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Chapter III

Illex illecebrosus, Northern Short-Finned Squid

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Abstract

Short-finned squid (*Illex illecebrosus*) eggs and paralarvae are distributed by the Gulf Stream at least from the Florida Straits to oceanic waters south of Newfoundland, with older stages extending inshore and further north, as far as the southern Labrador shelf. Adults feed in the north and migrate south to spawn. Fishery records only go back to 1880, but jigging for cod bait in Newfoundland may have been among the first occupations for Europeans in North America. For a decade starting in 1975, this squid was the target of an offshore trawl fishery that returned nearly a million tons before collapsing, and extensive field and laboratory research during this period made it one of the best characterized ommastrephid species. This chapter includes re-analyses of these data based on new age estimates. Present efforts, focused on monitoring a slow recovery from the longest series of recruitment failures on record, represent a valuable case study of squid recruitment processes.

1. Introduction

The short-finned squid *Illex illecebrosus* (Lesueur, 1821) is associated with fisheries from Delaware Bay to the Labrador Sea, but its range probably extends further south into the Caribbean and Gulf of Mexico and east into the Atlantic. In the northern region it is very common (Lu, 1973); in peak years its biomass has been estimated at up to 3,000,000 t

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(Froerman, 1980). Its economic importance as bait for the Grand Banks cod fishery is probably centuries old and, as Figure 1 shows, records of the inshore jig fishery, prosecuted mainly for this purpose, go back to the 1800's (Mercer, 1973a).

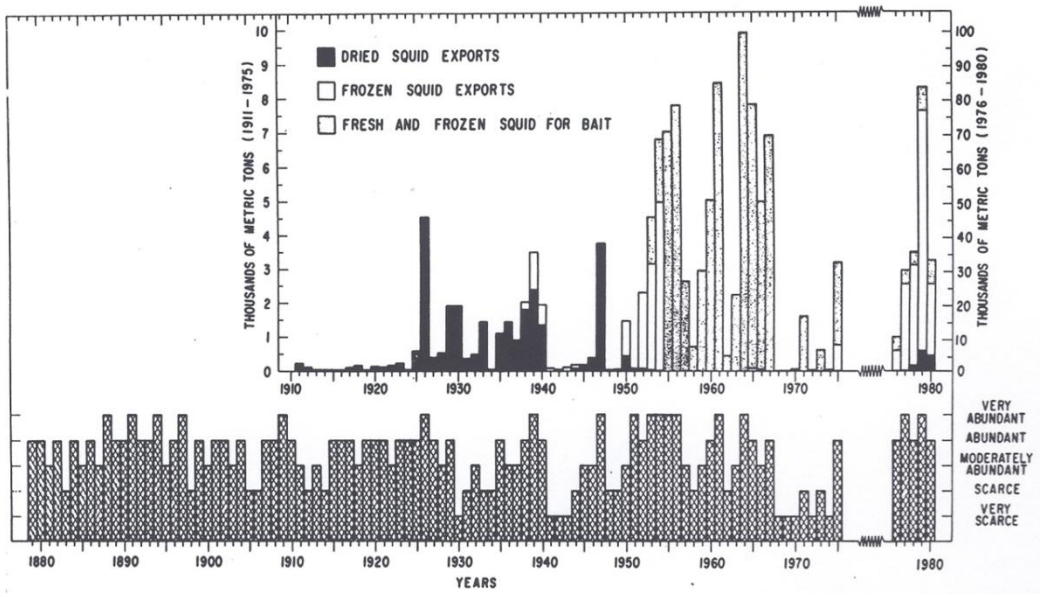

Figure 1. Qualitative estimates of inshore abundance estimates of squid (*Illex illecebrosus*) in Newfoundland, 1879–1980, and a breakdown of inshore catch, 1911–1980 (Note scale change on the catch ordinate for 1976–1980, from Dawe, 1981).

Squires (1957) gave an extensive account of the biology of this squid for the approximately six-month period it spends inshore near Newfoundland. During the late 1970's and early 1980's a greatly expanded fishery for this species provided the impetus for extensive research into its life cycle, including the reproductive and youngest stages. Several summaries of this work have appeared (Aldrich and Arnold, 1991; Balch et al., 1978; O'Dor, 1983; O'Dor and Dawe, 1998; Rowell et al., 1985a), and in recent years efforts have focused on an unusually long period of recruitment failure during the past three decades in Canadian waters (Dawe and Hendrickson, 1998; Hendrickson and Showell, 2010; O'Dor, 1995; O'Dor and Dawe, 1998). This chapter updates previous reviews by summarizing the existing information, including new information on mechanisms that regulate abundance and recent trends in fisheries.

2. Life History Biology

Although the overall distribution limits of *I. illecebrosus* remain unclear, the young stages are associated with the continental edge of the Gulf Stream and subsequently with the adjacent shelf (Figure 2, Dawe and Warren, 1993). Seasonally, large juveniles and adults may occur as far north as the Labrador Sea in summer, but accumulating evidence indicates that abundance near the northern limit varies annually with climatic conditions (Dawe and Warren, 1993; Dawe et al., 2000, 2007). By late autumn, most have emigrated from such northern areas, heading

offshore to greater depths and south. Squid from as far north as Newfoundland emigrate to warm waters on the shelf off the southern United States (Dawe, 1999; Dawe et al., 1981a; Hendrickson, 2004), presumably because eggs fail to develop at temperatures below 12°C.

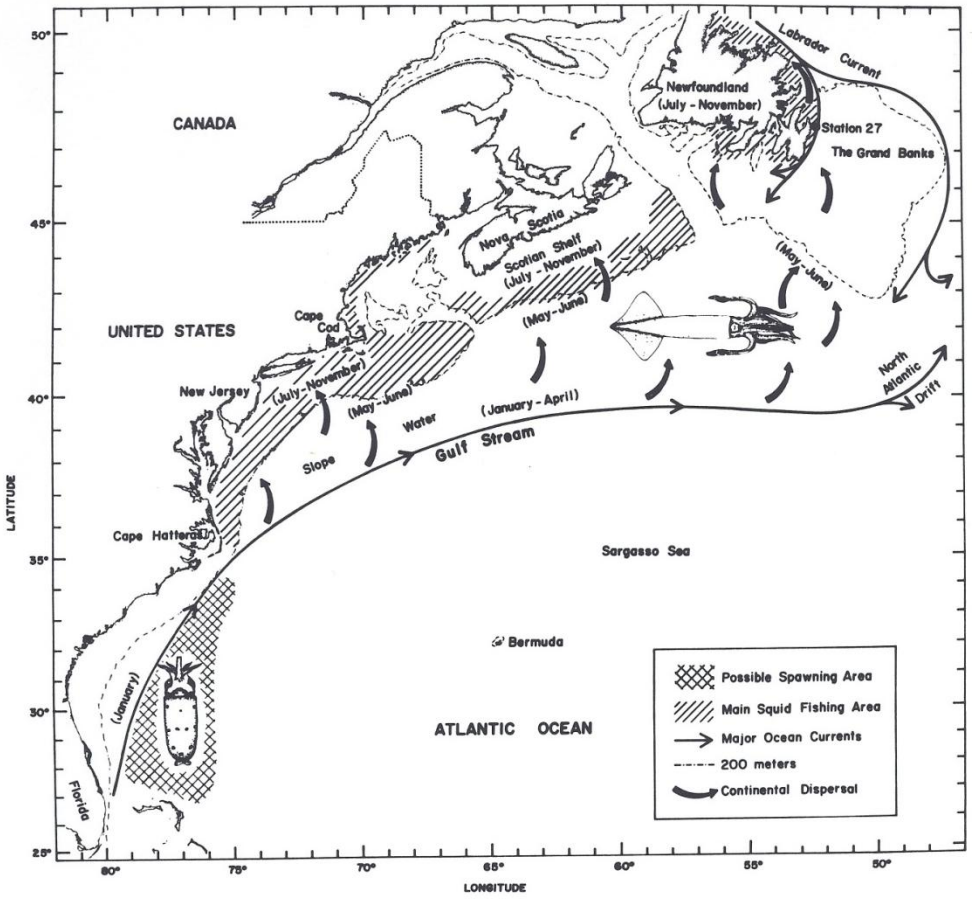

Figure 2. Diagrammatic representation of the life cycle of *Illex illecebrosus* in relation to the main northwest Atlantic Ocean currents and sampling sites (from Dawe and Warren, 1993).

The southward migration may reach a natural block where the high velocity Gulf Stream passes north through the Florida Straits. There are several submersible sightings of large schools of short-finned squids resting on bottom in this area (Voss and Brakoniecki, 1985) and high concentrations in the stomach contents of swordfish there (Toll and Hess, 1981). Near Ft. Pierce, Florida, in late January, 1977, at about 80 m depth, dead, post-spawning specimens of short-finned squid were seen and sampled from a submersible (J.K. Reed, Harbor Branch Foundation *unpubl. data*) at a site where currents would sweep the nearly neutrally buoyant egg masses into the Gulf Stream.

Although these specimens were tentatively identified as *Illex oxygonius* (C.F.E Roper *unpubl. data*), eggs carried north in such masses would release hatchlings that would be transported to the frontal zone between the warm slope waters and the shoreward edge of the Gulf Stream (Bakun and Csirke, 1998) where larval and juvenile *I. illecebrosus* have been

found in greatest abundance (Dawe and Beck, 1985; Fedulov and Froerman, 1980; Hatanaka et al., 1985; Rowell et al., 1985b).

This squid ranges from the surface to depths of 1000 m or more and is taken in waters from 0.5° to 27.3°C (Whitaker, 1980) and from 30 to 36.5 psu salinity (Amaratunga et al., 1980a; Palmer and O'Dor, 1978). Biomass estimates for the Scotian shelf (based on a standardized, annual survey) have ranged over two orders of magnitude (from 2000 t in 1970 to 200,000 t in 1976, Koeller, 1980).

2.1. Characteristics

Externally there is no apparent difference between the sexes until the size at which gonad development begins in males, about 13–15 cm mantle length (ML). However, when the mantle is slit ventrally the two small nidamental glands lying on either side of the mid-line just posterior to the heart can, with practice, be recognized in females >10 cm ML. From June onward, at lengths greater than 13–15 cm, the rate of somatic growth in males decreases so that they are, on average, 5 to 10% shorter than females. The difference in weight is less than that in length because males tend to be slightly heavier at a given length, but there is always considerable overlap in size between the sexes. Differentiation of the hectocotylus begins at the same time the size difference develops. This change may affect either arm R III or L III. Prior to emigration the length of the hectocotylized part may reach 2 cm (Squires, 1957). This species may achieve a maximum length of about 33 cm and a total body weight of 700 g, with females achieving largest sizes.

Length is convenient to measure and often gives a good correlation with age, but weight estimates are more appropriate for relating feeding and catch rates to growth. However, most studies of size and growth have utilized length as the size variable. Total body weight may be estimated from mantle length by applying length-weight relationships. Such relationships vary considerably due to sex, year, month and locality (Dawe, 1988). Lange and Johnson (1979) recommended the composite equation, $W = 0.0481\ L^{2.72}$ for relating ML (cm) to weight (g). This equation was derived for adults for use in estimating biomass from length-frequency data, but holds within reasonable limits for all lengths. It predicts a weight of 0.12 mg for a hatchling (which is half the weight of an egg) and is, at worst high by about 50% for large juveniles. Most such fitted equations are out 10- to 100-fold if extrapolated this far.

Weight-at-length also represents an index of condition for use in studies of feeding, energetics or growth. Dawe (1988) found that early-season weight-at-length, and seasonal change in weight-at-length, were related to the prevalence of fish in the short-finned squid diet at Newfoundland.

2.2. Age and Growth

Growth rates can be determined from changes in length over time if there is clear evidence for population homogeneity, if the age of individuals is known or if growth increments can be directly linked to time (Bizikov, 1991). Early analyses assumed that local concentrations of this species were homogeneous.

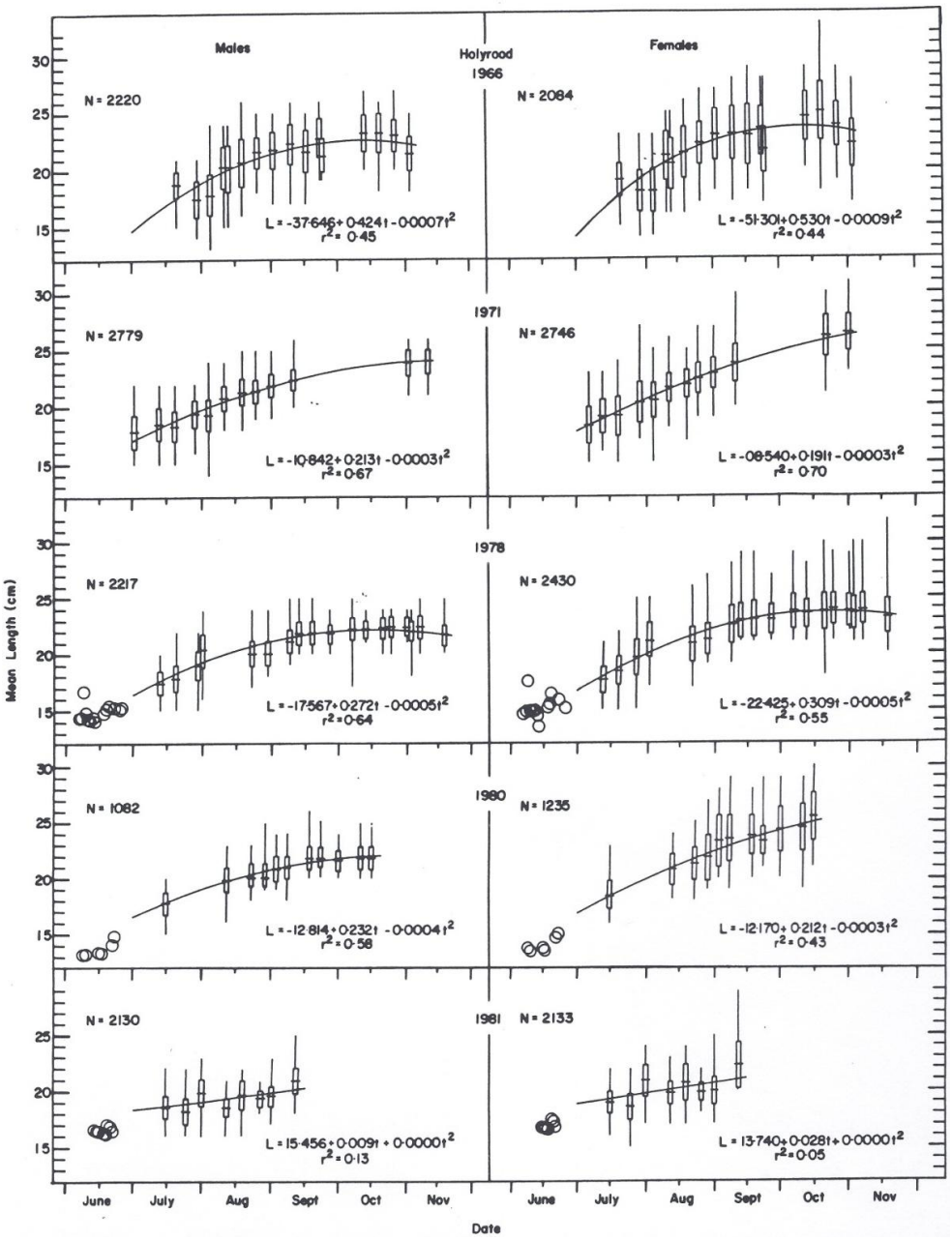

Figure 3. Annual variation in seasonal trends of mantle length for both sexes of *Illex illecebrosus* from the commercial jig fishery in Newfoundland waters. Box and whiskers show mean, SD and range. Circles indicate bottom trawl data from the Grand Banks slope, not included in quadratic models (O'Dor and Dawe, 1998).

This assumption for the Scotian shelf (Amaratunga, l980a) and Newfoundland (Squires, 1967; Beck et al., 1980) was based on the observation of unimodal length-frequency distributions with length increasing consistently through the year. This is not the case in the south where a second mode suggests a second breeding period (Mesnil, 1977; Lange, 1981; Coelho and O'Dor, 1993).

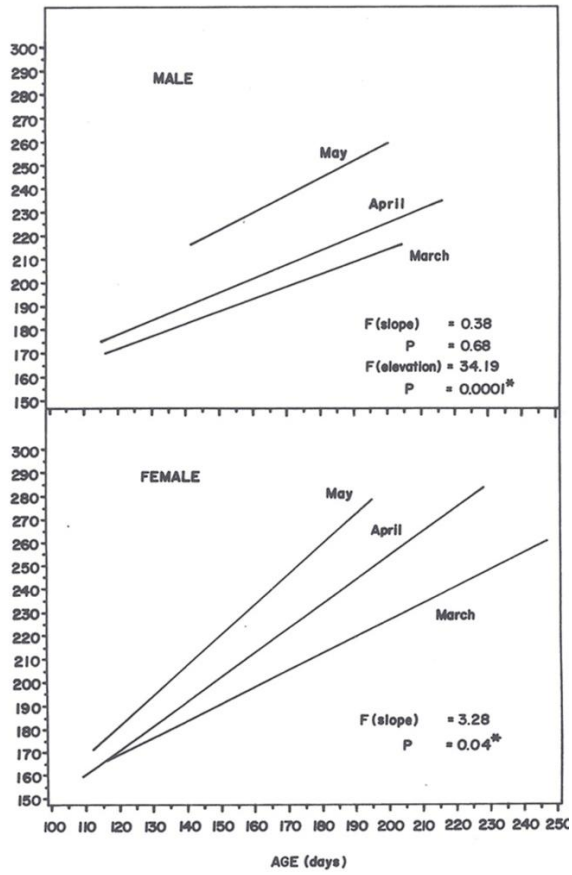

Figure 4. Mantle length at age for *Illex illecebrosus* in Newfoundland waters in 1990 separated by sex. Linear regressions show size dimorphism and different growth patterns between sexes, with progressive increases in growth rates over the season for individuals hatched in different months (Dawe and Beck, 1997).

Early growth studies from Newfoundland (Squires, 1967) and the Scotian shelf (Amaratunga, 1980a) were based on modelling seasonal progression in length using the von Bertalanffy growth model.

However a general quadratic model is more appropriate as a descriptive model because it accounts for the observed late-season decrease in length (Figure 3). Such length-based models suggested that growth in length continued at about 1.5 mm d^{-1}, as suggested for juveniles.

The apparent decline in growth rate from July to September was thought to be due to limited food supply. The apparent asymptotic or late-season negative growth was attributed to emigration of the largest squid. The few unusually small squid found in late winter and early spring were considered stragglers.

More recent studies have been able to utilize data on squid age or growth history determined from examination of statoliths or gladii, respectively (Arkhipkin and Perez, 1998; Perez and O'Dor, 1998, 2000). One such study, based on statolith ageing at Newfoundland, showed that length-based models are not appropriate for describing growth because there was constant interchange within the local population (Dawe and Beck, 1997).

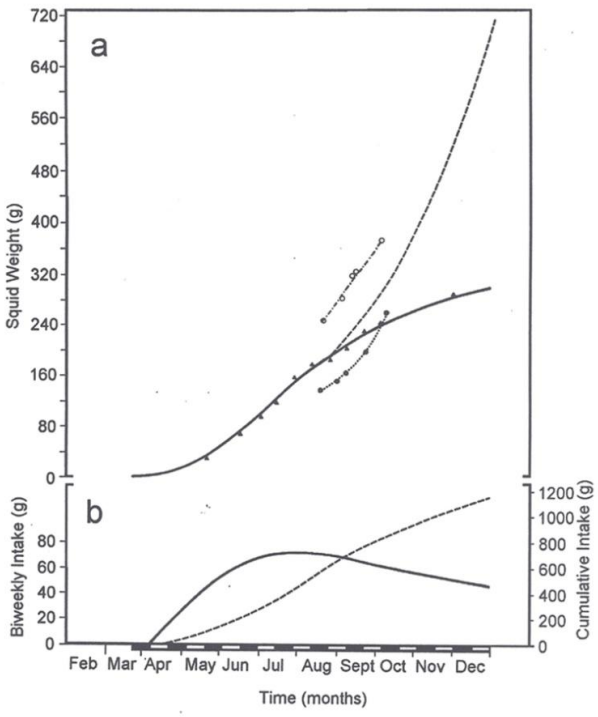

Figure 5. (a) Seasonal weight changes in wild and captive *Illex illecebrosus*. triangle = wild caught squid, 1977; filled circle = a captive population fed *ad libitum* on fish, 1978; empty circle = a single tagged captive. The dashed line projects the weights of the wild population, if they had continued growth at the rate of the captives. (b) Food consumption for an average squid estimated from the sizes of the wild population and the feeding rate/growth rate relationship seen in captives (solid line = bi-weekly consumption, dashed line = cumulative consumption). Note that these calculations assumed a stable wild population and underestimate the requirements of cycling migrant squids. (From O'Dor et al., 1980a).

As Figure 4 shows, growth in length did not decline but was linear throughout the season for animals hatched in the same month. Such rapid seasonal growth, in relation to earlier length-based estimates agreed generally with observations of growth in captivity better than field observations (Figure 5a, O'Dor, 1983). Age-based estimates showed that growth varies greatly among individuals and with time of hatching (Dawe and Beck, 1997). While such (within-study) relative differences in individual, seasonal or annual growth rates are valid, Gonzalez et al. (2000) showed that absolute age estimates may be biased by method of statolith age determination. Accordingly, they advised caution in comparing between studies of age and growth that are based on differing methodologies or age readers. A more recent approach to studying growth performance has been to model weight-at-length (condition) as a function of age (Ragonese et al., 2003). While this method may also be affected by bias in statolith age determination, it offers advantages above traditional size-at-age modelling, including concurrent use of two size metrics, reduced effects of sampling bias, and avoidance of theoretical constraints regarding the form of growth in absolute size. This approach provided comparable or superior model fits when compared with traditional size-at-age models.

2.3. Maturation and Fecundity

Sexual maturation does not occur concurrently between the sexes. Males begin to mature in summer and achieve advanced stages by late fall, whereas females show little evidence of maturation during the fishing season. A commonly used male maturity index has four stages: 1) Immature - all male ducts transparent; 2) Maturing I - thin white mid-lateral streak in spermatophoric organ; 3) Maturing II - vas deferens thick and creamy white; 4) Mature - spermatophores in spermatophoric sac (Mercer, 1973b). In routine use 1) and 2) have been combined (Amaratunga and Durward, 1979). There is a need for a better definition of 'mature' because observations of mating behaviour (see below) make it clear that males are not functionally mature until they have produced a thousand or more spermatophores (O'Dor et al., 1980b). However, spermatophore counts *per se* are not useful since they change with mating. Spermatophore length which tends to increase with squid length (Squires, 1957) and the proportion of arm length hectocotylized (Haimovici et al., 1998; Schuldt, 1979) have been examined (Coelho et al., 1985), but no satisfactory relationship has yet been found.

Female *I. illecebrosus* emigrate from fishing areas before maturing so that many details of maturation are known only from studies of captives which advance to maturity in 2 to 3 months (Figure 6). Rowe and Mangold (1975) suggested that such rapid maturation in captivity was a result of experimental starvation, and O'Dor et al. (1977) attributed it to lengthened artificial photoperiod regimes.

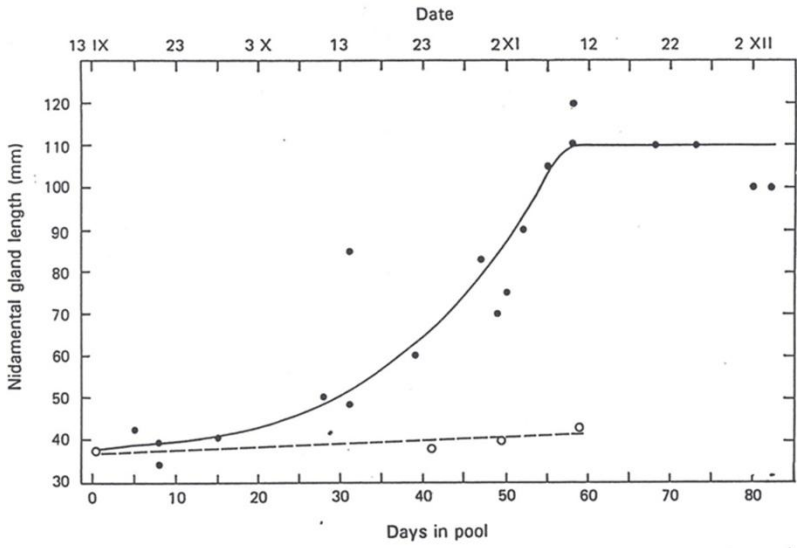

Figure 6. A comparison of maturity, as indicated by nidamental gland length, of wild-caught Nova Scotian inshore female squid (open circles) with captives (closed circles) held over the same period (from O'Dor et al., 1977). Originally presented as evidence for precocious maturation of captives, these data are now interpreted as evidence for population turnover and provide an estimate of natural maturation rates.

This maturation was considered precocious because the maturity of captives was much more advanced than that of the local population in nature at the same time. Since statolith ageing has now shown clearly that the natural population in any location is continually

moving on to be replaced by younger squid (Figure 7, Dawe and Beck, 1997), it now seems likely that the rapid maturation rate of captives is normal.

Although the age structure at a particular locale remains relatively constant throughout the season, due to dynamic migrations, as indicated by the median ages in Figure 7, Figure 8 shows that the animals increase their maturity at a given age (rate of maturation) as the season advances. This is probably because high temperatures accelerate the maturation process (although they do not appear to trigger it, Richard, 1966). Thus increasing maturation rate (and decreasing size and age at maturity) in nature probably reflects the exposure of each successive wave of young squid to progressively higher temperatures as the season advances rather than the progression of a local population. A similar effect of temperature on feeding and growth likely accounts for the increasing seasonal growth seen in Figure 4. This effect of temperature on growth and maturation is reflected in larger body size, and size-at-maturity, of the predominant winter spawning group than of later (spring and summer) spawning groups (Coelho and O'Dor, 1993; Coelho et al., 1994).

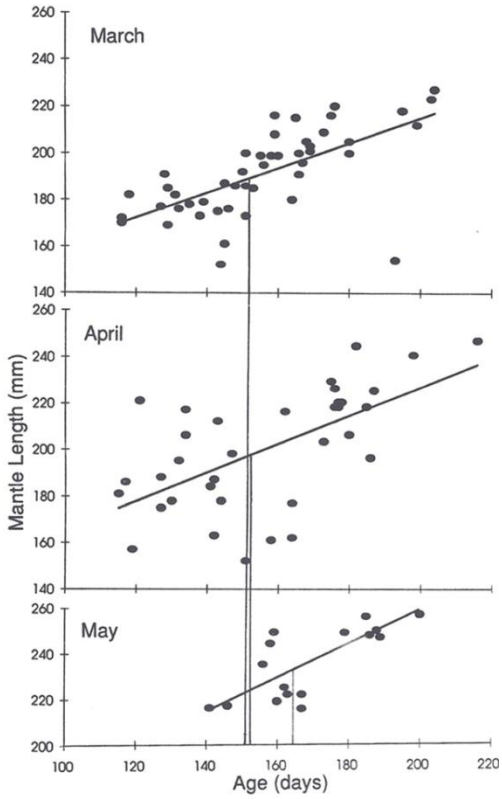

Figure 7. Mantle-length-at-age for male *Illex illecebrosus* in Newfoundland waters in 1990. Linear regressions indicate trends for animals hatched in the three principal months. Although hatching dates advanced by 60 d, median ages at capture (marked by lines dropping to the axis) advanced by only 12 d and the predicted size at this age increased from 190 to 235 mm (adapted from Dawe and Beck, 1997).

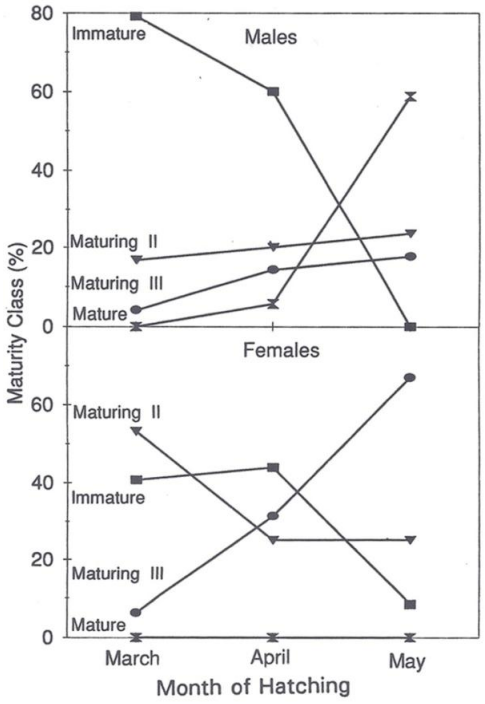

Figure 8. Maturity stages of *Illex illecebrosus* in Newfoundland waters in 1990 for individuals hatched in different months. Late hatching leads to accelerated maturation, since ages at capture typically differ by only a few days (from Dawe and Beck, 1997).

This effect of temperature is also reflected in spatial trends with smaller size and size-at-maturity in southern than in northern areas. Hendrickson et al., (1996) showed that mature (including mated) females caught in a bottom trawl survey in May 2000 on the slope of the southern USA shelf were smaller and younger than immature females typically caught in autumn by the jig fishery at Newfoundland, likely reflecting both seasonal and spatial effects of temperature. The maturation process in females is summarized in Table 1 which relates easily observed morphological features to histologically observed gametogenesis, the ovary to body weight ratio (OW/BW) and the nidamental gland to mantle length ratio (NGL/ML). The NGL/ML ratio is a good index of female maturation for population studies because it is easily determined, continuously variable (and can therefore be easily and meaningfully averaged) and well correlated with other developmental events. Table 1 is based on data from captive *I. illecebrosus*, but gametogenesis and maturation indices are similar for naturally maturing *I. argentinus* (Schuldt, 1979). Available records of mature female *I. illecebrosus* are also consistent with Table 1 (Dawe and Drew, 1981). There is a tendency for segregation of the sexes into separate schools which can produce dramatic shifts in sex ratios as populations turn over (Figure 9). Some inshore populations may be up to 95% female (O'Dor et al., 1980b). Males may predominate (ca. 60%) offshore early in the season, but their proportion may drop to as little as 26% in November (Amaratunga, 1980a). Both the segregation and the shifting ratios may be accounted for by the cannibalistic tendencies of large females.

Table 1. Characteristics of the maturation stages in female *Illex illecebrosus* (Durward et al., 1980)

Maturity Stage	Range of NGL/ML	Range of NGL (mm)	Range of OW/BW	Range of OW (g)	Follicle			Distinguishing Morphological Feature
					Stage[a]	Size[b] (μg)	Dimension[c] (mm)	
I	m≤0.09	11-25	m≤0.0026	0.14-0.90	1	2.1	0.20 x 0.14	NG thin and transparent
II	0.09<m≤0.125	25-35	0.0026<m≤0.0051	0.68-1.60	2	3.5	0.26 x 0.16	NG transparent to translucent ovary granular
III	0.125<m≤0.20	25-60	0.0051<m≤0.015	1.10-5.42	3	11.5	0.35 x 0.25	NG translucent to opaque
IV	0.20<m≤0.35	55-90	0.015<m≤0.09	6.0-30.0	4	-	-	NG white, oviducts forming
V	0.35<m	110-120	0.09<m	50.0-104.0	5	187	0.90 x 0.63	eggs in oviducts

NGL/ML = nidamental gland to mantle length ratio, OW/BW = ovary to body weight ratio.

[a] As defined by Selman and Arnold (1977).

[b] Calculated using the formula for a prolate sphere, $4/3\ \pi ab^2$ where a and b are the major and minor semi-axes respectively, and a specific gravity of 1.0. These values are lower by up to one-third than previously published values (O'Dor 1983, Durward et al., 1980), as the published values were incorrectly calculated using equations for oblate spheroids. This increases the fecundity estimates given in the text.

[c] Dimensions refer to major and minor axes; measurements of follicles fixed in Bouin's solution.

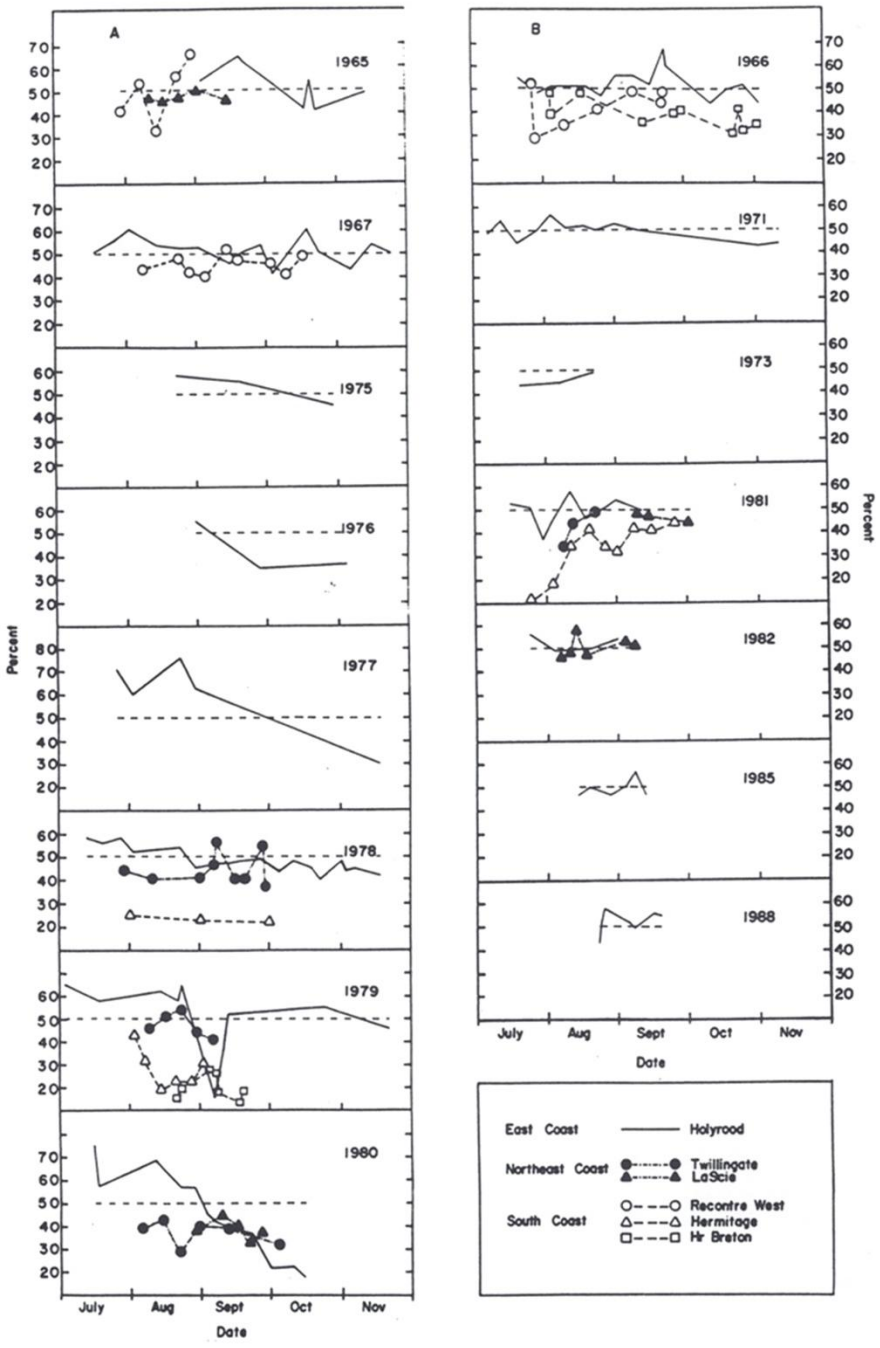

Figure 9. The percentage of male *Illex illecebrosus* varies dramatically with location, season and year. Schools segregate by size and sex, probably because of the prevalence of cannibalism. (O'Dor and Dawe, 1998).

As noted above, males begin to invest energy in gametes earlier and are outgrown by females of the same age. Either cannibalism or early emigration of mature males to avoid it could produce the changes in sex ratios.

Egg numbers are the most commonly used estimator of fecundity, but this is valid only if the fertilization rate is high. Both the changing sex ratio and laboratory records of low fertilization rates suggest that males are potentially limiting in this species. Final egg size is independent of body size, but egg numbers are higher in larger squid. The oviducts of captive females held without males contained eggs amounting to 23% BW at death with little ovary remaining, equivalent to about 1200 eggs per gram BW. When males are present, mating and spawning often occur before all of the ovarian eggs are finished. Females usually die shortly after spawning (O'Dor et al., 1980b), suggesting that actual fecundity may be considerably less than the maximum, unless the sexes are segregated in nature. Captives also rarely exhaust their oviducal egg supply, so a reasonable guess at the spawning fecundity of a typical 400 g female may be 200,000 eggs. Low fertilization and hatching rates may decrease it further.

2.4. Mating and Spawning

The sex ratio may be a determinant of spawning success and fecundity because males appear to be the initiators of mating behaviour (O'Dor et al., 1980b). Figure 10 summarizes an experiment in which two schools of squid were held in a 15-m pool for several months. The pattern observed suggests that when a male is 'fully mature' (precisely what this means remains unclear, Coelho et al., 1985) it will mate with several females. With only one exception mated females were vitellogenic (stage IV) and with only two exceptions they had oviducal eggs present (late state IV or stage V). This selectivity may reflect an element of female receptiveness since some females resist. Only one or two brief mating encounters have been observed despite extensive efforts, indicating that courtship in *I. illecebrosus* is likely much less dramatic than that described for loliginids (Arnold, 1962; Drew, 1911; Fields, 1965).

Spermatophores are transferred to the inside of the mantle cavity near the oviducal gland, and attached to the mantle, gills or the gland itself during a copulation in which the male grips the female from below (as in *Loligo*, *e.g*., Figure 1, Plate 1 in Drew 1911) judging from the sucker scars on the dorsal mantle of mated females. Our observations suggest mating takes only a few seconds and does not involve the long rituals common in *Loligo*. The discharge of the sperm is not immediate, however, and intact spermatophores have been taken from captive females up to five days after the death of the last male in a captive school. There are no oral spermathecae in *I. illecebrosus*, and the retention of sperm in the attached spermatophores is the only known means of sperm storage (Hamabe et al., 1974). How long sperm remains viable is unknown. Implantation of the spermatophores is the probable stimulus for spawning which seems to follow within a few days of mating. Two types of spawning have been observed in captivity, both occurring in the afternoon. Two females have been observed spawning on the bottom in a modified 'resting position' (Bradbury and Aldrich, 1969) where the usual cryptic pattern is replaced by a stark pattern of sharply contrasting dark bands (near the lip of the mantle, the fin tip and the arm tips) on a white background. While resting on the bottom both animals made strong, rapid mantle contractions (42 min^{-1} vs. 35 min^{-1} at rest). These contractions did not move the animal suggesting that the funnel was closed or blocked. Mechanical activity presumably mixes ova from the oviducts, gelling agent from the nidamental and oviducal glands and broken spermatophores with water to form the substance of the egg mass.

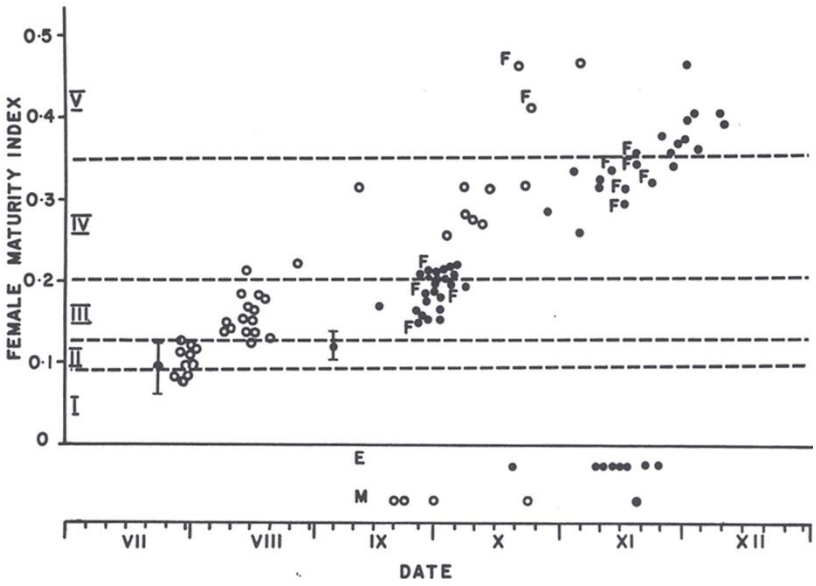

Figure 10. The progress of female sexual maturation and related events in two schools (open vs. closed circles) of *Illex illecebrosus* held in the same tank in 1979. The circles with bars indicate the initial means and standard deviations of the maturity indices (See Table 2, NGL/ML) at the time of capture; other circles are for individuals measured at death. The letter F indicates spermatophores were present in the mantle. Egg masses were noted at the dates indicated (E) and the death dates of males are indicated (M) (from O'Dor et al., 1980b).

This gel was pumped out between the arms to accumulate in front of the female as a large mass on the bottom similar to those described by Hamabe (1963) for *Todarodes pacificus*. In captivity, single *I. illecebrosus* females produce several (six is the maximum count) of these nearly spherical egg masses up to one metre in diameter. Ten to fifty thousand eggs per mass is typical, but the largest may contain up to 100,000 (Durward et al., 1980).

One *I. illecebrosus* has also been filmed spawning in midwater in a large pool (O'Dor and Balch, 1985). This squid apparently preformed a concentrated gel mixture in the mantle while resting on bottom and then inflated it in 1 to 2 min while hovering in midwater using rapid fin movements. Frame-by-frame analysis shows that the egg mass swells rapidly and becomes more tenuous, like a balloon full of gelatin being inflated with hot water. The mass is held in outstretched arms and sinks when released.

2.5. Egg Balloons and Embryonic Development

Although these gel balloons are slightly denser than the seawater incorporated into them, changes in water density of as little as 0.05 kg m^{-3} have lifted balloons off the bottom (O'Dor and Balch, 1985). Because of their large size and lack of internal convection, thermal equilibration in such masses is slow and chemical equilibration even slower. Balloons made of warm surface water would sink very slowly into cooler, denser water at depth, allowing time for the rapid development of these small eggs. Balloons formed in the lower salinity surface water of the Gulf Stream would become buoyant as they sank into its higher salinity core.

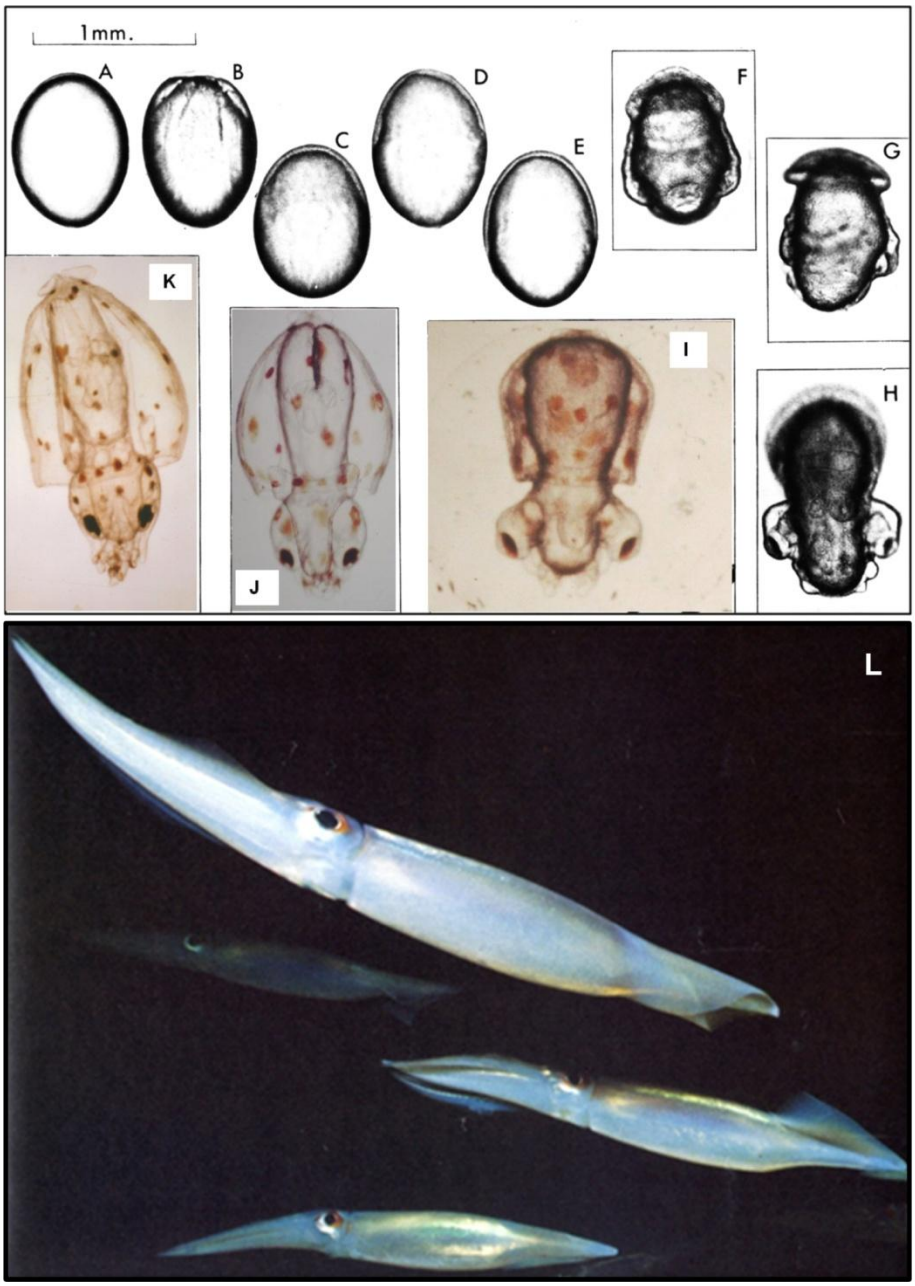

Figure 11. Egg development in *Illex illecebrosus* at 22°C. A = unfertilized egg, B = fifth cleavage, 5 h, C = stage III (Naef 1921-1923), trilaminar blastoderm, 1/3 cellulated, 24 h, D = stage V, 1/2 cellulated, 2 d, E = stage VII, cellulation nearly complete, eye and mouth placodes visibly thickened, 3 d, F = stage IX, mantle development begins, yellow pigmentation of eyes, chorion expanding, 4 d, G = stage XI, arm primordia I, II, III, IV (tentacles) visible, chromatophores forming on mantle, 5 d, H = stage XIII, mantle reaches mid-line and begins to contract, funnel tube complete, 6 d, (I) stage XV, expanded chorion, eye lens, and sucker primordia visible, eye stalks and fins prominent, 7 d, J = stage XVII, eyes move inward as yolk sac elongates and bifurcates, tentacles fused, mantle covers funnel, 8 d, K = stage XX, yolk sac being consumed; ink sac, fins and buccal mass functional, extensible proboscis, 9 d. (from O'Dor et al., 1982). L) Adult *Illex* in Dalhousie's Aquatron Pool Tank where the egg masses were produced. Image from Bob Seple, Fisheries and Oceans Canada.

Even balloons formed on the bottom could be lifted up by storms or shifting currents that cause local increases in water density or even by isopycnal changes in one variable. A gel made of cold, low-salinity water would become less dense as heat was transferred from isopycnal, warm, high-salinity water. Because heat transfer is faster than salt diffusion, the warm, low-salinity water in the gel would become less dense. Warming can also cause supersaturation, forming minute gas bubbles in the gel which would produce floatation. Ammonium ion production from protein breakdown during development could also contribute to increased buoyancy.

The only published record of eggs of the genus *Illex* from nature is of a large floating mass from the Mediterranean near Naples (Naef, 1928) which was later identified as *Illex coindetii* (Boletzky et al., 1973). The rarity of reports of floating squid masses in general (Clarke, 1966) suggest that their buoyancy features may isolate them from both benthic and planktonic predators in midwater pycnoclines or currents. Capturing such egg balloons in midwater is exceedingly difficult, even in captivity with optimal visibility (Balch et al., 1985); the pressure wave in front of a plankton net easily deflects them and they would certainly be destroyed by larger mesh bottom and midwater trawls. Thus they are not only difficult to collect as specimens but also probably hard to eat!

Finished eggs weigh 200 – 250 μg each and are ovoids ranging from 0.9 by 0.6 to 1.0 by 0.8 mm with a distinct micropyle at the larger, animal pole. As an aid to identification of egg masses, Figure 11 provides a brief description of embryonic development. Premature hatching may occur after as little as 10 days at 13°C, but full development requires 16 days at this temperature (O'Dor et al., 1982). Laboratory experiments indicate that the rate of development increases with temperature up to at least 26°C where development requires only 6 days (Balch et al., 1985). The minimum temperature at which normally spawned eggs will develop is about 12°C (O'Dor et al., 1982). At 7°C no development occurs; although eggs fertilized at this temperature will develop if the temperature is raised. Eggs developing at 17°C degenerated when the temperature was lowered to 7°C. The large egg balloons protect the eggs from rapid temperature changes which can cause abnormal development.

2.6. Spawning Area and Season

The observations of midwater spawning dramatically increase the number of potential spawning sites and the complexity of discriminating stocks. Spawning could occur and produce normal development in the Gulf Stream or anywhere in the north Atlantic central waters (O'Dor and Balch, 1985). Even egg masses formed at temperatures too low for immediate egg development could be 'activated' by contact with warmer water. For example, winter temperatures in the shelf waters are too low for development, but where these southward moving coastal waters meet the Gulf Stream south of Cape Hatteras there is intense mixing and production of warmer slope waters where normal development could proceed (Pickart, 1994; Trites, 1983).

No *I. illecebrosus* egg masses have ever been found in nature, so spawning seasons were traditionally estimated from squid size and the timing of advanced male maturity stages, as well as the appearance of paralarvae in the plankton (Dawe and Beck, 1985; Lange, 1981; Lu and Roper, 1979; Hatanaka et al., 1985; Rowell et al., 1985b; Squires, 1957, 1967). All such

data suggest that the main spawning period is in winter. Ageing techniques represent a much more powerful approach, but only a few such studies have provided estimates of hatching date (Dawe and Beck, 1997; Dawe et al., 1985).

There are relatively few records of advanced maturity stages for female *I. illecebrosus* in nature because the fishery is concentrated on immature populations on their feeding grounds. The records of fully mature females from spring and early summer cruises (Mercer and Paulmier, 1974; Lipinski, 1979; Squires, 1967; reviewed by Dawe and Drew, 1981) and of maturing specimens from winter surveys (Amaratunga et al., 1980b), are so few that they seem unlikely to represent the major spawning population. A 1979 bottom trawl survey of the continental slope from Georges Bank to Cape Canaveral found relatively large concentrations of *I. illecebrosus*, including squid up to 34 cm ML and nearly fully mature females in the 300 to 1000 m zone during October and November (Rathjen, 1981). Until recently only two records of mated females from nature existed (spermatophores present in the mantle cavity); one in July from an unreported site between Cape Hatteras and the Scotian shelf (Hamabe et al., 1974), and one in June from Browns Bank (Mercer and Paulmier, 1974). However Hendrickson (2004) reported the capture of 24 mated females during a May 2000 bottom trawl survey. These females were caught on the shelf slope in the mid-Atlantic bight, north of Cape Hatteras, and it was deduced that this represented a spawning area. However that seems unlikely given the absence of any spent females, and the evidence that spawning generally occurs south of Cape Hatteras. It is more likely that these spring-spawning mated females would move further south and offshore to spawn within the Gulf Stream.

If spawning occurs predominately in late winter at an appropriate site, the egg masses might be picked up by or rise into the Gulf Stream as they develop and be delivered back to sites along the shelf edge just in time to meet the next spring bloom. At 7 km h^{-1}, the average speed of the Gulf Stream, 10 days would allow an egg mass to move from almost any point on the coast to any other.

3. Ecology

3.1. Effects of Ocean Climate Variability

Recent studies have shown that this species is highly adapted to physical and biotic ecosystem variability. (Dawe et al., 2000, 2007). Variation in population abundance is closely related to variability in multiple interacting ocean climate processes. Dawe et al. (2000) showed that squid abundance is positively related to a favourable oceanographic regime associated with a negative North Atlantic Oscillation (NAO) index (weak winter northwesterly winds), high water temperatures off Newfoundland and a southward shift in the position of Gulf Stream and the boundary between the shelf waters and the offshore slope waters. In addition, decreased meandering of the Gulf Stream appears to promote increased abundance, probably through enhanced downstream transport of squid. Such ocean climate relationships with squid indices are believed to reflect effects of broad-scale winter atmospheric circulation patterns on Gulf Stream dynamics, which largely regulate year-class strength of the dominant winter-spawning group early in life. This is highly adaptive in that environmental conditions which promote strong year-classes also favour population

expansion through expedient advection of young stages and a suitable oceanographic regime in the northern-most area. Individuals of the broadly distributed winter-spawning group are strongly selected for large body size because near maximum growth and delayed maturation may be necessary to survive the lengthy spawning migration and complete the life cycle. In direct support of this strategy, it appears that squid body size and physical condition (Dawe, 1988) at Newfoundland are directly positively related to recruitment magnitude, indicating early peak spawning or rapid growth rate in warm years of high abundance.

It has been hypothesized (Dawe et al., 2007) that there is a limited carrying capacity for squid and the southern (USA) region approaches its relatively stable limit each year. The carrying capacity near the northeastern limit of distribution, in Canadian waters may be much more variable with higher capacity in warm years. Furthermore, short-finned squid shares its habitat with a sympatric long-finned squid (*Loligo pealei*) in the southern (USA) region. A recent study showed that these species share habitat and a common niche through opposing responses at the population level to environmental variation, such that their populations vary inversely (Dawe et al., 2007). The neritic long-finned squid is associated with higher bottom temperature conditions than is the oceanic short-finned squid on the USA shelf. (Brodziak and Hendrickson, 1999). Strong atmospheric forcing (positive NAO) generally results in high bottom temperatures in the southern area, favourable for long-finned squid, whereas weak atmospheric forcing (negative NAO) results in southward displacement of the Gulf Stream and associated fronts as well as warm bottom temperatures at the northern extreme, conditions favourable for short-finned squid.

3.2. Life History Strategy

All available data suggest that longevity for this species is about one year (Dawe and Beck 1997; Dawe et al., 1985; Squires, 1967), although this is probably somewhat variable (Coelho et al., 1994; Squires, 1967). Maximum age estimated at Newfoundland in one limited study did not exceed 250 days (Dawe and Beck, 1997), whereas *Illex argentinus* of about 360 days of age (Arkhipkin and Laptikhovsky, 1994) have been collected on the Patagonian shelf. This difference is probably related to the remote location of the northern-most fishery area for *I. illecebrosus* (Newfoundland) from its spawning area, relative to that for *I. argentinus* (Coelho and O'Dor, 1993; Coelho et al., 1994; O'Dor, 1998).

Spawning likely occurs throughout the year with some seasonally intense periods. The most intense spawning is apparently in winter (Squires, 1967), with a secondary peak in summer (Coelho et al., 1994; Lange, 1981). These seasonal peaks appear to be adaptively timed so that juveniles may avail of major seasonal productivity peaks in spring and autumn respectively (O'Dor, 1998). It appears that the usually most abundant winter-spawned squid are the most broadly dispersed, supporting fisheries in northern-most areas when climatic conditions are suitable, whereas summer spawners remain in closer proximity to the spawning grounds (Coelho and O'Dor, 1993; Coelho et al., 1994; O'Dor, 1998). Abundance of winter-spawned squid is highly variable in most northern (Canadian) fishery areas, whereas it is more stable (perhaps serving as a 'reserve') in the southern-most (USA) area.

An annual species such as this must be capable of adapting to an annually variable climate. This is apparently accomplished by maximizing the distribution of both reproductive effort over time and individuals over space (Coelho et al., 1994). With limited food supply,

cannibalism provides the final energy reserve for the spawning migration (O'Dor, 1998). It has been suggested that the major winter group may become depleted and it would subsequently 're-evolve' from other seasonal spawning groups. An alternative possibility is that this major group does not become depleted because its southern 'reserve' is relatively stable; it is probably not dispersed to northern fishery areas when the total population is low and the climate is unfavourable (Dawe and Warren, 1993; Dawe et al., 2000, 2007). This major seasonal group may simply shift its time of peak spawning with climatic variation. It is presently unknown whether the March to May peak hatching months of squid sampled in 1990 at Newfoundland (Dawe and Beck, 1997) represented the usual peak hatching time or, alternatively, whether it reflected delayed spawning in a year of low squid abundance and an unfavourable climate.

Certain aspects of population structure remain unclear, particularly the processes which cause the late-season decrease in mean length and seasonal decline in the proportion of males in some years. The seasonal decline in prevalence of males may be due to cannibalism by large squid (especially females) or emigration of mature, and presumably large, males. Cannibalism would promote seasonal increase in mean length whereas emigration of males would promote seasonal decrease in mean length of males only. However, the late seasonal decline in mean length is similar between the sexes (Figure 3), and observed age structure in one year showed no evidence of males emigrating before females (Dawe and Beck, 1997).

Cannibalism and male maturation probably affect size distributions and sex ratio, but seasonal decrease in mean length is more likely related to the dynamic interchange within northern fishery areas, as described above. Seasonal length increase is inhibited by the late-season arrival in low numbers in some years of particularly small (and presumably young) squid (Squires, 1957) which likely resulted from late-spring or summer spawning (Lange, 1981; Lange and Sissenwine, 1983). Such late-spawned squid have a limited feeding season available so they reach feeding areas at a young age. They probably grow quickly (Dawe and Beck, 1997) and may mature at a relatively young age and small size. Their arrival in northern areas at a very young age may be related to seasonal variation in physical transport mechanisms or to northward extension of the spawning area during the warmest season (Trites, 1983).

Although these squid may move inshore in pursuit of food, they spend much of their lives on the outer shelf and continental slope. Rhynchoteuthions and juveniles are abundant in the slope water of the Gulf Stream and in the adjacent upwelling regions at times of maximum production such as the spring plankton bloom. As the initial biomass of the bloom is transferred up through various trophic levels the squid grow at a pace which allows them to feed continuously at the level where biomass is peaking. By the time these fluctuations in the food supply have levelled out, the squid, which can eat prey almost as large as themselves (O'Dor et al., 1980a), can manage to take fish several years old. Some squid move inshore in June-July, probably following fish such as herring, mackerel and capelin. Others remain on the shelf where they feed throughout the water column on prey ranging from surface swarming euphausiids (Brown et al., 1981; Nicol and O'Dor, 1985) to bathyal myctophids (Amaratunga, 1980b). They surface at night, feed intensively before dawn and then descend to depths of several hundred metres during the day (Amaratunga, 1980b; Amaratunga et al., 1979, 1980b). Not every squid makes such vertical migrations each day, they probably only do so when hunger drives them there in search of crustaceans which remain their principal food. The surface is both risky, due to the predatory birds and mammals, and energy

expensive; these squid must do work to overcome their negative buoyancy and also have much higher metabolic rates at the higher surface temperatures (DeMont, 1981). The cryptic resting posture is probably an adaptation to the avoidance of benthic predators on the bottom during the day.

The vertical migrations may also be energetically linked to extensive horizontal migrations. Since squid are negatively buoyant like tuna they can save energy by using climb and glide swimming. A squid at the surface near the edge of the shelf may spend several hours and cover many kilometres by gliding down at a flat angle (O'Dor, 1988). Such behaviour, particularly in the presence of favourable currents, could make long migrations much less costly than would be predicted from the cost of steady swimming (Webber and O'Dor, 1986). The precise length of the spawning migration is unknown, but tag recoveries indicate that they can cover distances of over 2000 km (from Newfoundland to Maryland) averaging nearly 20 km d^{-1} (Dawe et al., 1981a). The direction is generally southward with a clear ontogenetic descent in the autumn as the large squid move into deeper water (Amaratunga, 1981a; Amaratunga et al., 1980a; Dawe, 1999). This scenario would return them to suitable spawning sites at >12°C, as deep Gulf Stream counter-currents provide a push towards suitable areas on the southern shelf (Pickart, 1994; Trites, 1983) and is substantiated by concentrations in deep slope waters (Dawe, 1999; Hendrickson, 2004; Rathjen, 1981).

Limited data indicate a possible nocturnal ascent of juveniles (Dawe et al., 1981b). During the night, 75% of the catch in the first 500 m occurs in the first 100 m while in the day the figure drops to 40 (Amaratunga et al., 1980a). Froerman (1980) has noted, however, that total catchability in the first 500 m during the day is only 25 to 35% of that at night so that differences may reflect net avoidance. The low proportion of juveniles taken with gut contents (13%, Amaratunga, 1980b), is also consistent with a diurnal feeding cycle. Few of these juveniles had identifiable prey items present, but in the larger ones (45–94 mm ML) amphipods, mysids and copepods were common and over half contained fragments of other juvenile squid (*I. illecebrosus*).

3.3. Feeding Ecology and Behaviour

The great variability in size-at-age and growth of individuals may be related to variability in feeding rates (Figure 12). In captivity, feeding hierarchies seem to be established in which some squid take several prey items before others feed at all and a similar situation may exist in nature. Meals of up to 25% body weight (BW) are occasionally taken, but feeding rates in excess of 10% BW per day are not sustained. This rate yields optimum efficiency in conversion of fish weight to squid weight, which may exceed 50% for individuals, giving daily growth rates of over 5% BW. For whole schools, efficiencies are lower by 25% to 35% as shown in Table 2. Feeding rates and growth rates seem to increase with temperature and decrease with weight, but the relationships are not well defined. O'Dor and Wells (1987) examined the interaction of temperature and body size on metabolic rate and feeding rate. The relationships suggest that maintenance food requirements are peaking for large squid at seasonal maximum temperatures of about 15°C in September. In combination with low food availability this could produce declining growth rates.

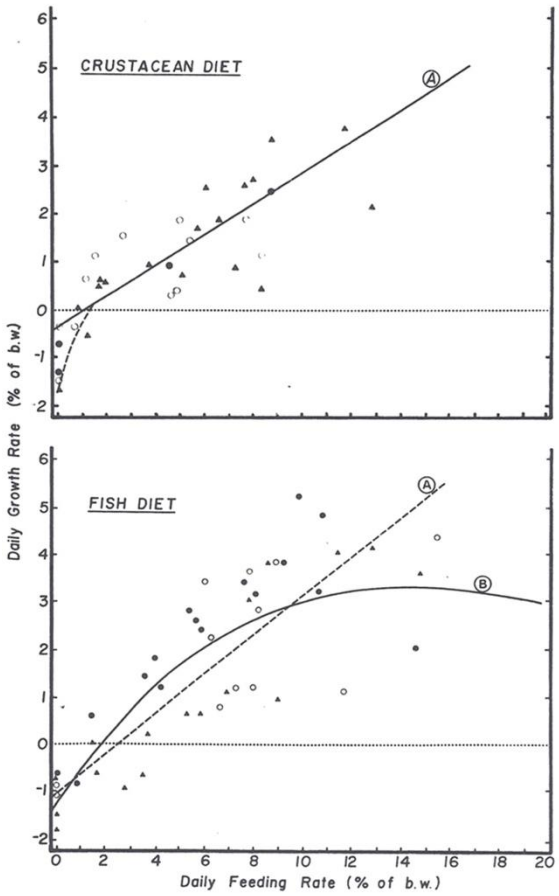

Figure 12. Daily growth (DGR) and feeding rates (DFR) for individual, tagged squid in a school fed ad libitum, twice daily on either crustaceans (*Crangon* sp.) or fish (*Fundulus* sp.). Squid were weighed and diets alternated at 3 d intervals (• = 75–89 g squid, ❍ = 90–99 g, ⍋ = >100 g). Crustacean diet A: fitted regression (DGR = 0.32 D · FR - 0.37, r = 0.79, n = 40). Fish diet A: linear regression for all observations (DGR = 0.39 D · FR - 0.99, r = 0.79, n = 60); B: DGR = 0.86 D · FR exp (-0.069 DFR) - 1.3(r =0.85, n = 60). Note the high individual variation in feeding and growth rates, as well as food preference. From Hirtle et al., 1981.

This squid plays an important role in the ecosystem as a prey species as well as a predator (Dawe and Brodziak, 1998). The predominance of prey types within its diet changes with the season and ontogeny from crustacea to fish and then to squid. Fish consumption is greatest in summer especially on the U.S. shelf and in Newfoundland coastal waters. Fish is not as prevalent a prey type on the Scotian shelf where the diet tends to shift directly from crustaceans to squid.

In the spring 60% to 70% of the squid examined in each fishing area have food in their guts, but by late autumn only 20% to 25% do. Since digestion requires at least 8 to 12 h and more than 24 h for large meals (Boucher-Rodoni, 1975; Wallace et al., 1981) the average time between meals must be more than a day in autumn. This is consistent with the model calculations shown in Figure 5b which suggest that squid eat more in their first four months than in the next five. However, the assumption that field data represent a stable population is no longer accepted (see below), so the case is certainly overstated.

Table 2. Growth parameters for *Illex illecebrosus* fed *ad libitum* on fish (*Fundulus* sp.) at various body weights and temperatures

Date	Mean Wt (g)	Mean Temp.(˚C)	Daily feeding rate (% BW)	Daily growth rate (% BW)	Food conversion rate (%)
28.6.79 - 10.7.79[a]	104	7.0	5.2	1.3	25
1.8.78 - 7.8.78[b]	159	9.7	3.6	1.0	29
11.8.78 - 24.8.78 [b]	183	10.3	3.8	1.4	36
25.8.78 – 7.9.78 [b]	232	15.5	6.7	1.9	28

[a] Averages for marked individuals (Hirtle et al.1981).
[b] Based on feeding and growth of whole schools (O'Dor et al. 1980a).

Fish appears to become a more suitable prey type than crustaceans during summer, probably because of rapid squid growth and the need for progressively larger prey. It appears that physical condition (weight-at-length) of squid at Newfoundland was directly related to the prevalence of fish in the diet (Dawe, 1988).

This suggests that absolute abundance of fish prey or competition for fish prey may have considerable impact upon local squid populations. Similarly, predation by squid could be an important source of mortality in fish populations. Squid at Newfoundland prey first on large, presumably post-spawning, capelin (*Mallotus villosus*) in July and then switch to smaller juvenile fish (predominately gadoids) (Dawe et al., 1997). They resort to cannibalism in autumn as other prey types become depleted, unavailable (Ennis and Collins, 1979; Squires, 1957) or unsuitable (Dawe et al., 1997)

Cannibalism appears to be an important element in the life cycle of this species. In nature it increases as total feeding decreases, and the largest squid are the most cannibalistic (Amaratunga, 1980b; Dawe and Brodziak, 1998).

The same pattern is seen within schools of captive squid where about three days of starvation are needed to induce cannibalism; a single victim may be divided between several cannibals with each getting approximately its maintenance ration (O'Dor et al., 1980a). This would ensure survival of a breeding stock, and would provide an interesting population control since sexual dimorphism makes the smaller males the likely victims. This pattern of cannibalism may also create 'apparent growth' in population studies since selective removal of small animals will increase the average weight even if no individuals grow. A starving population may therefore appear to grow faster than a moderately well-fed one (Arkhipkin and Perez, 1998).

4. Fisheries

4.1. Fishing Areas and Catch Trends

Trends in *I. illecebrosus* fisheries in any of the three fishery areas (Figure 2) have not been reviewed for more than a decade (Dawe, 1981; Dawe and Hendrickson, 1998; Hurley, 1980; Lange and Sissenwine, 1983; O'Dor and Dawe, 1998).

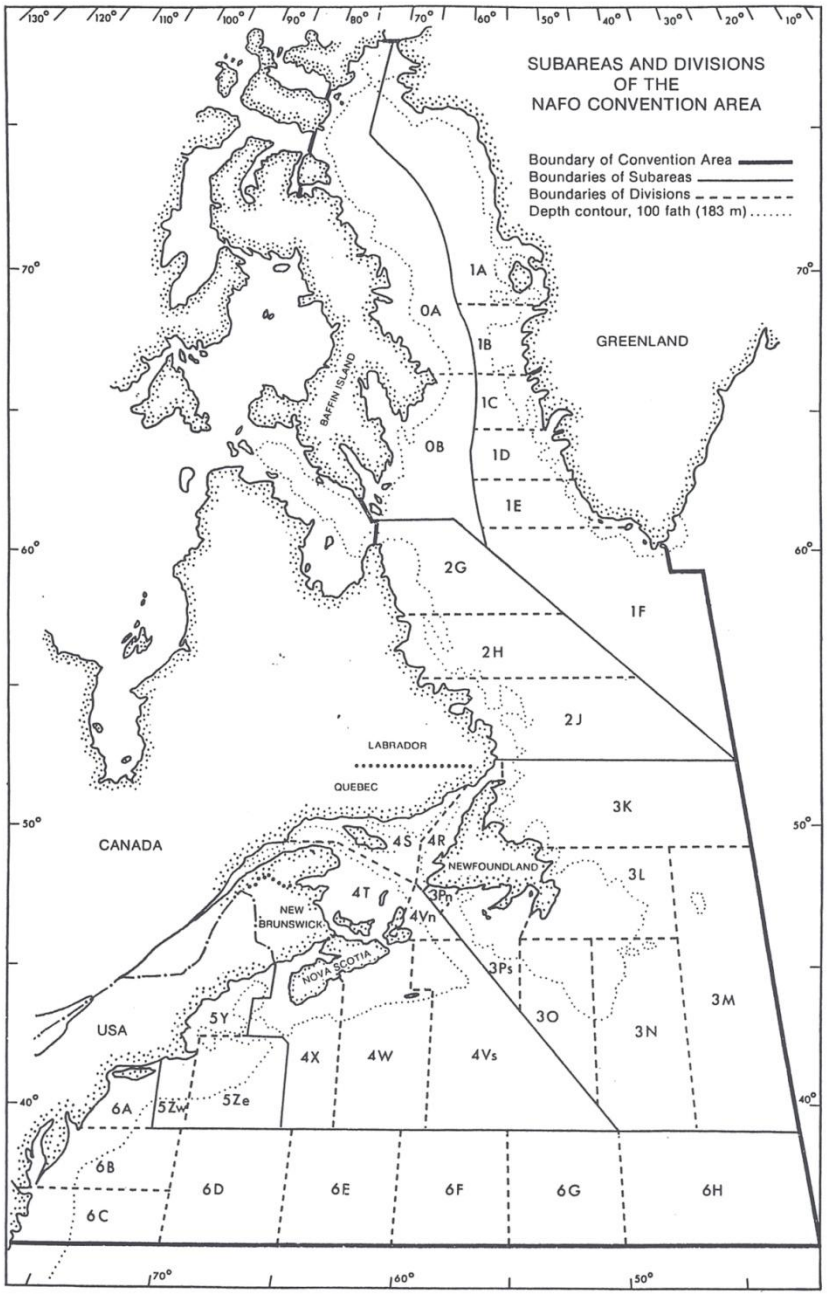

Figure 13. Map of the northwest Atlantic, showing NAFO (and ICNAF) subareas discussed in the text.

The three fishery areas correspond to management areas (Subareas) of the International Commission for the Northwest Atlantic Fisheries (ICNAF) and its successor, the Northwest Atlantic Fisheries Organization (NAFO). These areas (Figure 13) include Newfoundland (Subarea 3), Nova Scotia (Subarea 4), and the northeastern USA (Subarea 5+6).

The oldest directed fishery is the artisanal inshore fishery at Newfoundland (Dawe, 1981; Squires, 1957; Templeman, 1966). This fishery is a passive one, prosecuted very near shore in small open boats. Very little of the annual catch is derived from offshore waters; the

maximum proportion caught offshore was 11% (5,050 t) in 1978. The small offshore Subarea 3 catches are usually taken on the southwestern portion of the Grand Bank and St. Pierre Bank (NAFO Divisions 3PNO, Figure 13). However in some years squid may be distributed to the northern and eastern edges of the Grand Bank as well as on the Flemish Cap (Hurley and Beck, 1979; Vázquez, 1991, 1992). Inshore catches are mostly from the jig fishery, in which multiple barbless jigs are fished in series on monofilament lines. Several lines are usually concurrently fished using hand-operated reels. In certain areas some of the catch is taken using traps. In some years a very small proportion of the catch is derived from Labrador (Subarea 2); these catches are included in the Subarea 3 catch here, for convenience.

Commercial catch data from this fishery date back to 1911 and a subjective ranking of inshore squid abundance at Newfoundland dates back to 1879 (Figure 1). This fishery developed in three stages, related primarily to market developments. Initially, squid were fished mainly for drying (Hurley 1980) and export to China (Figure 1). Annual catches remained below 5,000 t during this period. They increased during the next stage (about 1950–1975), peaking at about 10,000 t in 1964. These larger annual catches were related to the development of a market for squid as bait, for European interests fishing in the northwest Atlantic. A huge market developed in the mid 1970's for squid as food, mainly in Japan, due especially to declining Japanese domestic squid catches. With strong foreign markets for both frozen whole and dried squid, the Newfoundland annual catch increased regularly from 1974 to peak at about 89,000 t in 1979. Annual catches declined regularly since 1979 to only about 5 t in 1983 (Figure 14) due to low abundance of squid. Since 1983 abundance has remained generally low, with peaks of about 4,400 t in 1990, 12,700 t in 1997, and 7,000 t in 2006 (Hendrickson and Showell, 2010). This 27-year period of poor fishery performance at Newfoundland represents the longest period of poor recruitment and low squid abundance in the history of the Newfoundland inshore squid fishery (Figs. 1 and 14). However recent peaks in 1997 and 2006 do not well reflect abundance, as fishing effort was low due to reduced market value and low price in recent years.

In the two more southern fishery areas (Nova Scotia and northeastern USA) the squid fisheries have for more than three decades been predominantly prosecuted offshore using trawls. Trawl fisheries have been mainly by foreign fleets in both areas but with a more prominent domestic component in the northeastern USA fishery than on the Scotian shelf. Squid may be available as early as April in both offshore areas, whereas squid virtually never become available to the inshore Newfoundland fishery before July. Historical catch data date back to 1920 for Nova Scotia (Lange and Sissenwine, 1983; Mercer 1973a). Catch statistics date back to 1887 for the USA total squid fishery (*I. illecebrosus* and *Loligo pealei* combined), and are available by squid species beginning in 1963 (Lange and Sissenwine, 1983; Tibbetts, 1977).

Annual catch at Nova Scotia remained below 800 t during 1920–1968, with the exception of three years (1921, 1925 and 1926) when annual catch levels rose to between 1000 and 2000 t (Lange and Sissenwine, 1983). Catches during that period were mostly incidental from other trap fisheries. Annual catch increased to about 1,300 t in 1970 and 7,300 t in 1971 (Figure 14) due mainly to offshore catches by the USSR and, to a lesser extent, Japan (ICNAF 1978). Further expansion occurred during 1975 and 1976 due to increased recruitment of squid on the Scotian shelf and a great increase in participation by foreign fleets. Foreign fleets participating in this fishery increased from three in 1974 to ten in 1976 (ICNAF 1978).

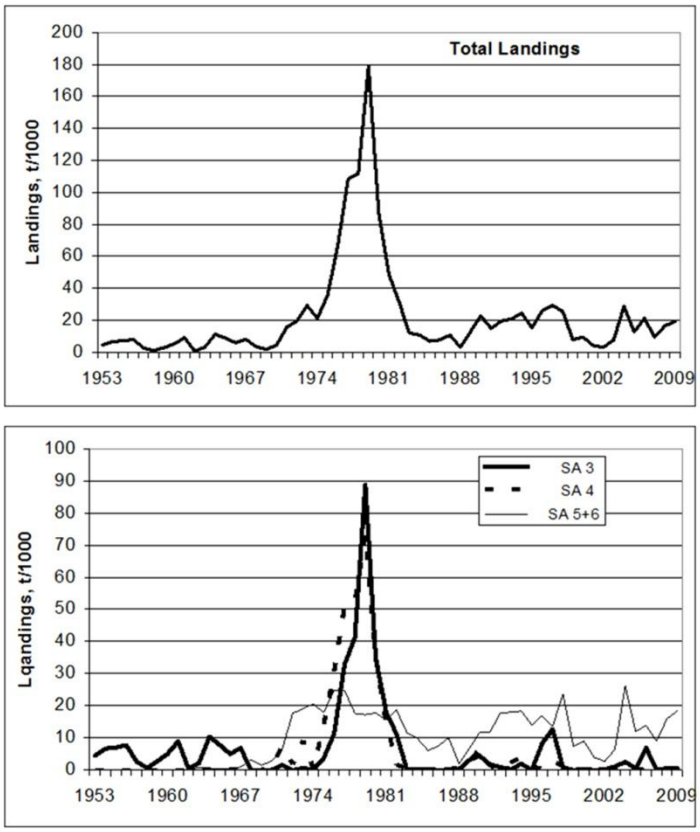

Figure 14. Recent catch statistics for *Illex illecebrosus* in total (above) and by NAFO region (below) showing the relative stability of the fishery in the southern region.

The Subarea 4 catch increased from about 400 t in 1974 to 14,000 t in 1975 and continued to increase regularly to about 73,000 t in 1979 (Figure 14). It subsequently declined regularly to about 400 t in 1983 and has remained generally low since, with a peak of about 6,500 t in 1990 and 4,000 t in 1994 (Hendrickson and Showell, 2010). Much of the Scotian shelf squid catch is taken as by-catch in the small-meshed bottom trawl fishery directed for silver hake (Waldron, 1978). Midwater trawls, also used in the directed squid fishery, catch mostly squid, the small by-catch consisting mainly of silver hake. In 1979 about 6,000 t was taken offshore in Subarea 4 by the Japanese jigging fleet (NAFO, 1980).

The northeastern USA squid fishery was also initially incidental to other (trawl and inshore trap) fisheries (Lange and Sissenwine, 1983). During 1887–1962 peak catch for *I. illecebrosus* and *L. pealei* combined was about 3,600 t in 1928. Foreign fishing began with the USSR first participating in 1964. However, during 1963-1967 the annual catch of *I. illecebrosus* remained below 1,000 t. Annual *I. illecebrosus* catch subsequently increased, though not regularly (Figure 14), due to increasing participation by foreign fleets. It increased from about 6,600 t in 1971, with five foreign fleets participating, to peak at about 25,000 t in 1976, with 11 foreign fleets participating. During that period of fishery expansion the maximum domestic catch was about 1,600 t in 1976. Annual catches generally declined to 10,000 t in 1984 and to a minimum of 2,000 t in 1988 before increasing regularly to about

18,000 t in each of 1992 and 1993. Since 1981 the USA domestic fishery has expanded and there has been no foreign participation in this fishery since 1986.

In Newfoundland the annual catch is generally taken throughout July to November, with peak catches usually occurring in September or October (Beck et al., 1994; Mercer, 1973a). Most of the catch is taken along the northeast coast of Newfoundland (NAFO Divisions 3L and 3K, Figure 13), with greatest catches usually occurring in Division 3L. In years of very low inshore squid abundance, however, local concentrations of squid may occur almost anywhere around Newfoundland.

The Subarea 4 catch is mostly taken along the edge and slope of the Nova Scotian shelf (NAFO Divisions 4VWX, Figure 13). The fishery may extend April through November. Peak catches occur earlier than at Newfoundland, with greatest offshore catches having been taken between late July and early September during 1977–79 (Amaratunga, 1981a, b). However the Subarea 4 inshore catch peaks much later. For example, in 1977 when total offshore catches and Canadian catch rate peaked in late July, the small inshore fishery peaked in September, only one month earlier than the peak catch at Newfoundland (Amaratunga et al., 1978).

Most of the short-finned squid catch in Subarea 5+6 has traditionally been taken offshore in a mixed trawl fishery that also catches *L. pealei*. Although both species are fished from the Gulf of Maine to Cape Hatteras, *L. pealei* generally has a more southerly distribution than *I. illecebrosus* (Brodziak and Hendrickson, 1999; Lange and Sissenwine, 1983). In recent years however, most of the short-finned squid catch in Subarea 5+6 has been taken from southern areas of the mid-Atlantic bight (NEFSC 1994). The *L. pealei* and short-finned squid fisheries are somewhat separated by season, with catches of *L. pealei* occurring in all months but peaking during winter in recent years. Catches of *I. illecebrosus* generally occur in all months as well, but the vast majority of the catch is taken offshore during June-September (NEFSC, 1994). Inshore catches of *L. pealei* generally peak during May-June, whereas inshore catches of *I. illecebrosus* peak during September–October (Lange and Sissenwine, 1980).

Although annual catches are strongly affected by variable fishing effort, it is believed that, for the Scotian shelf and Newfoundland, catches generally reflect annual recruitment since about 1972 (with some exceptions). Obviously, trends in catch (and recruitment) are highly variable but in synchrony at Newfoundland and on the Scotian shelf whereas the trend is for greater stability at a moderate level on the northeastern USA shelf. Relative stability in recruitment to the southern-most fishery area may be related to a relatively mild ocean climate, close proximity to the spawning ground, and recruitment from squid spawned in all seasons (Coelho and O'Dor, 1993; O'Dor and Coelho, 1993; O'Dor, 1998). In contrast, the fishery in Canadian waters depends almost exclusively on recruitment of squid spawned during winter (or in some years winter-early spring) (Coelho et al. 1994). Recruitment, especially at the most northern area (Newfoundland) is related to ocean climate (Dawe and Warren, 1993; Dawe et al., 2000, 2007). Especially evident is that uncommon prolonged periods of poor squid recruitment (1968–1974 and 1982–1993, Figure 14) are associated with unusually cold periods of ocean climate (Beck et al., 1994). One working hypothesis is that squid recruitment is limited to a moderate level on the northeastern USA shelf due to low carrying capacity (Dawe et al., 2000) that may be related to intense competition with other predators and that population increases are achieved by expansion to more northern areas when climatic conditions are favourable. Furthermore, squid abundance may co-vary with that of its most important predators, competitors and prey in an adaptive manner such that the

population increases and expands when niche space becomes available (Dawe et al., 2007; O'Dor, 1998).

4.2. Resource Management

A detailed account of the development of management regulations for each of the three fishery areas has been provided by Lange and Sissenwine (1983), O'Dor and Dawe (1998) and Dawe and Hendrickson (1998) and will be summarized and updated here. All northwest Atlantic squid resources were initially managed through ICNAF. Pre-emptive quotas, first established due to increases in catches by foreign fleets, were set at 71,000 t in 1974 (and again in 1975), for both commercially exploited squid species combined for Subareas 5+6. A separate TAC (total allowable catch) was established for short-finned squid, of 30,000 t for 1976, which was increased to 35,000 t in 1977 (Lange and Sissenwine, 1980). The Subarea 3+4 TAC was first set in 1975, at 25,000 t (ICNAF, 1975).

In 1977, both the USA and Canada extended their jurisdiction to assume responsibility for fishery resources within 200 mi of their coastlines. Since that time the USA has managed its squid resources independently. However, Canada has continued to manage its short-finned squid resource through ICNAF and NAFO.

Under the USA management system, an allowable biological catch (ABC) for short-finned squid is established annually for SA 5+6 by the Mid-Atlantic Fishery Management Council (MAFMC) (Dawe and Hendrickson, 1998). During 1978-1995, the SA 5+6 ABC was 30,000 t. It was reduced from 21,000 t in 1996 to 19,000 t in 1997 and 1998, based on the most recent stock assessment (Hendrickson et al., 1996), which concluded that the MSY was approximately 24,000 t during 1982-93, rather than 30,000 t as had been previously estimated. The TAC has since remained at 24,000 t (NAFO 2011). Commercial catch is monitored via a mandatory dealer reporting system whereby weekly purchase quantities are reported to NMFS. Under this system, the directed fishery is closed when 95% of the ABC is landed. The ABC has never been exceeded. A moratorium on the number of vessels for which short-finned squid fishing permits could be obtained went into effect in June of 1997. Since then there have been approximately 50 vessels in the directed fishery and captains are required to submit logbook reports of their fishing activities.

A minimum mesh size of 60 mm was also established for bottom trawls fishing for squid (ICNAF 1978). Information on resource status in Subarea 5+6 is based largely on indices of the abundance of pre-recruit and recruited squid from spring and autumn bottom trawl surveys. Recognizing that short-finned squid resources in USA and Canadian waters likely comprise a single population, joint management of this species across all areas is advisable. Given the annual life cycle of this species, the basis for an annual Subarea 5+6 TAC of 24,000 t should be reviewed. There may be considerable potential for recruitment overfishing in fisheries for annual species. This may be particularly true for the USA fishery area because that area may serve as a stable 'reserve' for short-finned squid in years of low total population abundance.

The TAC for Canadian waters (Subarea 3+4) was maintained at 25,000 t throughout 1975–77 but in addition, countries without specific allocations were permitted to take 3,000 t each (ICNAF, 1978). The TAC was increased from 25,000 t to 100,000 t during 1978 (ICNAF, 1978). In that year the TAC was first partitioned between Subarea 3 (45,000 t) and

Subarea 4 (55,000 t). It was further increased to 120,000 t in 1979. The 1979 TAC was exceeded by about 42,000 t and the TAC was established in 1980 at 150,000 t (NAFO, 1980). That TAC level remained in place until it was reduced to 75,000 t in 1999 and to 34,000 t in 2000. The 2000 level of 34,000 t was determined (Rivard et al., 1998) by calculating the relative fishing mortality (relative F) for the year of peak Subarea 3+4 landings (1979), by dividing the landings by the Subarea 4 July survey biomass index of that year. Assuming the 1979 fishing mortality rate would be appropriate to more recent years of low abundance, this relative F was then applied to the average survey biomass index for the period 1983-1997, to calculate the corresponding mean annual removal level that might be sustained under the recent period of 'low productivity' (Rivard et al., 1998). The 34,000 t TAC has remained in place since 2000 (Hendrickson and Showell, 2010; NAFO, 2011). Information on resource status in Subarea 3+4 is based largely on indices of the biomass from multiple bottom trawl surveys including an autumn survey in SA 5+6 as well as summer (July) and fall surveys in Canadian waters (SA 3+4) (Hendrickson and Showell, 2010). Annual assessments have concluded that the resource has remained in a state of 'low productivity' since 1983 (NAFO, 2011).

In 1977 a minimum codend mesh size was established of 130 mm for all bottom trawls fishing inside the slope area of the Scotian shelf, as defined by a small-mesh gear line (ICNAF, 1978). Outside the small-mesh gear line, short-finned squid may be taken in a directed fishery or as a by-catch in the silver hake fishery which utilizes small-meshed bottom trawls. In that slope area, where most of the Subarea 4 squid and silver hake fishery is directed, there is a minimum codend mesh size regulation for bottom trawls of 60 mm (NAFO, 1984).

In 1978 effort regulations were first introduced in the Subarea 4 foreign trawl fishery, recognizing that high TAC's could result in excessive exploitation in years of poor squid recruitment (ICNAF, 1978). Fishing days were allocated in 1978 based on catch rates achieved in the previous year. Thus, if squid abundance was lower in 1978 than in the previous year, the effort allocation would preclude the TAC being taken and would limit risk of over-exploitation. Effort regulation was discontinued with the virtual absence of directed trawl fisheries for squid following the early 1980's. It was found however that effort is somewhat self-regulating in that when squid recruitment declined to some marginal level (in 1982), foreign fleets did not fully utilize their allocated fishing days for squid, and directed their fishing activity towards other species (NAFO, 1983). There are no specific effort regulations for the Newfoundland inshore fishery. That fishery relies mostly upon passive gear (jigs and traps), and effort expenditure usually decreases with squid availability.

The season for foreign vessels fishing for squid in Canadian waters was established as beginning on June 15 in 1978 (ICNAF, 1978) and on July 1 for 1979 (ICNAF, 1979). Currently, the Subarea 3+4 season for foreign vessels extends from July 1-December 31, whereas the Canadian fishery (both inshore and offshore) is April 1-December 31.

4.3. Conservation Concerns

Trends in relative fishing mortality for SA 3+4 indicated that fishing mortality in Canadian waters was highest during the 1976-81 period of highest removals (Rivard et al., 1998). However, Dawe (1999) showed that when total fishery removals (including those from

USA waters) were considered it appears that overall fishing mortality was relatively low during the 1976-1981 period of peak catch when most of the catch was derived from SA 3+4. Highest fishing mortality occurred in 1973, when 66% of the total catch was derived from SA 5+6 (Dawe and Hendrickson 1998). It was noted that the main peak of fishing mortality in 1973 was soon followed by a regular increase in catches during 1975-1979, which corresponded to a warm oceanographic regime (Dawe et al., 2000). In contrast, a secondary peak in relative fishing mortality during 1982-1983 coincided with the onset of a prolonged period of low biomass and a cold oceanographic regime. While low total biomass from 1983 to the mid-1990s has been related to a cold thermal regime (Dawe et al., 2000, 2007), abundance has generally since remained low, despite the persistence of a warm oceanographic regime in the Canadian Atlantic since the mid-1990's (Colbourne et al., 2009). It is possible that antropogenic effects on climate variability may have resulted in de-coupling of some of the interacting ocean climate processes that regulate abundance (Dawe et al., 2007). However, the possibility that high fishing mortality during a period of low abundance was a contributing factor cannot be dismissed. This further highlights the advisability of managing this fishery resource on a total population basis across all fishery regions.

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