamics of *I. argentinus* during the entire fishery period.

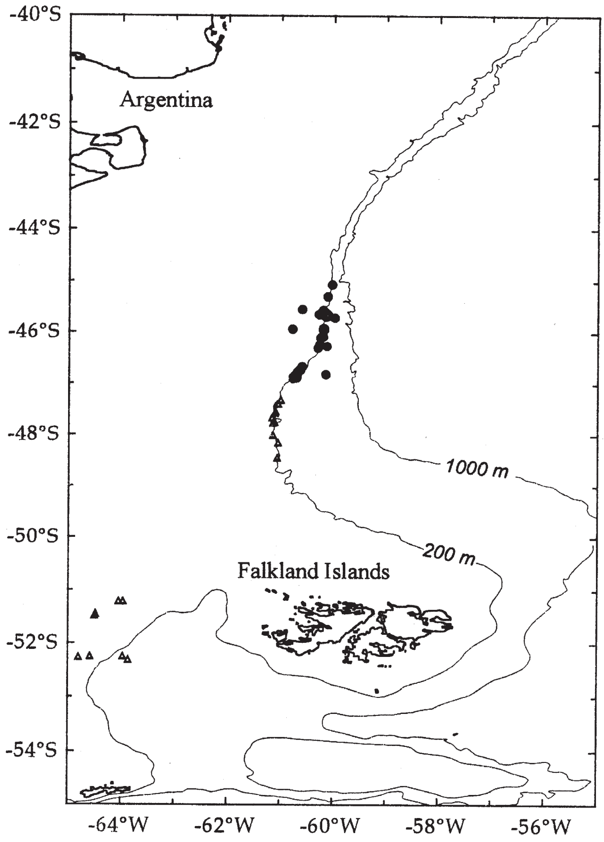

Figure 1

Sampling locations of *Illex argentinus* off (circles) and within (triangles) the Exclusive Economic Zone of Argentina (EEZA) in the southwest Atlantic in January–April 1991.

Materials and methods

Data on the Argentine shortfin squid, *Illex argentinus*, for the present study were collected during four experimental surveys carried out in the fishery region of 45–47°S outside the EEZA by the Soviet research vessels *Anchar* and *Volzhanin* (2700 GRT) and within the EEZA (in 47–49°S and 51–52°S) by the fishing trawlers *Petropavlovskaya krepost* and *Batiliman* (4000 gross registered tonnage [GRT]) between January and April 1991 (Fig. 1). Trawls were conducted with different types of rope trawls with a mean horizontal opening of 60–75 m and mean vertical opening of 40–50 m. Trawls were made in the superficial water layer at night and near bottom in the daytime at bottom depths ranging from 140 to 190 m in January–March and from 190 to 660 m in April. The duration of trawls ranged from 4 to 8 hours, and the average towing speed was 6–8 km/h.

Every ten days, average daily catch per unit of effort (CPUE) was calculated as a mean of daily CPUEs of the Soviet fishing trawlers that caught squid in each fishery region. Mean CPUEs were calculated separately for the fishery region of 45–47°S outside the EEZA (where a majority of fishing vessels are 2700-GRT trawlers) and for the fishery regions within the EEZA (where all fishing vessels were 4000-GRT trawlers). To obtain an objective picture of the squid fishery, CPUEs of the 2700 GRT trawlers may be adjusted to those of 4000-GRT trawlers by a coefficient of 0.7 (Arkhipkin, 1993).

Length-frequency sampling

A random sample of one hundred squid was taken by scientific observers from each of two catches (at night and day) everyday on board each of the four vessels. Dorsal mantle length (ML) was measured to the nearest 1 mm, total body weight (BW) was weighed to the nearest 1 g. Sex and maturity stages were identified according to the maturity scale elaborated for *Illex argentinus* (Nigmatullin, 1989a). Sex ratio was determined. A total of 16,436 squid were analyzed in the fishery region of 45–47°S outside the EEZA and 9893 squid were analyzed within the EEZA. Every ten days, three length-frequency curves of males and females were constructed for three maturity periods: immature (maturity stages 1–2), maturing (maturity stages 3–5_1) and mature (maturity stages 5_2–5_3).

Age sampling and statolith processing

Every ten days, from January to April, statoliths were dissected from 100–150 individuals of *Illex argentinus* from two successful catches on board each of the four vessels. The length-frequency distribution of the 10-day age sample was proportional to the length-frequency distribution of squid caught during these ten days. Statoliths were washed in distilled water and stored in oil-paper envelopes in 96% ethanol. A total of 1700 statoliths were sampled in the fishery region of 45–47°S outside the EEZA, and 1150 statoliths were collected within the EEZA.

All statoliths sampled were processed by statolith aging techniques in the Laboratory of Commercial Invertebrates of AtlantNIRO (Arkhipkin, 1991). Statolith terminology follows Clarke (1978) and Lipinski et al. (1991). Statoliths were attached to the microscopic slides with Pro-texx mounting medium and were ground on both sides on a wet waterproof sandpaper of 1000-grit grade. During grinding, the statolith rostrum was completely removed, so that growth increments could be easily distinguished from the nucleus to the edge of the dorsal dome. Ground statoliths were embedded in Canada balsam and covered with glass covers. Ready preparations were placed in an oven at 90–100°C for one hour to dry the balsam and improve the readability of growth increments. Statoliths were read under a Biolam R1 light microscope at 450–500× magnification. To avoid possible counting errors, each statolith was counted twice by two observers using the gradation of an eye-piece micrometer. The total number of growth increments for each specimen was obtained as a mean of these replicate counts if the deviation between the two counts was less than 5%. If deviation exceeded 5%, the statolith was recounted by the two observers once more. If such deviation did not decrease after the recounting, the statolith was rejected from further analysis. From the whole sample, 1597 statoliths from the region outside the EEZA (93.9%) and 1067 statoliths from the region within the EEZA (92.7%) were prepared and read.

Length-at-age data analysis

Deposition of putative growth increments within *I. argentinus* statoliths has not yet been validated. However, incorporation of either tetracycline or strontium marks into statoliths of the congeneric species *I. illecebrosus* kept in captivity has shown that growth increments are formed daily (Dawe et al., 1985). Statolith microstructure in both species is similar; therefore growth increments within statoliths of *I. argentinus* are considered to form daily in the present paper. Hence, their total number was considered to represent squid age in days. Hatching dates were backcalculated. Month classes of hatching were defined by pooling squid into each month of hatching (Arkhipkin, 1990; Rodhouse and Hatfield, 1990). Length-at-age data were analyzed separately for both sexes. The 10-day age structure was determined by construction of age-length keys. Age-length keys were constructed by using numbers of squid for each month class separately for each sex and maturity period (Arkhipkin et al., 1996).

Results

CPUE dynamics

Region 45–47°S *Illex argentinus* were caught in all trawls of the research vessels (Fig. 2). In January, schools of squid aggregated mainly north of the region. Trawl catches were variable (from 1 to 20 t per vessel day, t/d), and mean January CPUEs were low (8–9 t/d).

During the first 10-day period of February, concentrations of *I. argentinus* were observed in all parts of the region. Squid concentrated near the bottom during the daytime and ascended to the upper water layers at night. The CPUE was twice as high as in January, and the squid fishery stabilized at 16–17 t/d. However, aggregations of *I. argentinus* quickly dispersed, and during the second 10-day period of February, the CPUE fell sharply to the January level (Fig. 2). Catches of squid were low but stable (around 10 t) until the second 10-day period in April, when fishing vessels shifted from the shelf edge (170–190 m depth) to the continental slope (440–660 m depth) and changed fishing tactics. The vessels performed near-bottom trawls at the shelf edge during the daytime, and on the continental slope at night. These tactics considerably increased CPUE (up to 15–18 t/d) for the third 10-day period of April and in the beginning of May because the fleet began to target not only shelf aggregations but also the slope aggregations of *I. argentinus* that were beginning to appear at that time.

Region 47–49°S Fishing trawlers operated in this region between February and the second 10-day period of March. The fishing tactics were the same as those used in the previous region. Abundance of *I. argentinus* was considerably greater than that in the region outside the EEZA (Fig. 2). The peak of CPUE was observed in the third 10-day period of February (51 t/d).

Region 51–52°S All fishing vessels that had operated in the 47–49°S region moved to the fishing region west of the Falkland Islands during the second 10-day period of March and fished there until the middle of May (Fig. 2). The fishing tactics were different from those used in the two previous regions. Trawlers fished for squid in midwater both at night and in the daytime. CPUE in March–April was high, similar to those in the 47–49°S region with a prominent peak (53 t) during the second 10-day period of April. At the beginning of May, CPUE decreased sharply and the fleet ceased fishing for squid in the region.

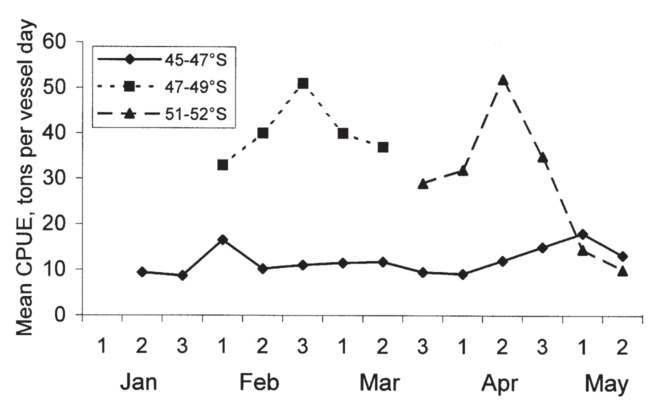

Figure 2

Mean CPUE (tons per vessel day) of the Russian trawlers in the *Illex argentinus* fishery in three fishery regions of the Southwest Atlantic in 1991: 45–47°S (bold solid line), 47–49°S (dotted line) and 51–52°S (dashed line).

Sex ratios

Region 45–47°S The proportion of females was the highest during the second 10-day period of January (ca 80% of the total sample). From the end of January through the beginning of February, the proportion of females decreased sharply (to 55–60%). Sex ratio was close to 1:1 between the second 10-day period of February and the first 10-day period of April, when the proportion of females occurring on the shelf edge decreased to 30%. However during the third 10-day period of April on the continental slope at depths of 480 m, the sex ratio was found to be close to 1:1, and females prevailed in catches (65%) at deeper depths (630 m) (Fig. 3).

Region 47–49°S Except the first 10-day period of February (when the sex ratio was close to 1:1), males always predominated in catches at a ratio of 2:1 (Fig. 3).

Region 51–52°S The sex ratio was close to 1:1, but the proportion of females tended to decrease from 55% to 45% (Fig. 3).

Length and hatching-month composition

Region 45–47°S During the second 10-day period of January, June-hatched maturing females (modal sizes 210 mm ML) and mature males (200 mm) predominated in catches. The proportion of mature May-hatched squid was low. Hatching-month composition changed considerably during the third 10-day period of January owing to an appearance of maturing and mature May-hatched squid (males of 200 mm and females of 220–250 mm ML) in the region (Fig. 4).

Massive appearances of dense schools of immigrating June and July-hatched immature and maturing females (200–220 mm ML) and mature males (200–210 mm ML) were observed in the first 10-day period of February which resulted in a double increase in CPUE of the fishing fleet (Fig. 2) and in corresponding changes in the hatching-month compositions of squid: June-hatched squid

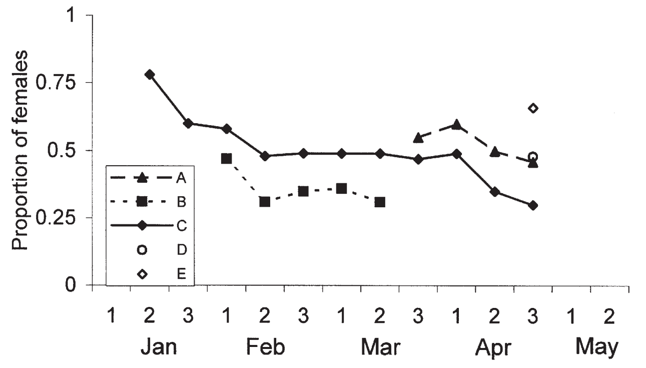

Figure 3

Proportion of females in sex ratio of *Illex argentinus* in three fishery regions of the Southwest Atlantic in 1991: (A) 51–52°S; (B) 47–49°S; and (C–E) 45–47°S. Depths for the last region were 160–190 m (C), 480 m (D), and 630 m (E).

became the most abundant in catches, as in the middle of January. During the second and third 10-day periods of February, hatching-month composition was the same as that of January, with June- and July-hatched squid predominating. However during the third 10-day period, the number of large mature females (280 mm ML) increased considerably (Fig. 4).

In March, the hatching-month composition of the *I. argentinus* catch was approximately similar to that of the second 10-day period of February; June- and July- hatched squid were the most abundant. The proportion of July-hatched squid increased by the end of March with a corresponding decrease in June-hatched squid. Modal sizes of males increased from 220–230 mm ML in the beginning to 230–240 mm ML at the end of the month. Length composition of females was bimodal (240–250 and 290–300 mm ML). The proportion of immature females decreased, whereas the proportion of mature females increased by the end of March (Fig. 5).

In April, hatching-month composition of *I. argentinus* caught over the shelf edge (170–190 m depths) remained almost similar to that of the second and third 10-day periods of March; July-hatched squid were predominant. Almost all males were mature. Immature females disappeared from catches in the first and second 10-day periods of April, but were caught in small numbers in the third 10-day period. At the beginning of the month, the length composition of both maturing and mature females was bimodal (260–270 and 300 mm ML). During the second 10-day period, large maturing and mature females (310 mm ML) began concentrating over the shelf edge, whereas medium-size females (270–280 mm ML) were still dispersed (Fig. 6). These concentrations caused another increase in CPUE for the fishing fleet (Fig. 2). During the third 10-day period of April, large mature squid (females of 310–320 mm ML and males of 270 mm ML) appeared in deeper waters over the continental slope, and they became most abundant at 480–630 m depths. Medium-size squid (maturing females of 280 mm ML and mature males of 250 mm ML) remained over the shelf edge (Fig. 6).

Region 47–49°S During the first 10-day period of February, the length composition of males was unimodal (230 mm ML) and most of these males were mature. Among females, two different modal groups occurred in the catches: immature June-hatched females (220 mm ML) and maturing and mature April- and May-hatched females (260 mm ML). Large catches of June- and July-hatched squid were evident between the second 10-day period of February and first 10-day period of March (Fig. 2).

Hatching-month compositions did not change significantly in this period, June- and July-hatched squid were caught almost in equal proportions. Mature males increased slightly in length from 230 to 240 mm ML. The proportion of immature females decreased and that of maturing and mature females increased by the second 10-day period of March (Fig. 7).

Region 51–52°S Hatching-month composition was similar between the third 10-day period of March and second 10-day period of April; July-hatched males and females were predominant in catches. Length compositions were unimodal for both sexes. Except during the third 10-day period of March when about a third of males were maturing, most of the males were mature, and their sizes increased from 260 mm ML at the end of March to 280 mm ML at the end of April. Females grew more rapidly in length than did males (from 280 to 320 mm ML). They matured quickly; immature females prevailed at the end of March, whereas maturing females were predominant at the end of April. During the third 10-day period of April, age composition of *I. argentinus* changed owing to a high proportion of August-hatched squid (Fig. 8).

Comparative comments

Simultaneous sampling in the regions of 45–47°S and 47–49°S between February and March and in the regions of 45–47°S and 51–52°S between March and April enabled a comparison of both length and hatching-month compositions of *I. argentinus* in these regions.

Hatching-month compositions were almost similar in the regions of 45–47°S and 47–49°S during the same 10-day periods (Figs. 4, 5, and 7). Modal sizes of mature males were about 10–20 mm greater in the southern region than those in the northern region. During the first 10-day period of February, the proportion of large mature females was much higher at 47–49°S (Fig. 7) than at 45–47°S (Fig. 4). After the second 10-day period of February, the opposite situa-

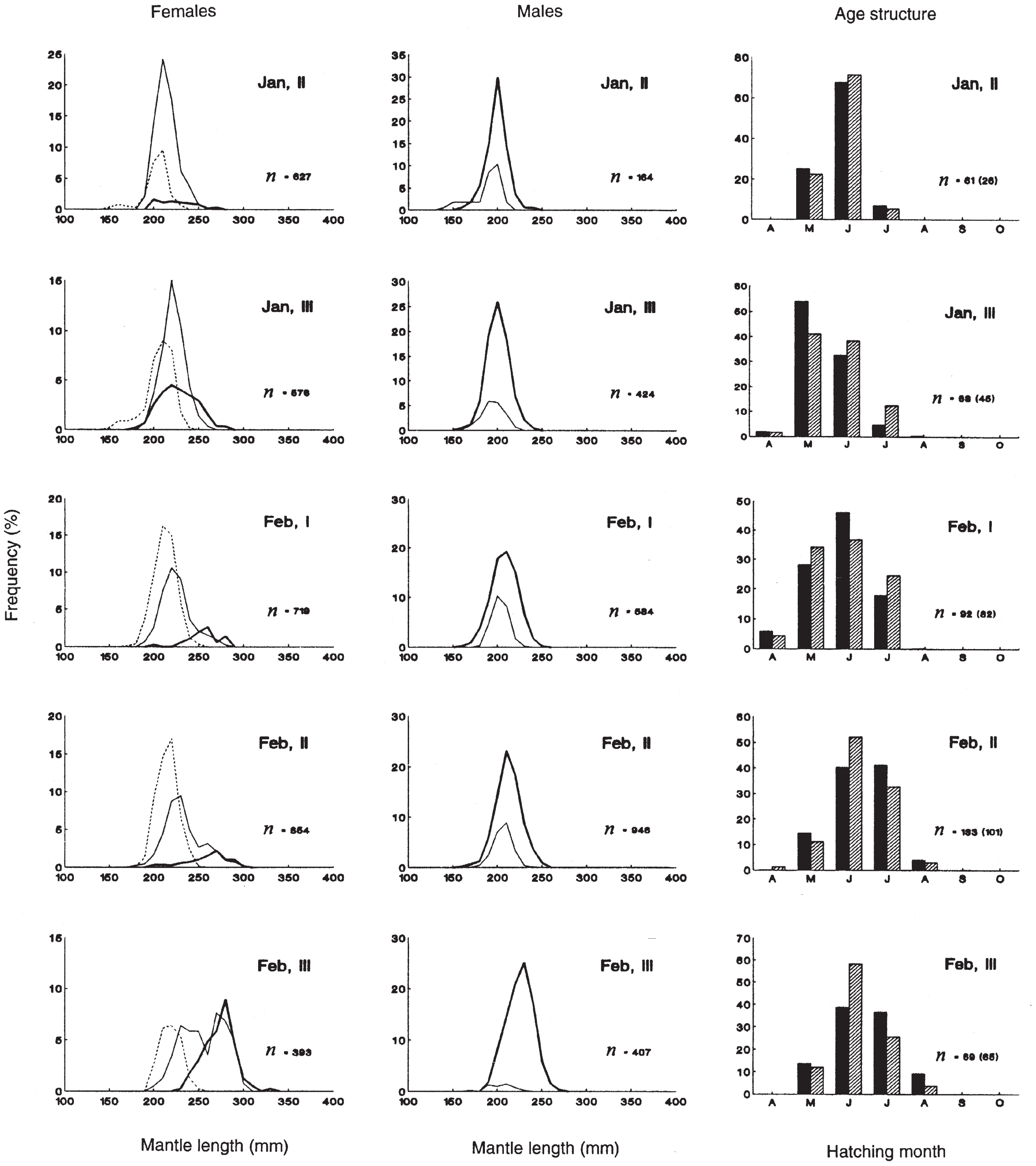

Figure 4

Length-frequency compositions of immature (dotted line), maturing (solid line) and mature (bold solid line) squid and hatching month compositions (age structures) of females (black bars) and males (dashed bars) of *Illex argentinus* in the fishery region of 45–47°S outside the EEZA in January–February 1991. Number of males in parentheses.

tion was observed; the proportion of mature females decreased at 47–49°S and increased at 45–47°S.

Both the length and hatching-month compositions of *I. argentinus* catches were different over the Patagonian Shelf at 45–47°S and 51–52°S. In the southern region, squid were 20–30 mm larger, about a month younger, and less mature than in the northern region, except during the third 10-day period of April when the

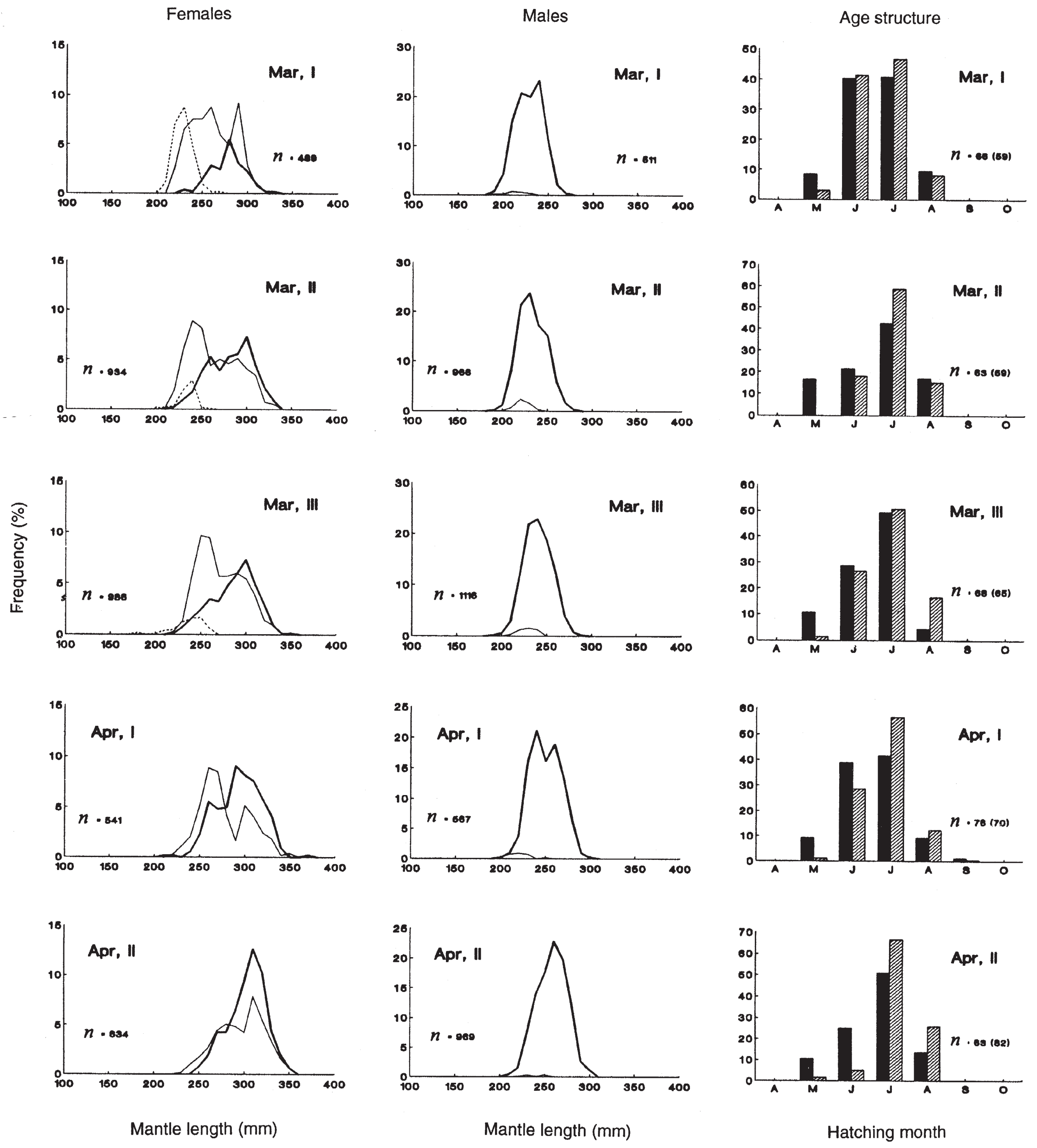

Figure 5

Length-frequency and hatching month compositions (age structures) of *Illex argentinus* in the fishery region of 45–47°S outside the EEZA in March–April 1991. Symbols are the same as in Figure 4.

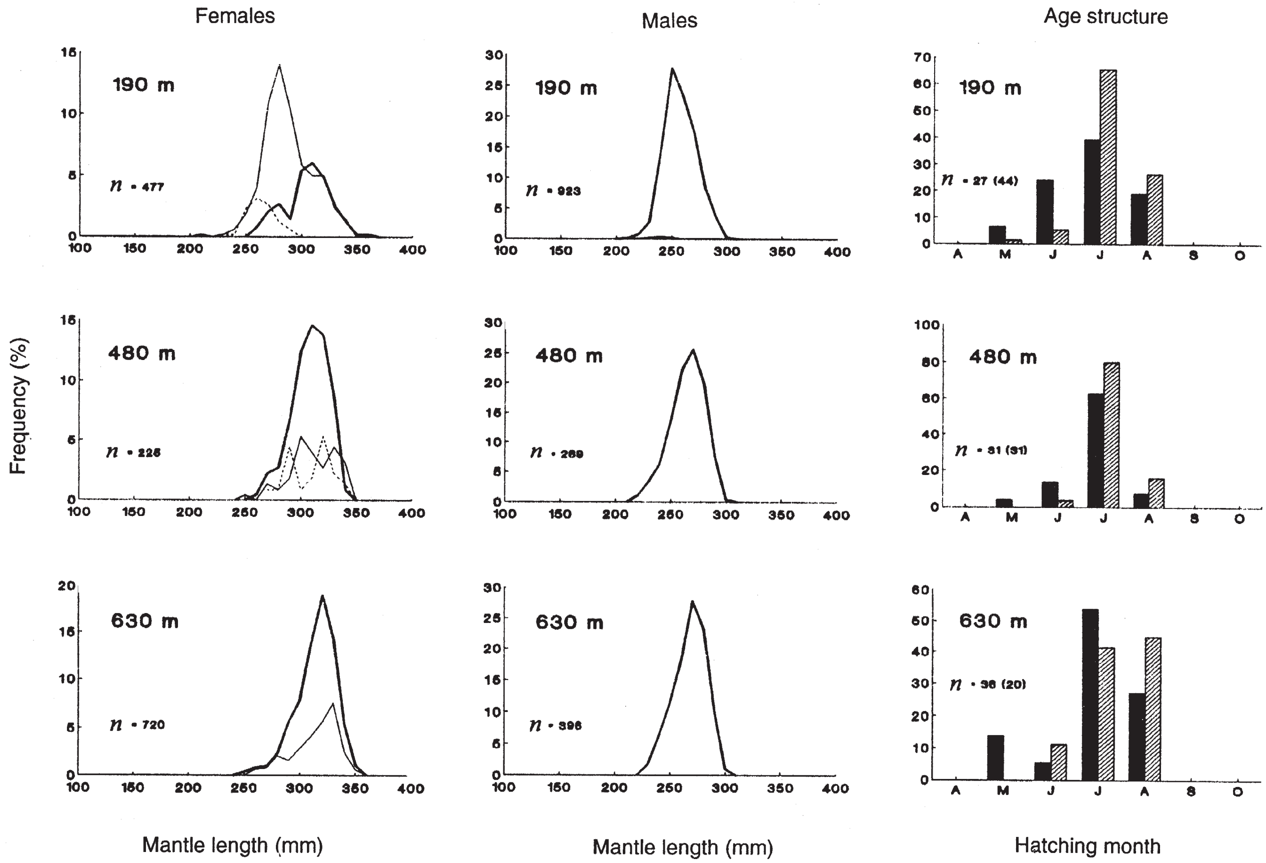

Figure 6

Length-frequency and hatching month compositions (age structures) of *Illex argentinus* at different depths of the fishery region of 45–47°S outside the EEZA between 21 and 30 April 1991. Symbols are the same as in Figure 4.

hatching-month compositions were practically similar to those for the continental slope (630 m) at 45–47°S and shelf (190–210 m) of 51–52°S. However, in spite of the similarity in modal length both in males and females in the last case, most of the females were mature in 45–47°S, whereas those at 51–52°S were still maturing (Figs. 5 and 8).

Discussion

Stock structure dynamics

Studies of the length-at-age structures for immature, maturing, and mature squid (separately) of both sexes, with a 10-day interval, revealed in detail the intrapopulation structure dynamics and migratory patterns of *I. argentinus* during the January–April feeding period on the Patagonian Shelf. Previous investigations, in which length-at-age data were pooled separately for each sex, revealed only general patterns in the age structure dynamics of *I. argentinus* (Rodhouse and Hatfield, 1990; Uozumi and Shiba, 1993).

Stock structure of winter-hatched *I. argentinus* was rather stable during the feeding period (January–April). After massive immigration of June- and July-hatched squid into the region 45–47°S from the end of January through the beginning of February, probably from an area farther north on the Patagonian Shelf (Hatanaka, 1988; Parfeniuk et al., 1992), the age structure of squid remained rather stable until the middle of April. During each 10-day period, from four to five month classes were observed, similar to the number obtained from the jigging fishery data (Uozumi and Shiba, 1993). Predominance of monthly classes changed gradually from June-hatched squid in February to July-hatched squid in March–April.

A considerable portion of the June and July-hatched squid continued their southward feeding migrations and reached 47–49°S by the end of February, which

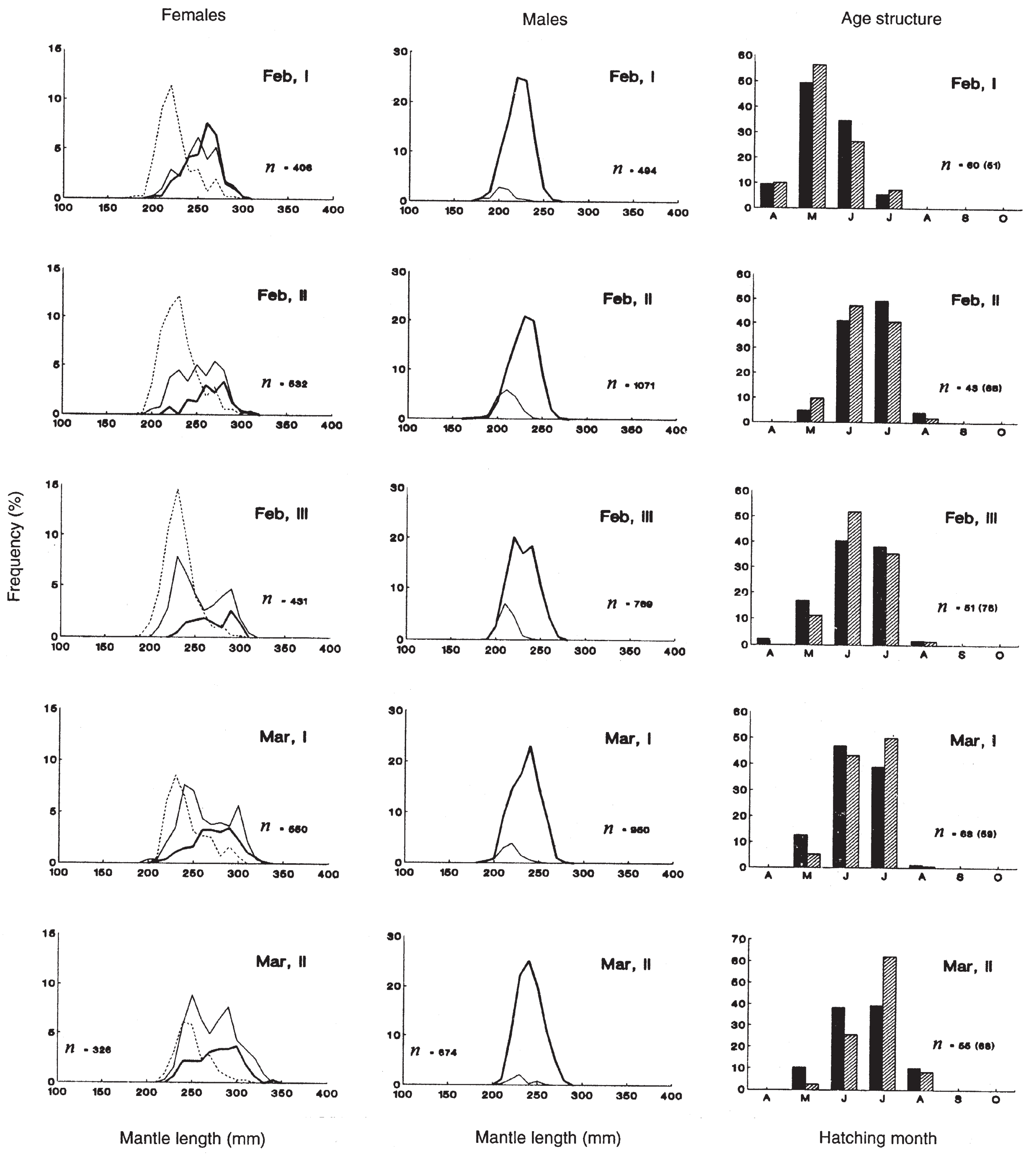

Figure 7

Length-frequency and hatching month compositions (age structures) of *Illex argentinus* of the fishery region of 47–49°S within the EEZA in February–March 1991. Symbols are the same as in Figure 4.

was confirmed both by similar hatching-month compositions and prominent peaks of the CPUE in both regions.

During the feeding period, winter-hatched *I. argentinus* grew rapidly and matured—males maturing at younger ages (from one to two months) than females

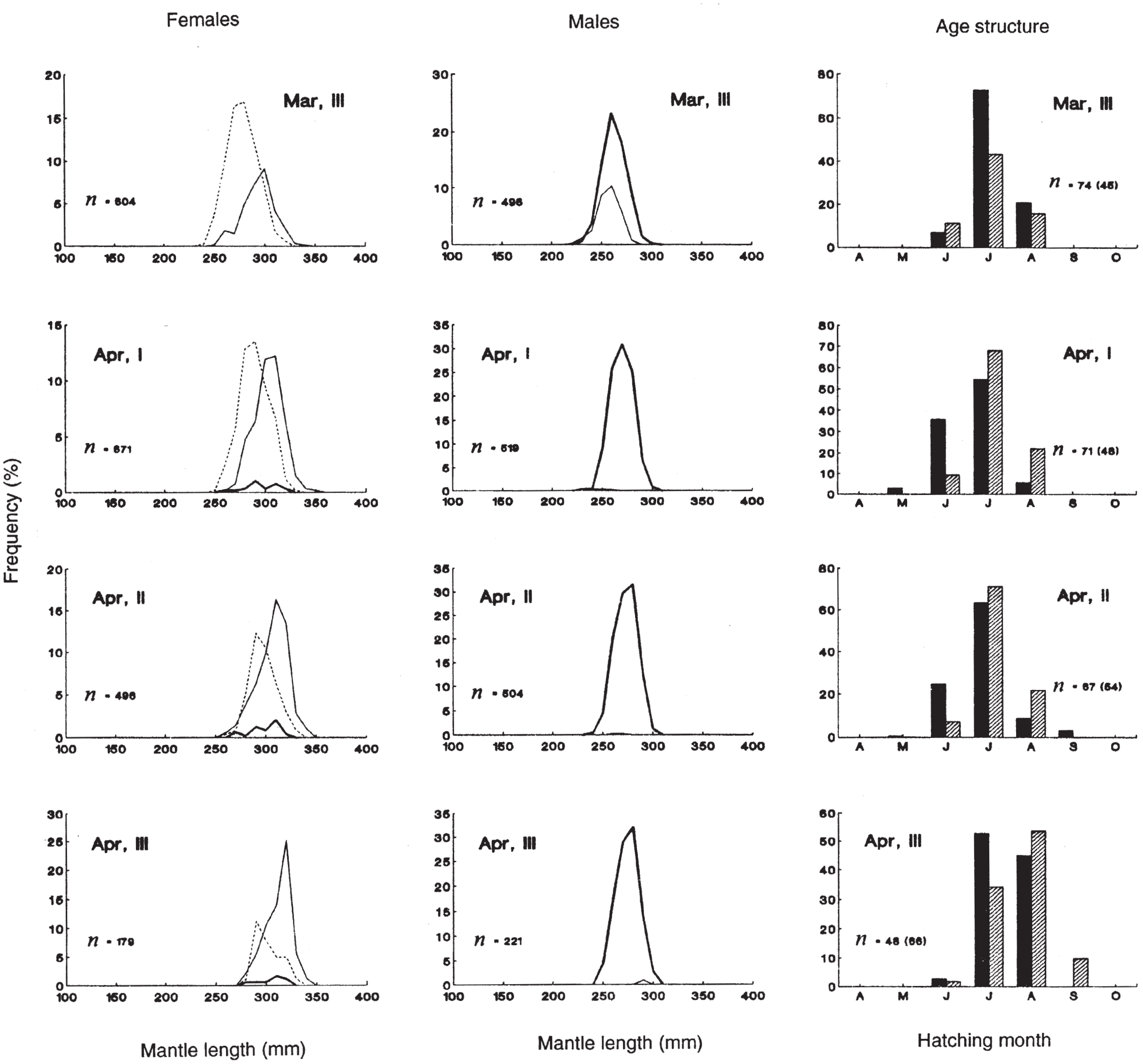

Figure 8

Length-frequency and hatching month compositions (age structures) of *Illex argentinus* of the fishery region of 51–52°S within the EEZA in March–April 1991. Symbols are the same as in Figure 4.

(Arkhipkin, 1990; Rodhouse and Hatfield, 1990). Taking into account the rather stable hatching month compositions during February–April, the squid were not performing any active spatial migrations after their arrival into the region of 45–49°S. Therefore, growth curves that were constructed on the basis of the increase in modal lengths of squid during February–April are valid, and growth rates calculated from these curves are probably close to actual growth rates (Koronkiewicz, 1986; Hatanaka, 1988). During feeding, some redistribution of the *I. argentinus* population was observed; large maturing and mature squid (mainly females) tended to shift from the shelf (130–150 m depth) in a northeast direction and to concentrate over the shelf edge (160–170 m depth). This shift resulted in an increase in their proportion in catches in the region outside the EEZA (45–47°S) and a simultaneous decrease in their proportion within the EEZA (47–49°S). A similar shift of maturing squid from the shelf to the shelf edge has been noted by Brunetti et al. (1998). Probably, this shift of maturing and mature females was also a reason for the considerable predominance of males (2:1) in catches within the EEZA in February–March. Similar sex ratios have also been noted in the fishery region north of the Falkland Islands (Koronkiewicz, 1995). Another explanation for the predominance of males in shelf catches may be the earlier migrations of mature males (in contrast to females) from the southern part of their feeding area through the region of 47–49°S. This migratory pattern occurs during prespawning migrations of *I. argentinus* from the southern part of the Patagonian Shelf (Arkhipkin, 1993).

In April large mature males and females, which had been aggregated over the shelf edge, began to shift to the continental slope and migrate to great depths (>600 m), where they mixed with the already migrating schools of July- and August-hatched squid that had fed in the southern part of the Patagonian Shelf and around the Falkland Islands (Arkhipkin, 1993). Such a redistribution of *I. argentinus* aggregations caused a rather sharp decrease in the CPUE of jigging vessels on the shelf in April–May and a simultaneous regrouping of trawlers—a shift from the shelf to one over the continental slope (Hatanaka, 1988; Nigmatullin, 1989b). Medium-size squid remained on the shelf and probably made their prespawning migrations along the shelf edge.

Stock structure of winter-hatched *Illex argentinus*

From the complex of biological characteristics (statolith microstructure, modal length in different months, sizes at maturity, types of feeding, and prespawning migrations), it is possible to consider the Patagonian Shelf south of 45°S as a feeding ground for two intraspecific groups of winter-hatched *I. argentinus*: the "shelf group that matures at medium sizes" (ShG) and the "slope group that matures at large sizes" (SlG). These two groups correspond well with the bonaerensis north Patagonian stock (BNPS) and south Patagonian stock (SPS) distinguished by Brunetti (1988) by using length-frequency analysis. Later, Brunetti et al. (1998) postulated that the spawning of both groups takes place near the shelf edge and over the continental slope; the BNPS squid spawn north of 43°S in winter, whereas the SPS squid spawn south of 43°S in autumn. It was shown however that the SPS squid definitely migrated from the southern part of the Patagonian and Falkland shelves along the continental slope farther north at 41–42°S (Arkhipkin, 1993), but location of their spawning grounds is still unknown (Haimovici et al., 1998).

The shelf group also corresponds to the winter shelf group (WSG), and the slope group corresponds well to the winter oceanic group (WOG), both (WSG and WOG) of which were distinguished by different locations of juvenile feeding and by type of life cycle (Parfeniuk et al., 1992; Nigmatullin and Laptikhovsky, 1996).

The shelf group of *I. argentinus* has a neritic life cycle, characterized by the following features: spawning in warm waters of the northern part of the species range (27–36°S); southward feeding migrations of juveniles <100–150 mm ML over the Patagonian Shelf; a "shelf" type dark zone within the statolith microstructure (Arkhipkin, 1993); fast juvenile growth but rather slow growth of immature squid; medium sizes at maturation (males at 160–220 mm ML, females at 180–240 mm ML); medium maximum sizes for mature squid (males of 180–260 mm ML, females of 220–320 mm ML); and northward prespawning migrations over the shelf. The slope group of *I. argentinus* has an oceanic-slope life cycle characterized by the following features: slope spawning in the northern part of the species area (27–36°S); southward feeding migrations of juveniles <100–150 mm ML in the open part of the Argentine Basin; an "oceanic" type dark zone within the statolith microstructure (Arkhipkin, 1993); slow juvenile growth but rather fast growth of immature squid; large sizes at maturation (males at 180–240 mm ML, females at 240–340 mm ML); large maximum sizes for mature squid (240–340 mm ML, females up to 280–400 mm ML); and northward prespawning migrations over the continental slope. The taxonomic status of the two groups of winter-spawned *I. argentinus* remains unclear (Arkhipkin and Scherbich, 1991; Parfeniuk et al., 1992; Nigmatullin and Laptikhovsky, 1996; Santos and Haimovici, 1997).

Interannual changes in stock structure

It has been shown that growth rates of *I. argentinus* from the same hatching month vary to a lesser extent between different years from those of the different months of hatching within one year (Arkhipkin and Laptikhovsky, 1994). Thus it is possible to make comparisons of modal lengths of squid from the same month of hatching but in different years. The results of this study (based on data collected by the trawl fishery in 1991) are somewhat different from those obtained from the Japanese jigging fishery in 1989–1990 (Uozumi and Shiba, 1993). Generally, during the same month and in the same region of sampling, a majority of males and females caught by jigs in 1989 were about a month younger and correspondingly 20–30 mm smaller than those sampled by the trawl fishery in 1991 (Figs. 8 and 9 in Uozumi and Shiba, 1993; and Figs. 4 and 5 of the present study). Unfortunately, there are no data on the length-frequency composition of trawl-caught *I. argentinus* in 1989 (Arkhipkin and Laptikhovsky, 1994), and thus it is difficult to explain the reasons for such a difference in length composition between the two years. It was found that *I. argentinus* caught by jigging gear were significantly larger and more mature (especially females) than trawl-caught squid fished in the same location and time (Koronkiewicz, 1995). Thus, differences in age and length compositions observed in 1989 and 1991 can be explained by interannual changes in population structure of *I. argentinus* rather than by various selectivity of the two different sampling gears.

The results of the present study show that in January–April, the international squid fishery in the southwest Atlantic catches aggregations of both groups of winter-spawned *I. argentinus*. Squid of the shelf group are captured by trawlers and jigging vessels over the depth range of 150–200 m mainly in the region of 45–49°S. Squid of the slope group are caught by trawlers and jigging vessels mainly in the southern part of the Patagonian Shelf within the EEZA (47–51°S) over the depth range of 150–250 m in February–March, and by trawlers over the continental slope (45–47°S) at depths of 600–700 m in April.

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Literature cited

Arkhipkin, A. I.
1990. Edad y crecimiento del calamar *Illex argentinus*. Frente Maritimo 6 (sec. A):25–35.
1991. Methods for cephalopod age and growth studies with emphasis on statolith ageing techniques. *In* P. Jereb, S. Ragonese, and S. von Boletzky (eds.), Squid age determination using statoliths, p. 11–17. Note Tecniche e Reprints dell'Istituto di Tecnologia della Pesca e del Pescato (N.T.R.-I.T.P.P.) Special Publ.
1993. Age, growth, stock structure and migratory rate of prespawning short-finned squid *Illex argentinus* based on statolith ageing investigations. Fish. Res. 16:313–338.

Arkhipkin, A.I., V. A. Bizikov, V. V. Krylov, and K. N. Nesis.
1996. Distribution, stock structure and growth of the squid *Berryteuthis magister* Berry, 1913 (Cephalopoda, Gonatidae) during summer and fall in the Western Bering Sea. Fish. Bull. 94(1):1–30.

Arkhipkin, A. I., and V. V. Laptikhovsky.
1994. Seasonal and interannual variability in growth and maturation of winter-spawning *Illex argentinus* (Teuthida, Ommastrephidae) in the Southwest Atlantic. Aquat. Living Resour. 7:221–232.

Arkhipkin, A. I., and Zh. N. Scherbich.
1991. Crecimiento y estructura intraespecifica del calamar *Illex argentinus* (Ommastrephidae) en imbierno y primavera en el Atlantico Sudoccidental. Scient. Mar. 55(4):619–627.

Brunetti, N.
1988. Contribucion al conocimiento biologico-pesquero del calamar argentino (Cephalopoda, Ommastrephidae, *Illex argentinus*). Trabajo de Tesis presentado para optar al grado de Doctor en Ciencias Naturales, Universidad de la Plata, Mar del Plata, Argentina, 135 p.

Brunetti, N., M. Ivanovic, G. Rossi, B. Elena, and S. Pineda.
1998. Fishery biology and life history of *Illex argentinus*. *In* T. Okutani (ed.), Contributed papers to international symposium on large pelagic squids (July 18–19, 1996), p. 217–232. JAMARC, Tokyo.

Clarke, M. R.
1978. The cephalopod statolith—an introduction to its form. J. Mar. Biol. Assoc. UK. 58:701–712.

Csirke, J.
1987. Los recursos pesqueros patagonicos y las pesquerias de altura en el Atlantico Sud-occidental. FAO Doc.Tec. Pesca 280, Rome, 78 p.

Dawe, E. G., R. K. O'Dor, P. H. O'Dense, and G. V. Hurley.
1985. Validation and application of an ageing technique for short-finned squid (*Illex illecebrosus*). J. Northwest Atl. Fish. Sci. 6:107–116.

FAO Yearbook.
1997. Fishery statistics. Catches and landings, 1995, vol. 80. FAO Fisheries Series 48, 714 p.

Haimovici, M., N. Brunetti, P. G. Rodhouse, J. Csirke, and H. R. Leta.
1998. *Illex argentinus*. *In* P. G. Rodhouse, E. G. Dawe, and R. K. O'Dor (eds.), Squid recruitment dynamics: the genus *Illex* as a model, the commercial *Illex* species and influences on variability, p. 27–58. FAO Fish. Tech. Pap. 376. FAO, Rome.

Hatanaka, H.
1986. Growth and life span of short-finned squid *Illex argentinus* in the waters off Argentina. Bull. Jap. Soc. Sci. Fish., 52:11–17.
1988. Feeding migration of short-finned squid *Illex argentinus* in the waters off Argentina. Nippon Suisan Gakkaishi 54(8):1343–1349.

Hatanaka, H., S. Kawahara, Y. Uozumi, and S. Kasahara.
1985. Comparison of life cycles of five ommastrephid squid fished by Japan: *Todarodes pacificus, Illex illecebrosus, Illex argentinus, Nototodarus sloani sloani* and *Nototodarus sloani gouldi.* NAFO Sci. Counc. Studies 9:59–65.

Koronkiewicz, A.
1986. Growth and life cycle of *Illex argentinus* from the Patagonian shelf and Polish squid fishery in the region, 1978–85. ICES C.M./K 27:1–25.
1995. Size and maturity differences between trawl and jigger caught short-finned squid *Illex argentinus* (Cephalopoda: Ommastrephidae). Acta Ichtyol. Pisc. 25 (1):97–112.

Leta, H. R.
1987. Descripcion de los huevos y juveniles de *Illex argentinus* (Ommastrephidae) y juveniles de *Loligo brasiliensis* (Loliginidae) en la Zona Comun de Pesca Argentino-Uruguaya. Publ. Cient. Instituto Nacional de Pesca (INAPE), Montevideo, Uruguay 1(1):1–8.

Lipinski, M. R., E. G. Dawe, and Y. Natsukari.

1991. Practical procedures of squid ageing using statoliths. A laboratory manual. Introduction. *In* P. Jereb, S. Ragonese, and S. von Boletzky (eds.), Squid age determination using statoliths, p. 77–81. Mazara del Vallo, N.T.R.-I.T.P.P. Special publication 1.

Nesis, K. N.

1987. Cephalopods of the world. T.F.H. Publications, Neptune City, NJ, 351 p.

Nigmatullin, Ch. M.

1989a. Las especies del calamar mas abundantes del Atlantico sudoeste y sinopsis sobre ecologia del calamar *Illex argentinus*. Frente Maritimo 5 (sect. A):7—81.

1989b. Squid of the world ocean. *In* V. V. Ivchenko (ed.), Development of the fishery in the open oceanic waters, p. 26–48. Kaliningrad Book Press, Kaliningrad. [In Russian].

Nigmatullin, Ch. M., and V. V. Laptikhovsky.

1996. Soviet/Russian fishery of the Argentine squid (*Illex argentinus)* in the Southwest Atlantic, its ecological fishing periodicity and probable reasons of anomalous fishery conditions in 1993–1995. *In* V. A. Sushin (ed.), Fishery and biological research carried out by AtlantNIRO in 1994–1995, p. 138–156. AtlantNIRO Press, Kaliningrad. [In Russian with English summary].

Parfeniuk, A. V., Yu. M. Froerman, and A. N. Golub.

1992. Particularidades de la distribucion de los juveniles de *Illex argentinus* en el area de la depresion argentina. Frente Maritimo 12 (sect. A):105–111.

Rodhouse, P. G., and E. M. C. Hatfield.

1990. Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 (Teuthoidea, Ommastrephidae). Phil. Trans. Roy. Soc. Lond. (ser. B) 329:229–241.

Santos, R. A., and M. Haimovici.

1997. Reproductive biology of winter-spring spawners of *Illex argentinus* (Cephalopoda: Ommastrephidae) off southern Brazil. Scient. Mar. 61(1):53–64.

Sato, T., and H. Hatanaka.

1983. A review of assessment of Japanese distant-water fisheries for cephalopods. *In* J. F. Caddy (ed.), Advances in assessment of world cephalopod resources, p. 14–180. FAO Fish. Tech. Pap. 231.

Tsygankov, V. Y.

1987. Squid polymorphous protein systems and an analysis of intraspecific differentiation of *Illex argentinus* (Castellanos). *In* Genetic investigations of marine hydrobionts, p. 243–251. Annals of the III All-Union symposium. Moscow, VNIRO. [In Russian].

Uozumi, Y., and C. Shiba.

1993. Growth and age composition of *Illex argentinus* (Cephalopoda: Oegopsida) based on daily increment counts in statoliths. *In* T. Okutani, R. K. O'Dor, and T. Kubodera (eds.), Recent advances in cephalopod fishery biology, p. 591–605. Tokai Univ. Press, Tokyo.