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Population Structure of the Squid *Illex illecebrosus*

by

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Introduction

There are four closely related species of Illex in the western Atlantic (Roper et al., 1969): Illex illecebrosus, I. oxygonius, I. coindetti and I. argentinus. I. argentinus has a discrete distribution in southern South America and is of no consequence to discussions in this paper. However, the other three species which may have overlapping distribution in the southern range of I. illecebrosus (Roper et al., 1969) is of consequence in I. illecebrosus stock considerations.

Among these three species, I. illecebrosus has the northernmost distribution and is the predominant commercial species. The known distribution of this species (Roper and Lu, 1979; Lu, 1973; Clark, 1966) extends from eastward of Labrador and Newfoundland in the north, to central Florida in the south (Fig. 1). Roper et al. (1969) noted that past records of the southern range of this species may very possibly have included misidentified specimens of the other two species, I. oxygonius and I. coindetti. Therefore, based on adult specimen data, the southernmost extent of I. illecebrosus they report is at 29°39.5'N. I. oxygonius is described to range between 24°N and 39°N and the northernmost extent of I. coindetti is at 27°37'N.

The morphological similarities of the adult forms of these species (Roper et al., 1969), under the best of conditions, make species seperation very difficult. The problem is further confounded by the absence of information on the larval and juvenile forms of I. oxygonius and I. coindetti. Consequently, in this report we are required to make two basic assumptions. We assume that: 1) I. illecebrosus reported by various authors referred to in this report are correctly identified; and 2) Illex larvae (Rhynchoteuthion type 'C') and juveniles discussed in this report are truly I. illecebrosus. Since I. illecebrosus is by far the most abundant species in areas considered, these assumptions are justified to some extent.

Distribution and Life Cycle Stages

I. illecebrosus exhibit a definite seasonality to their distribution. While Figure 1 depicts the overall distribution, various stages of their life cycle are usually associated with various temporal and spatial patterns. In late winter, larvae and juveniles have been recorded in large numbers in the off-shelf water masses extending into the Gulf Stream (Amaratunga et al., MS 1980). Subsequently, older juveniles and adults are recruited each year to the fishery when they migrate onto the continental shelf and inshore areas for the summer and fall. Their residency on the continental shelf and inshore areas ends in late fall and early winter when they migrate out of these areas to spawn in unknown areas (Amaratunga, MS 1980a). The present indications are that there is post-spawning mortality of pre-recruits which results in a totally new generation. This life cycle of I. illecebrosus is schematically depicted in Figure 2. Although the life cycle of this species is well understood, there is clarification required on the distribution of some of the life stages and consequently the population structure. Thus for convenience of discussion in this paper, the life cycle continuum is divided into discrete sections labelled as egg stage, larval-juvenile stages, and late-juvenile and adult stages.

Egg Stage

Naef's description (1928) of a large floating egg mass of I. coindetti from the Mediterranean has been the only published record of Illex sp. eggs in nature. Many I. illecebrosus egg masses have since been observed under laboratory conditions (O'Dor et al., 1982a). The I. illecebrosus egg mass consists of a nearly spherical homogeneous, tenuous, gelatinous mass of up to 1 m in diameter containing up to the order of 10^5 uniformly distributed small ovoid (approximately 0.6 x 0.9 mm) eggs (Durward et al., 1980). These masses tend to be slightly denser than the ambient seawater and are usually unattached at deposition. The gelatinous mass secreted by the nidamental gland was often bottom spawned in tank experiments, but slight water density changes caused them to float (Durward et al., 1980). More recently, however, one female was observed to spawn a free-floating egg mass, mid-water in the tank (O'Dor et al., MS 1982b). These observations have suggested that egg masses may in nature be easily transported by water currents and through changes in conditions such as density and temperature.

Copulation takes place some time before spawning, and females which have copulated have been observed carrying spermatophore bundles on various locations of the body. During egg mass deposition spermatophores are transferred into the nidamental jelly mass. Chemical properties of the jelly cause the release of spermatozoa permitting fertilization. Embryonic development then proceeds within the jelly mass.

Rate of cephalopod embryonic development is known to be temperature dependent. Choe (1966) and Hamabe (1962) reported faster development of eggs in species of squid and cuttlefish as the water temperature became warmer, while Boletzky (1974) noted that in some species the change in development period could change hatching time considerably. In Loligo vulgaris hatching time ranged from 20 days to 70 days at temperature changes from 20°C to 10°C. Similarly, McMohan and Summers (1971) showed that the rate of egg development of Loligo pealei could be modified at any stage of their development by altering the water temperature within their tolerable range. These relationships have important consequences on the population structure, with the entire life cycle time table liable to be shifted by water temperatures.

In I. illecebrosus also, rate of egg development was found to be temperature dependent (O'Dor et al., 1982a). In one laboratory experiment, naturally fertilized eggs required about 11 days to hatch at 13°C (Durward et al., 1980) although more recent experiments have estimated the time lapse from fertilization to hatching to range from 9 days at 21°C to 16 days at 13°C (O'Dor et al., 1982a). The lower temperature limit tested, 7°C, resulted in successful fertilization without embryological development, while successful egg development was apparently between 11°C and 13°C (O'Dor et al., 1982a). The upper temperature limit has not been tested.

In nature, spawning locations are not known. However, temperature requirements for successful development suggest the probable areas to be in the warmer waters southwestward of Georges Bank or in the vicinity of warm waters of the Gulf Stream in the more northeastern areas. Data supporting both possibilities are available (NAFO, 1980; 1981).

Larval-Juvenile Stages

Newly hatched *I. illecebrosus* bear the typical characteristic ommastrephid larval form. The larval form, which is characterized by the two tentacles fused into a proboscis, is termed the Rhynchoteuthion stage, a general designation that carried no nomenclatorial status (Roper and Lu, 1979). Chun (1903) originally recognized the form and described it as *Rhynchoteuthis*. Until recently specimens of larvae and juveniles of this species were few. Roper and Lu (1979), however, from field samples ranging from 1.5 mm to 18 mm mantle lengths, characterized the *I. illecebrosus* Rhynchoteuthion stage and juveniles. Subsequently, surveys in the oceanic water masses of the northwest Atlantic, extending from the continental shelf to the Sargasso Sea which have provided a large specimen data base (Amaratunga et al., MS 1980) and laboratory-induced spawning (Durward et al., 1980; O'Dor et al., 1982a), have elaborated our understanding of the morphological and behavioural characteristics.

The first recorded spawning in captivity in 1979 (Durward et al., 1980) and subsequent years of experiments have provided descriptions of spawning habits, embryonic development, and early larval forms. Rhynchoteuthion-stage larvae emerging from egg masses at about 1.1 mm in mantle length survived in the tanks to a maximum of 10 days on the yolk reserves from the telolecithal eggs. These hatchlings were unable to swim at first but were able to, by sporadic mantle contraction, scoot about at the bottom of the tank for a day or more. Durward _et_ _al_., (1980) suggest that in nature they spend this period within the gelatinous egg mass for protection against microbial attack. In these experiments the Rhynchoteuthion was later able to move up the water column by rapid mantle contractions. Similar-sized specimens collected near the Gulf Stream in the upper 100 m of the ocean (Hatanaka _et_ _al_., 1982) suggest that they are capable of maintaining elevation. At Rhynchotheuthion transition to the juvenile form, when the proboscis divides into two tentacles at about 8 mm mantle length, they are active swimmers.

Off-shelf (oceanic water masses) surveys between February and May since 1979 have produced several thousand specimens ranging from Rhynchoteuthion stages up to 120 mm mantle length (NAFO, 1981). These distributions range geographically from offshore waters off Cape Hatteras, N. Carolina, to off the Grand Bank, Newfoundland. They have been most commonly encountered in the upper 100 m of the landward boundary zone of the Gulf Stream at temperatures from about 10°C to 18°C and salinities from 35‰ to 36.5 ‰ (Amaratunga _et_ _al_., MS 1980). Near-surface bongo hauls particularly have resulted in the capture of many Rhynchoteuthion and early juvenile stages in these water masses prior to mid March, mostly southwestward of the Scotian Shelf.

Although the exact area of spawning is unresolved, one hypothesis suggests that spawning occurs over a broad area southwest of the Scotian Shelf, and that hatchlings are initially passively transported northeastward by the Gulf Stream flow (Froerman _et_ _al_., MS 1981). The Gulf Stream dynamics make the transport mechanism possible (Trites, MS 1982); and the temperatures within the Gulf Stream, which are above the minimum required for embryonic development (O'Dor _et_ _al_., 1982a), provide an ideal environment for development and distribution. However, catches within the Gulf Stream to date have been few, making it not possible to confirm the mechanism of hatchling transport. On the other hand, the more actively swimming juveniles ranging from post-Rhynchoteuthion stage to about 100 mm mantle length, spend their time in the northern boundary zone of the Gulf Stream before they actively swim northward in the direction of the continental shelves. Supportive data include large catches of these sizes in the northern boundary zone of the Gulf Stream and its meanders and also in the peripheral regions of warm-core eddies (Amaratunga and Budden, MS 1982; Hatanaka *et al.*, MS 1982). Similarly, progressively larger juveniles have been encountered progressively landward of the Gulf Stream in the Slope and Shelf Water masses (Froerman *et al.*, MS 1981).

Late Juvenile and Adult Stages

After their early stages of life associated with the Gulf Stream and oceanic water masses, juveniles 100-150 mm mantle length arrive on the continental shelves of Nova Scotia and the Grand Bank in spring (May/June) (Amaratunga, MS 1980a; Squires, 1957). For convenience this is referred to as the immigration phase (Caddy, MS 1979). Fedulov and Amaratunga (MS 1981) demonstrated that sea temperature was related to the date of immigration to the Scotian Shelf; however, their strategy is probably related to availability of preferred prey. Amaratunga (MS 1980b) observed that the immigrating squid exhibit an active period of feeding; their diet at the time, which consisted exclusively of euphausiids, coincided with the seasonal availability of *Meganyctiphanes norvegica*, *Thysanoessa inermis*, and *Th. rashii* on the Shelf. Nevertheless, their inshore and offshore distribution in Nova Scotia and Newfoundland waters is usually limited to the warmest period of the year, from spring to late fall (as late as December). Their local distribution and abundance may vary considerably from year to year.

A comprehensive study of the growth and maturation of squid on the Scotian Shelf was conducted by Amaratunga (MS 1980a).

Figure 3 shows fitted von Bertalanffy growth curves for three years of length frequency distributions studied. Length frequency distributions compiled by sex by week typically showed normal distributions with a consistent single modal class (Fig. 4) progressing through the season. However, inconsistent modes were also sometimes present. These less-pronounced modal classes were sometimes noted at various regions of the distributions, sometimes close to the major modal class. Especially in early and late season, distributions were often skewed (larger S.D. in Figure 3) and modes were sometimes apparent at considerably different sizes. The males usually had a narrower size range than females.

The von Bertalanffy curves (Fig. 3) of all three years were generally similar. Although the 1977 and 1979 animals first observed on the Shelf in May were smaller than those of 1978, mean sizes by the end of August in all three years were similar to each other. The constant t_o (the hypothetical age at which the animal would have had zero length) and L_∞ (the hypothetical greatest length of the animal) provided valuable estimates of the growth parameters. Table 1 shows these parameters for the three years.

The 1978 and 1979 growth curves were also used to study maturation patterns (Amaratunga, MS 1980a). In males, visually detectable stages (Amaratunga and Durward, 1979) are used to demarcate different phases of maturation. The transition into the "mature" phase is critical in that males entering it will soon be ready to breed (Phase 3 in Figure 5). This stage also relates to an imminent emigration phase (Caddy, MS 1979) from the continental shelf feeding grounds to the unknown spawning grounds.

Female staging is less subjective in using the nidamental gland length:mantle length ratio (Durward _et_ _al_., 1979). Stage 3, when maturation is activated by gonadatrophic hormones, is the critical stage. Fifty percent of the animals reached this stage of maturity in early December 1978 and late November 1979, a little later than the corresponding Stage 3 in males. Stage 3 in females also relates to an imminent emigration phase (Figure 5).

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As yet, emigration undertaken by mature squid has not been totally described. As stated earlier, one hypothesis suggests that spawning occurs in a broad area southwest of Georges Bank (NAFO, 1980). If they are to spawn in the warmer waters southwestward of Georges Bank, these animals in SA 3 and 4 must undertake a mass, long-distance emigration. Although mass migrations have not been observed, few tagged squid have in fact travelled such long distances in the fall. A squid tagged (September 6, 1979) in Notre Dame Bay, Newfoundland, was reported captured (December 22, 1979) 1,260 miles away, off the coast of Maryland, U.S.A. (Dawe _et al_., 1982). Hurley and Dawe (MS 1980) and Amaratunga (MS 1981) also reported fall south/southwestward movements (of up to 300 miles) of a few tagged squid from Newfoundland and Nova Scotia, supporting the probability of a spawning migration.

Another hypothesis suggests that spawning could occur in more northeastern areas (NAFO, 1980). If they are to spawn in the vicinity of the Gulf Stream in the more northeastern areas, their emigration would be normal to the continental shelf edge. Fall and early-winter aggregations of maturing squid have been observed on the Scotian Shelf edge (Amaratunga, MS 1980a). Larger and more mature animals were encountered progressively deeper at the Shelf edge (unpublished data, 1978), supporting the belief that squid (most ommastrephids) undertake an ontogenic spawning migration (Lu, 1973). Additionally in an August/September survey on the Shelf, six mature females (one of which was carrying spermatophores after copulation) were captured. These data suggest that spawning locations could also conceivably be in oceanic water adjacent to the Scotian Shelf.

Life Cycle Hypotheses

We have thus seen that the life cycle of _I. illecebrosus_ is composed of stages which are distinguishable by biological and distributional characteristics. Biological and distributional aspects of the egg, larval, and early-juvenile stages still require considerable elaboration; research on these aspects is recent and underway (NAFO, 1981). On the other hand, late-juvenile and adult stages during their residency on the continental shelf and inshore areas are much better described.

Studies between April and December in SA 3 to 5 have resulted in the current hypotheses of the life cycle, with postulated life spans ranging from 1 to 2 years.

Squires (1967), from length measurements and observations on maturation patterns of squid in Newfoundland waters, proposed a possible 1 or 2 year life span, but he favoured an age of 1 year at spawning. Similarly, in the adjacent Scotain Shelf, data support the annual life cycle hypothesis (Amaratunga, MS 1980a). Both study areas report single consistent modal classes (Fig. 5) annually. However, further southwestward, on Georges Bank, the modal class structure changes to contain three consistent modes, and Mesnil (1976) interpreted the data to contain two concurrent generations each with a life span of 16 to 18 months. One generation was described to have hatched in the winter (roughly February) and mature to spawn in the next year's late summer (roughly August), while the other generation hatched in the fall and matured to spawn in the next year's winter. This hypothesis attempts to rationalize the presence of two prominent modes, thus proposing a modification to the annual cycle proposed for the colder northeastern areas. Lange (MS 1981) on the other hand noted that in Georges Bank and southwestward, winter spawning is consistently seen each year while the importance of summer spawning varied and reached significant proportions in some years. Indeed two and three modes have been inconsistent and occasional in the Scotian Shelf (Amaratunga, MS 1980a; Dupouy, MS 1981). Squires (1967) also reported that in some years a few out-of-phase maturing animals are observed in May and young juveniles are observed in November. These, however, were believed to belong to the same generation and thus a component of a single protracted breeding season. Lange's (MS 1981) observations farther southwestward indicate they probably spawn to some extent through most of the year.

In conclusion, we see that the winter spawning period constitutes the major spawning for the species, and its recruits are consistently seen through much of its known distribution. Reports from the extensive data base for SA 3 and 4 distinctly show this and therefore support the annual life cycle hypothesis. We further propose that the winter spawners constitute the major component of the *I. illecebrosus* population. Although the tests were preliminary, biochemical evaluation of animals of a single year collected from various parts of the Scotian Shelf showed the squid to be genetically monomorphic and that there was a high degree of homogeneity between samples (Romero and Amaratunga, MS 1981).

The variations in spawning periods seen in areas southwestward of the Scotian Shelf may be attributed to the availability of more suited environmental conditions. In particular, there is an extended warm season in those areas. Thus it is hypothesized here that the protracted breeding season, described for animals in SA 3 and 4, is further protracted and more pronounced in areas southwestward.

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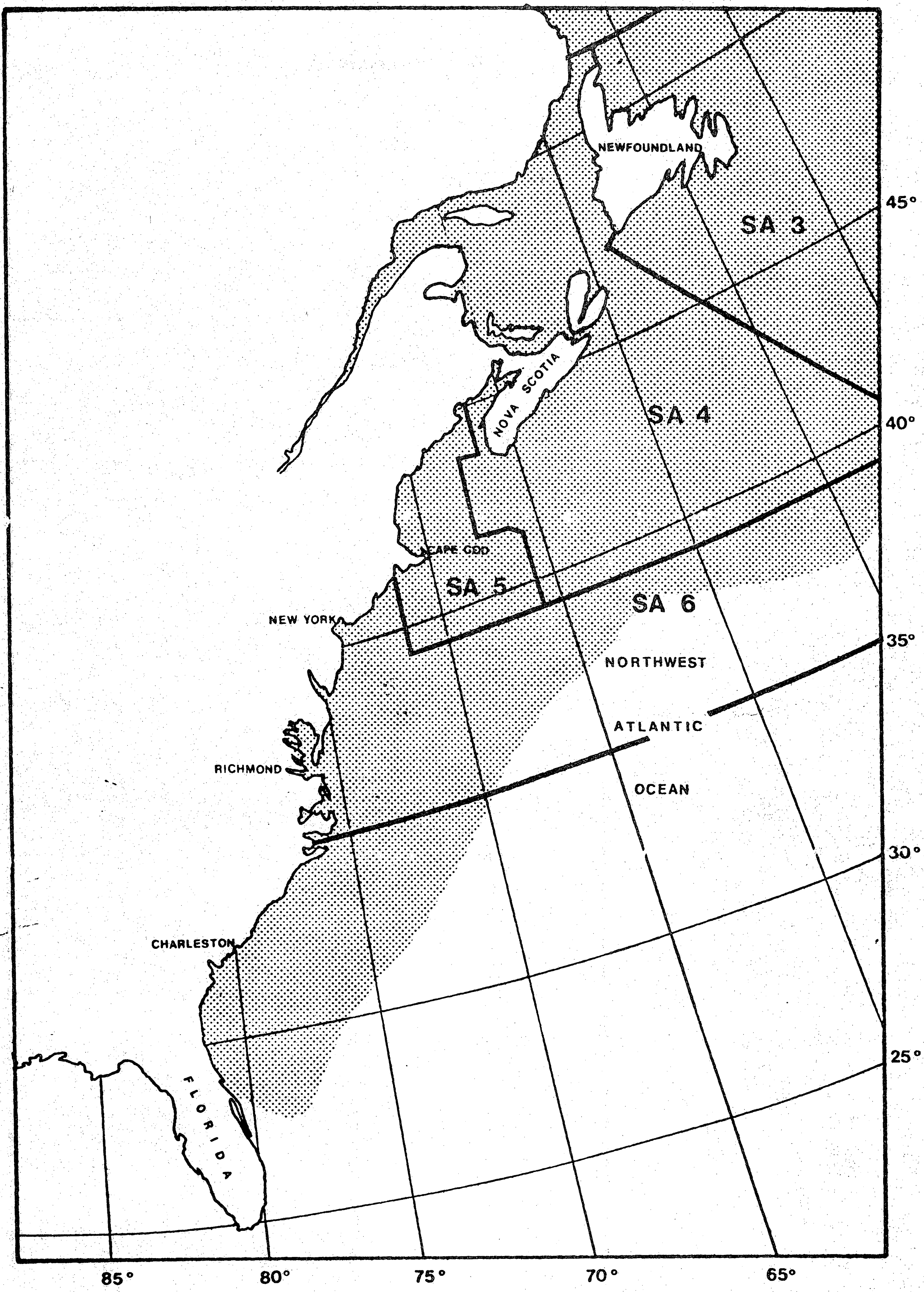

Fig. 1. Known distribution (shaded area) of *Illex illecebrosus* in the Northwest Atlantic region.

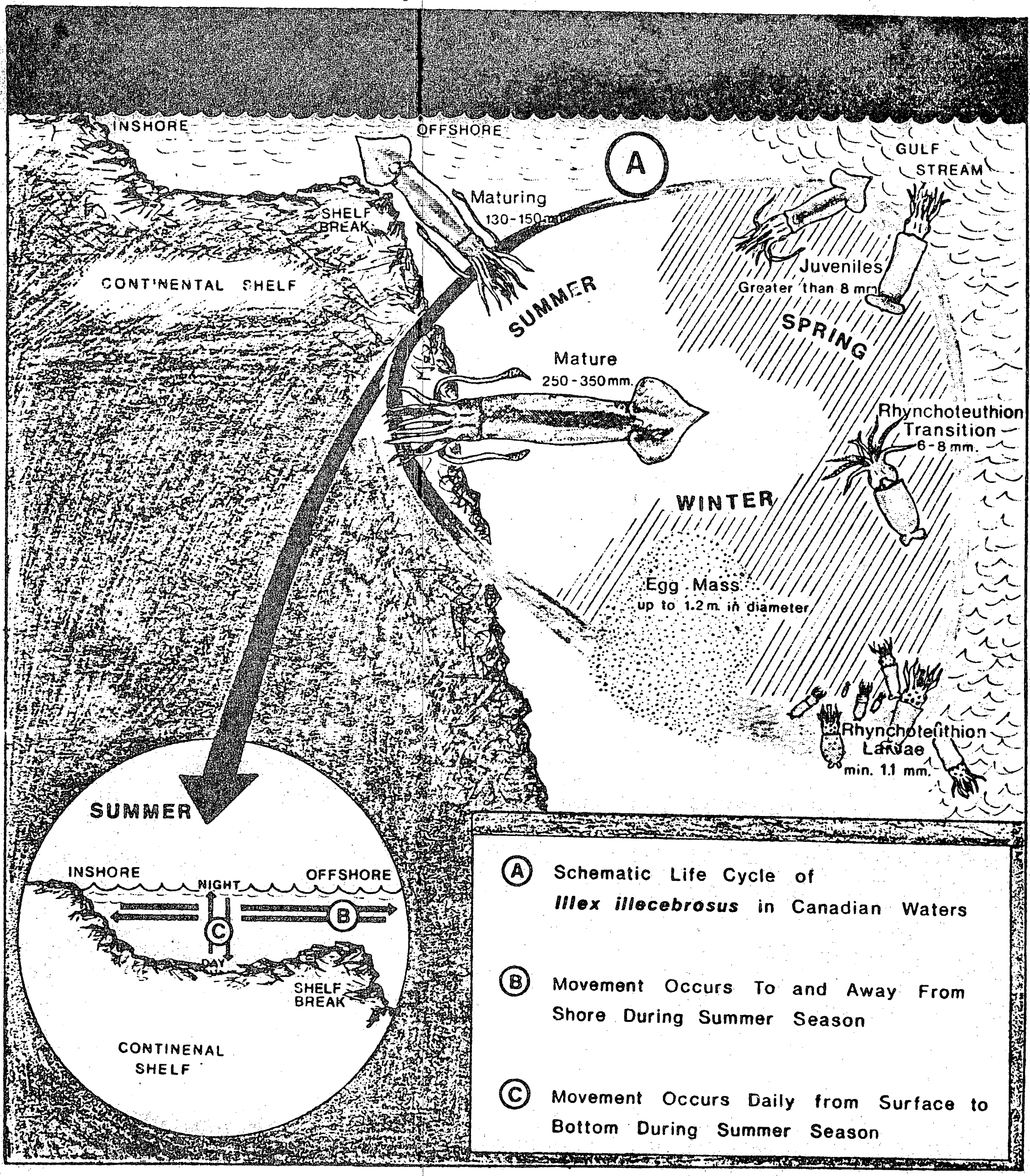

Fig. 2. Schematic representation of the life cycle of *Illex illecebrosus*. The unknown total distribution of the winter and spring stages are indicated with cross-hatching.

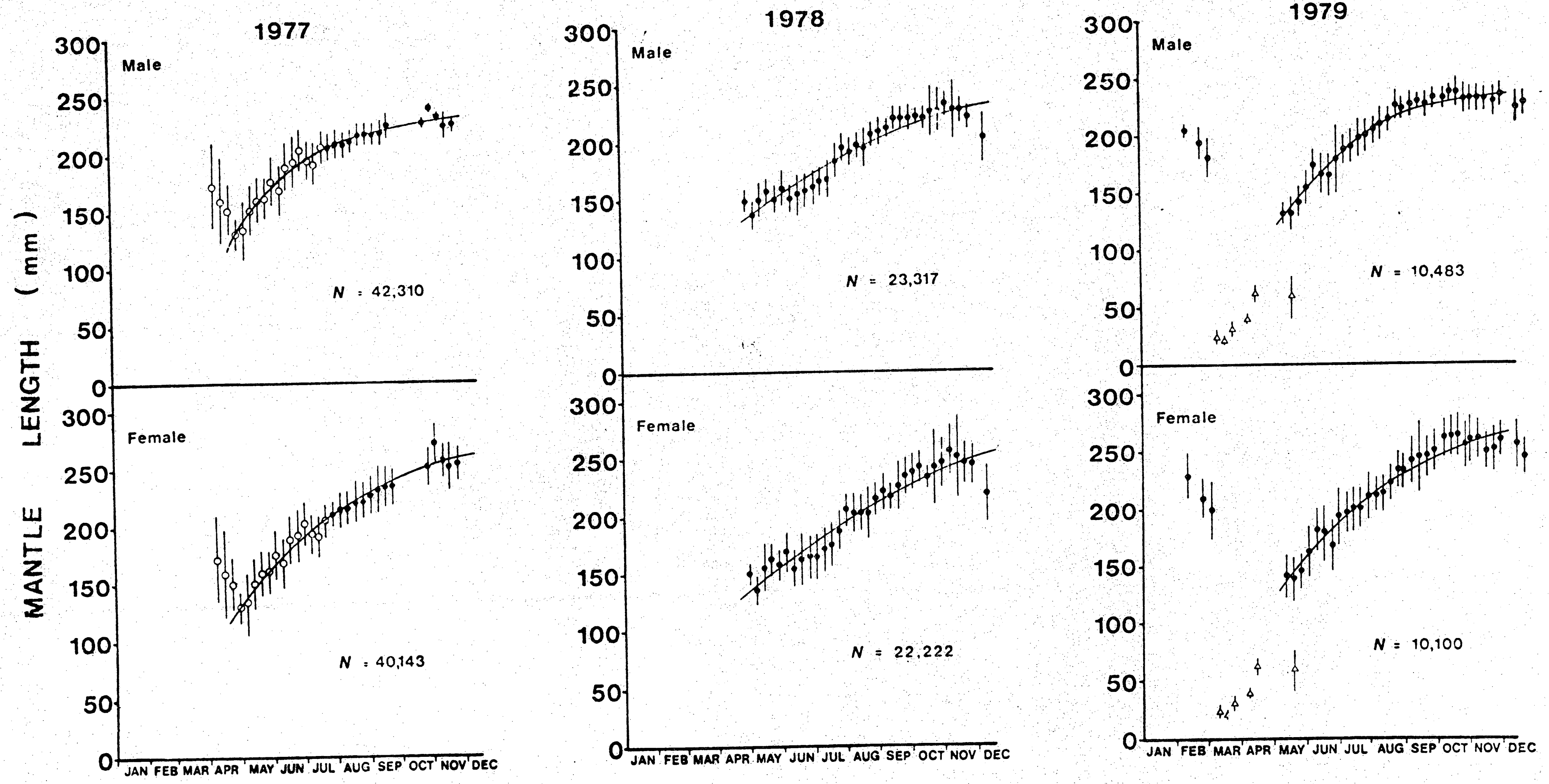

Fig. 3. Growth curves fitted with von Bertalanffy equation $L_t = L_\infty (1-e^{-Kt})$ to length-frequency data of *Illex illecebrosus* from 1977, 1978, and 1979 (N.B. 0 = unsexed; 0 - sexed; Δ - samples obtained from outside of Scotian Shelf; vertical bars - 1 S.D.

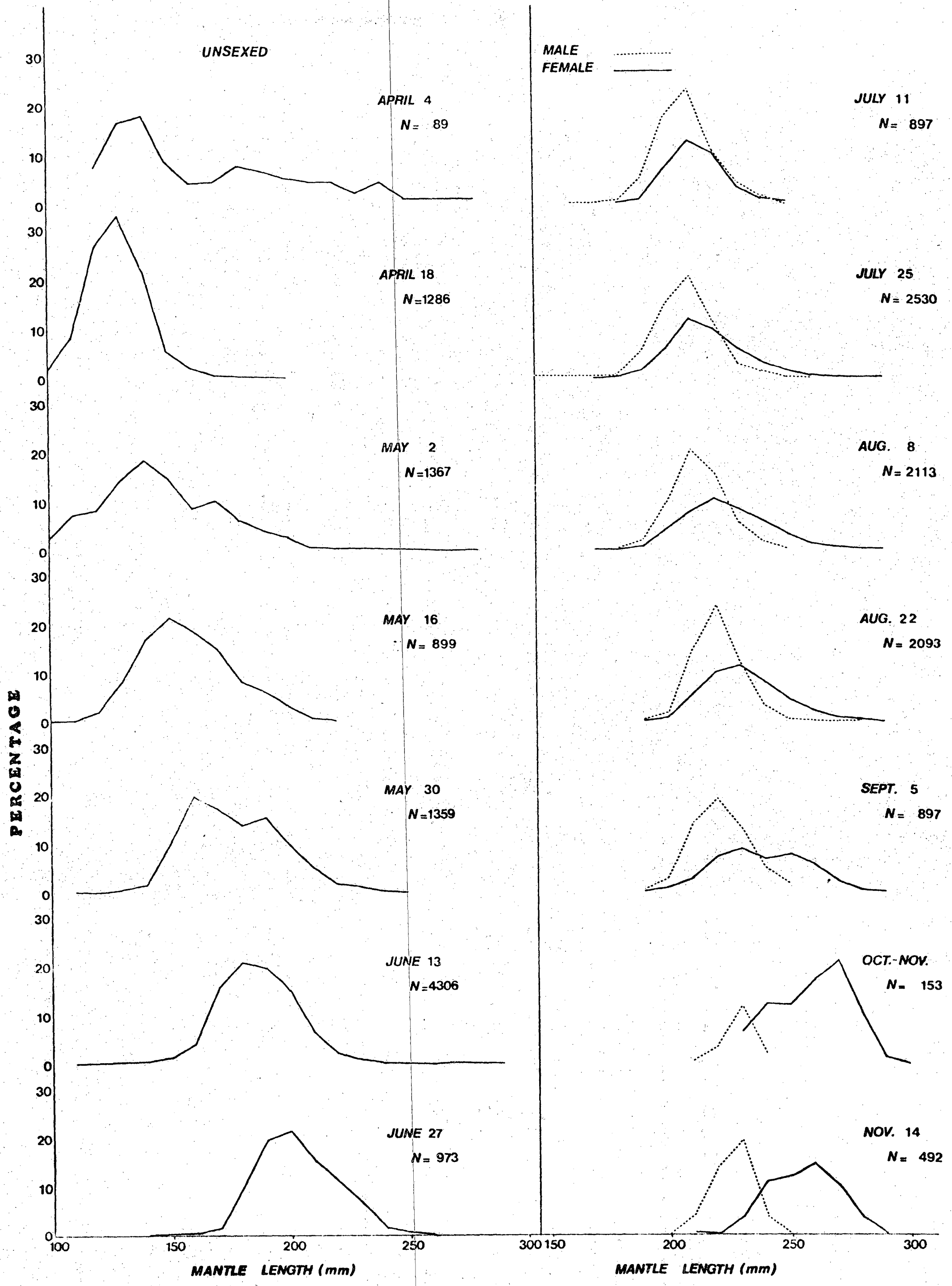

Fig. 4. Length-frequency distributions of *Illex illecebrosus* samples from the Scotian Shelf in 1977. Numbers (N) indicate sample sizes.

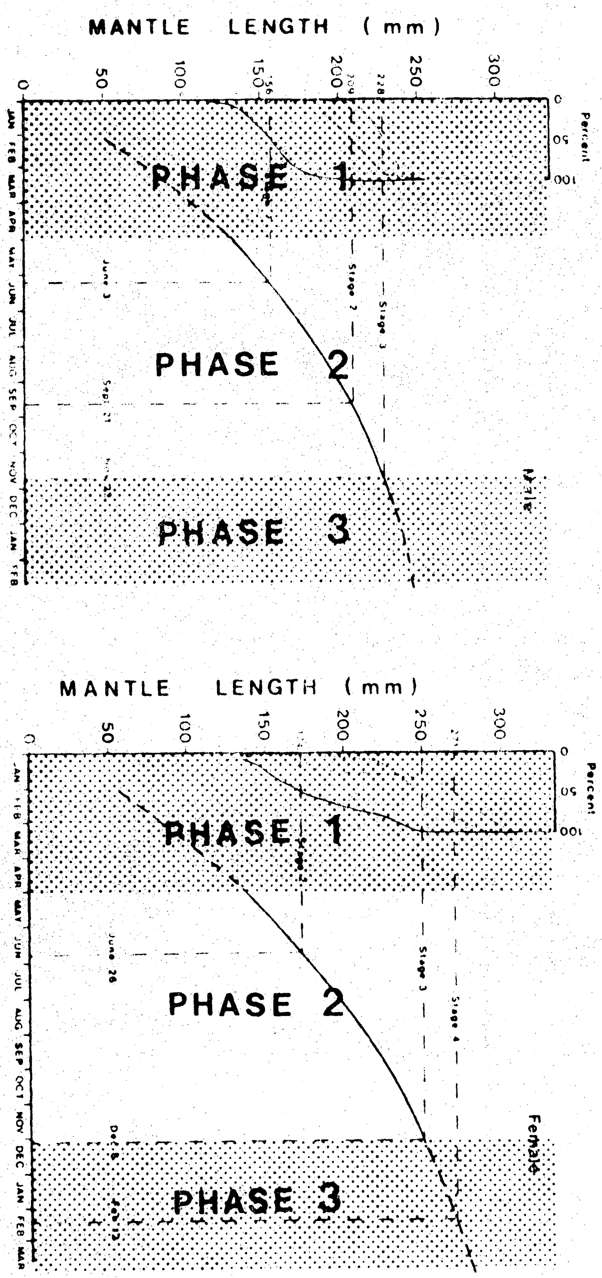

Fig. 5. 1978 fitted growth curves of Fig. 3 showing three phases of residency of *Illex illecebrosus* population on the Scotian Shelf. Phase 1 = immigration phase; Phase 2 = exploitation phase; Phase 3 = emigration phase.