Chapter 5

Illex illecebrosus

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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 the Labrador Sea; 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 reanalyses of that data based on new age estimates. Present efforts, focused on monitoring a slow recovery from the longest series of recruitment failures on record, are 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, as discussed in Chapter 1. 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 (Froerman 1980). Its economic importance as bait for the Grand Banks cod fishery is probably centuries old and, as Fig. 5.1 shows, records of the inshore jig fishery, prosecuted mainly for this purpose, go back to the 1800s (Squires 1957, Mercer 1973a). 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 1970s and early 1980s 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 (Balch *et al.* 1978, O'Dor 1983, Rowell *et al.* 1985a, Aldrich and Arnold 1991), and in recent years efforts have focused on an unusually long period of recruitment failure during the last decade in Canadian waters (O'Dor 1995). The collapse of this fishery and the subsequent rise in that for *I. argentinus* were major stimuli for this volume. This chapter summarizes the existing information and provides a background for some of the new approaches to interpretation of data which are presented in the chapters that follow.

2 Geographic distribution

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 (Fig. 5.2, 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). 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, presumably because eggs fail to develop at temperatures below 12°C. 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

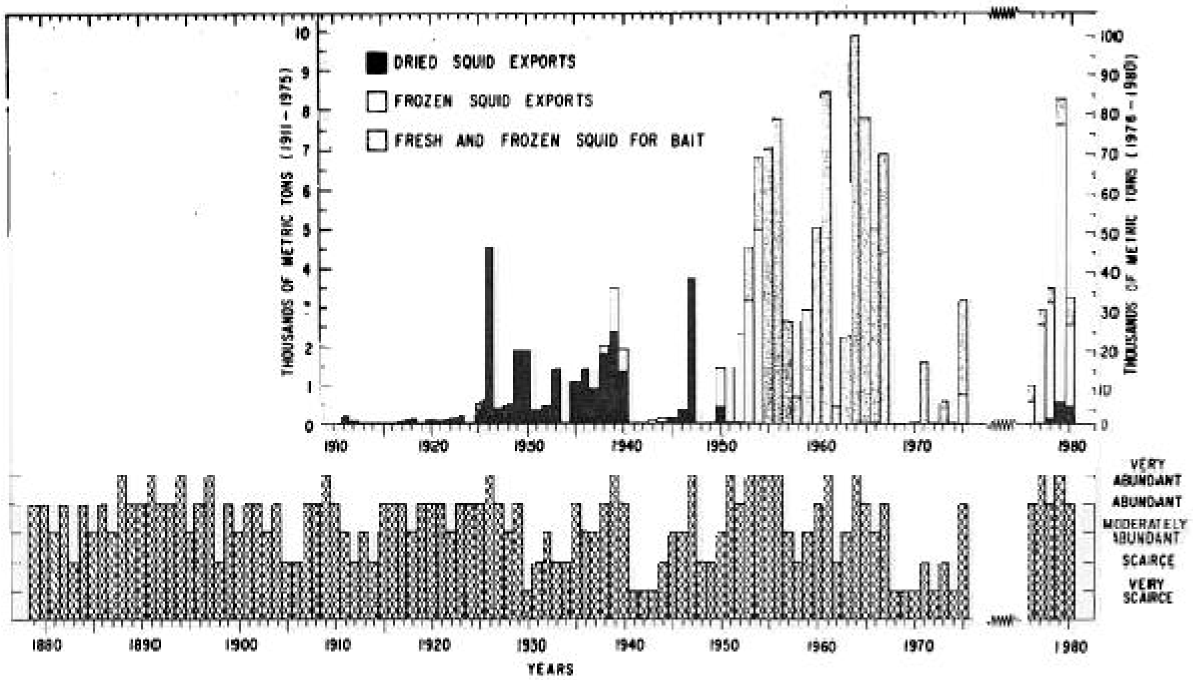


Figure 5.1. Qualitative estimates of inshore abundance estimates of squid (*Illex illecebrosus*) in Newfoundland, 1879–1980, and a breakdown of inshore catch, 1911–1980 (note scale change on the catch ordinate for 1976–1980, from Dawe 1981)

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 (*see Chapter 6*), where larval and juvenile *I. illecebrosus* have been found in greatest abundance (Fedulov and Froerman 1980, Dawe and Beck 1985, Rowell *et al.* 1985b, Hatanaka *et al.* 1985).

This squid ranges from the surface to depths of 1 000 m or more and is taken in waters from 0.5 to 27.3°C (Whitaker 1980) and from 30 to 36.5‰ salinity (Palmer and O'Dor 1978, Amaratunga *et al.* 1980a). Biomass estimates for the Scotian Shelf (based on a standardized, annual survey) have ranged over two orders of magnitude (from 2 000 t in 1970 to 200 000 t in 1976, Koeller 1980).

3 Biological 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 percent 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 (Lange and Johnson 1979, 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 percent 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.

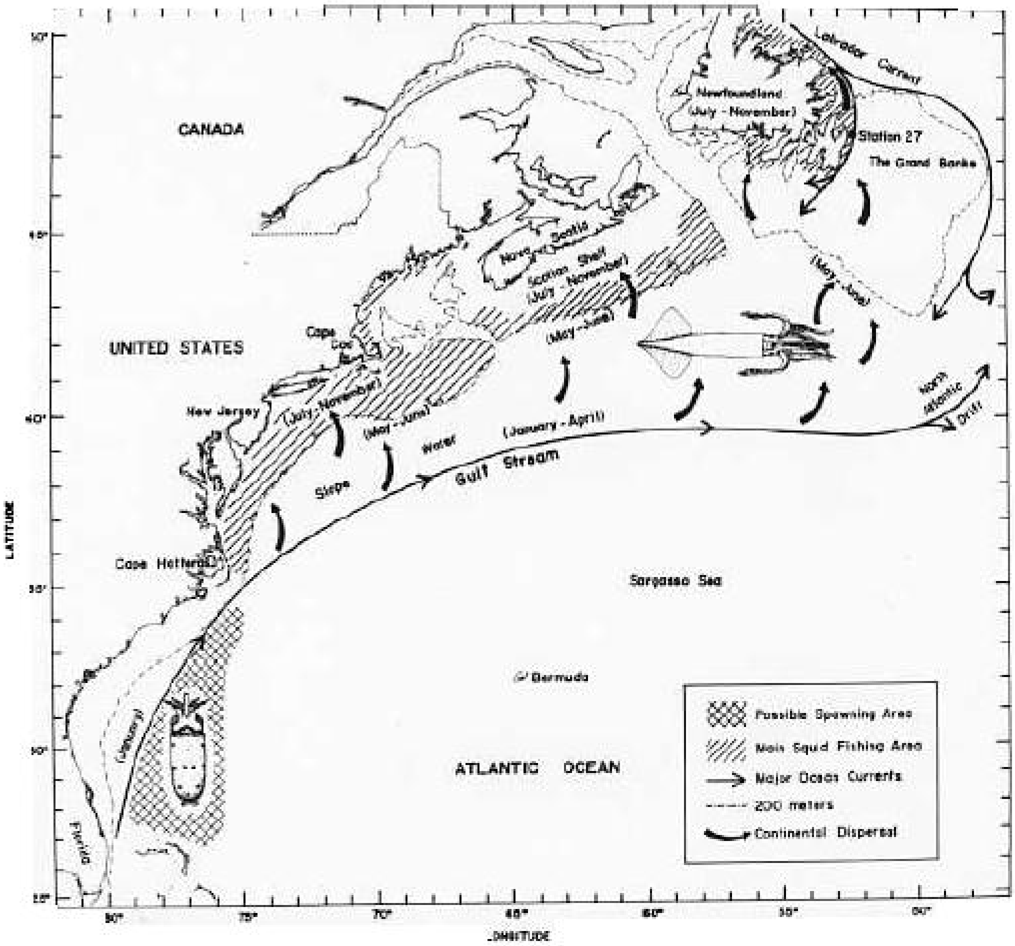


Figure 5.2. Diagrammatic representation of the life cycle of *Illex illecebrosus* in relation to the main northwest Atlantic Ocean currents and sampling sites (from Dawe and Warren 1993)

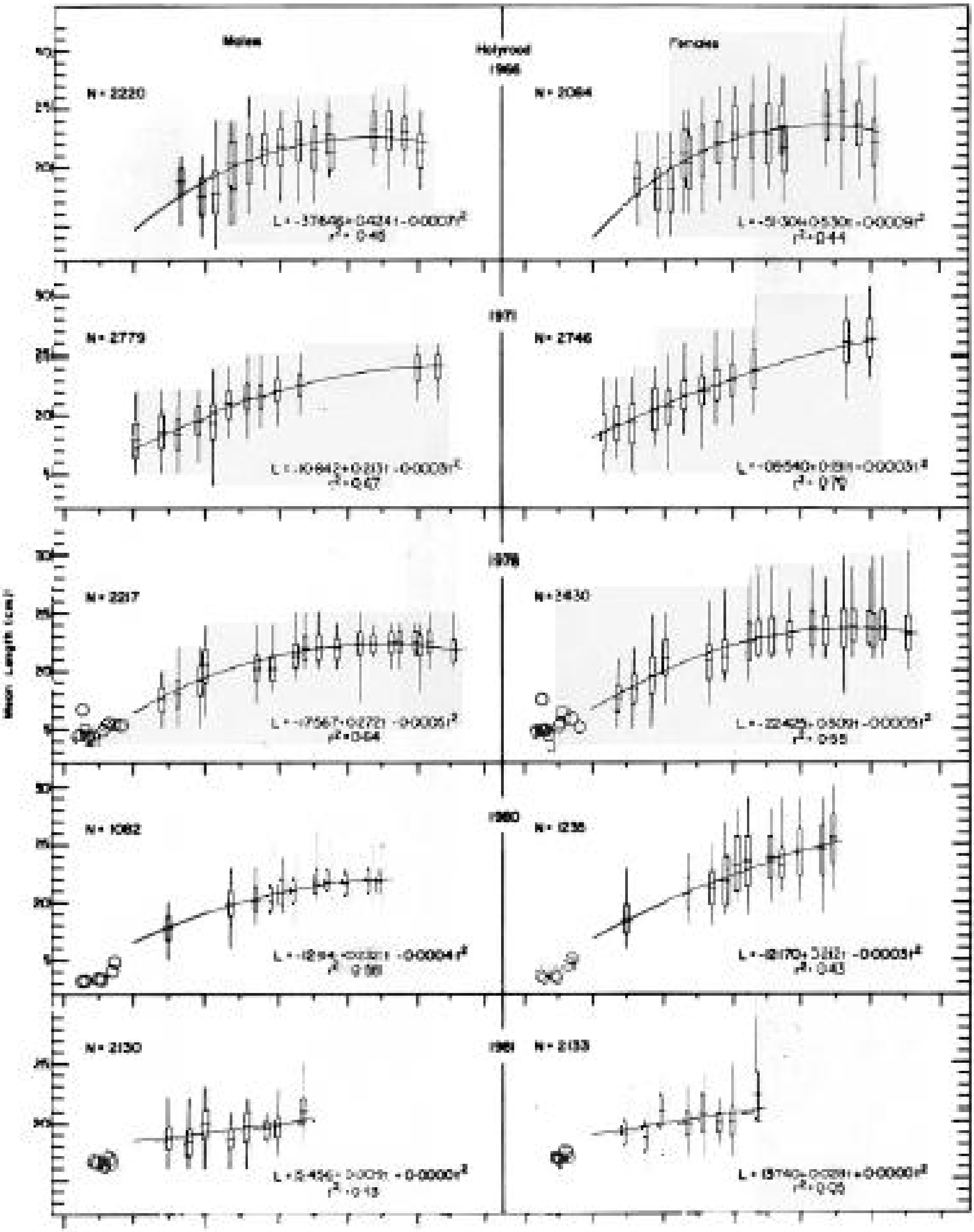


Figure 5.3. Annual variation in seasonal trends of mantle length for both sexes of *Illex illecebrosus* from the commercial jig fishery in Newfoundland waters; box and whiskers show mean, SD and range. Circles indicate bottom trawl data from the Grand Banks slope, not included in quadratic models (Dawe *unpubl. data*)

3.1 Length distribution 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. This assumption for the Scotian Shelf (Amaratunga 1980a) 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).

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 (Fig. 5.3). 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.

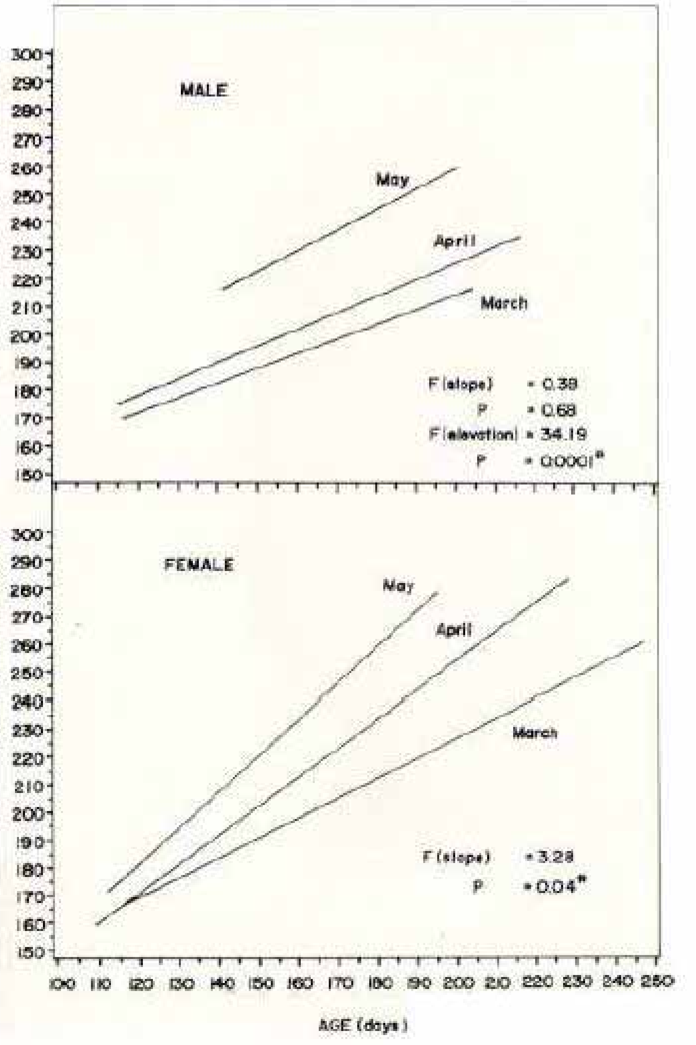


Figure 5.4. Mantle length at age for *Illex illecebrosus* in Newfoundland waters in 1990 separated by sex; linear regressions show size dimorphism and different growth patterns between sexes, with progressive increases in growth rates over the season for individuals hatched in different months (Dawe and Beck 1992).

Table 5.1. Growth parameters for *lllex illecebrosus* fed *ad libitum* on fish (*Fundulus* sp.) at various body weights and temperatures

Date	Mean wt (g)	Mean temp. (^{o}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
01.8.78 – 07.8.78[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 – 07.9.78[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)

More recent studies have been able to utilize data on squid age or growth history determined from examination of statoliths or gladii, respectively (*see Chapter 8*). 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 1992). As Fig. 5.4 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 (Fig. 5.5a, O'Dor 1983). Age-based estimates showed that growth varies greatly among individuals and with time of hatching (Dawe and Beck 1992).

4 Feeding

The great variability in size-at-age and growth of individuals may be related to variability in feeding rates (Fig. 5.6). In captivity, feeding hierarchies seem to be established in which some squid take several prey items before others feed at all; a similar situation may exist in nature. Meals of up to 25 percent body weight (BW) are occasionally taken, but feeding rates in excess of 10 percent BW per day are not sustained. This rate yields optimum efficiency in conversion of fish weight to squid weight, which may exceed 50 percent for individuals, giving daily growth rates of over 5 percent BW. For whole schools, efficiencies are lower by 25 to 35 percent as shown in Table 5.1. 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.

This squid plays an important role in the ecosystem as a prey species as well as a predator (*see Chapter 7*). 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. It 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 percent of the squid examined in each fishing area have food in their guts, but by late autumn only 20 to 25 percent 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 Fig. 5.5b, suggesting that squid eat

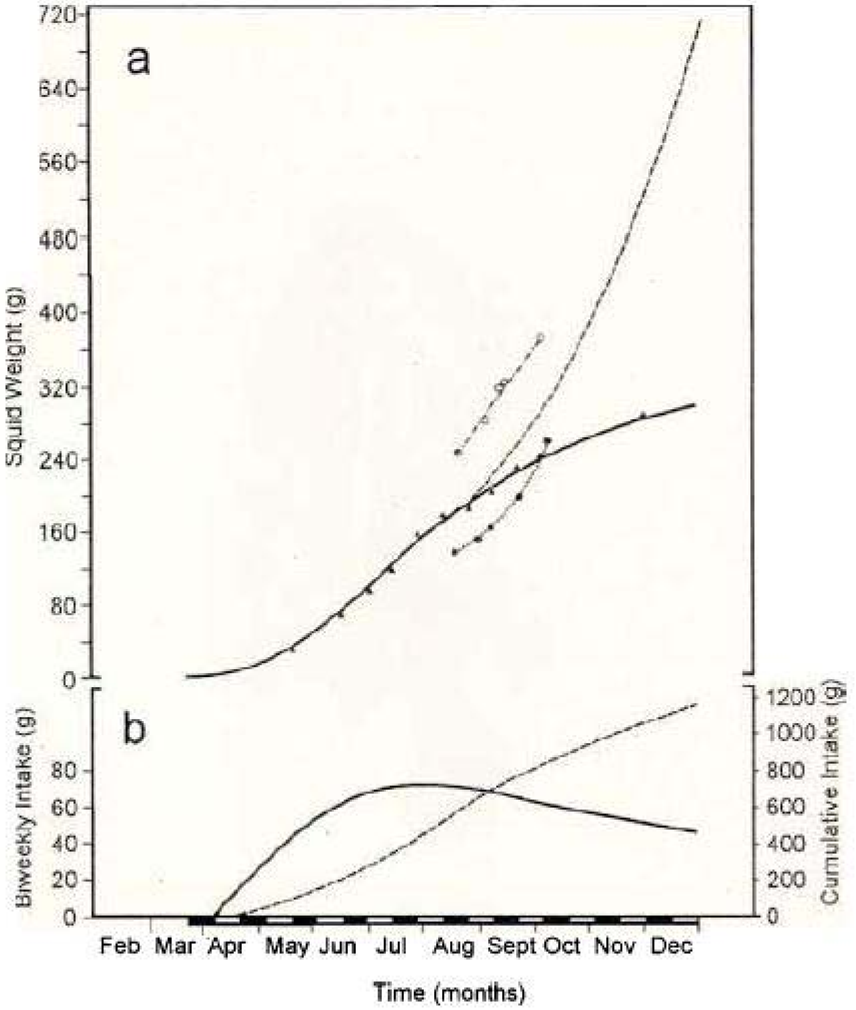


Figure 5.5. (a) Seasonal weight changes in wild and captive *Illex illecebrosus*; ▲ = wild caught squid, 1977; ·= a captive population fed *ad libitum* on fish, 1978; º = a single tagged captive; the dashed line projects the weights of the wild population, if they had continued growth at the rate of 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; - = bi-weekly consumption; - - - - - = 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 with permission NAFO)

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.

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 resort to cannibalism in autumn as other prey types become depleted or unavailable (Squires 1957, Ennis and Collins 1979).

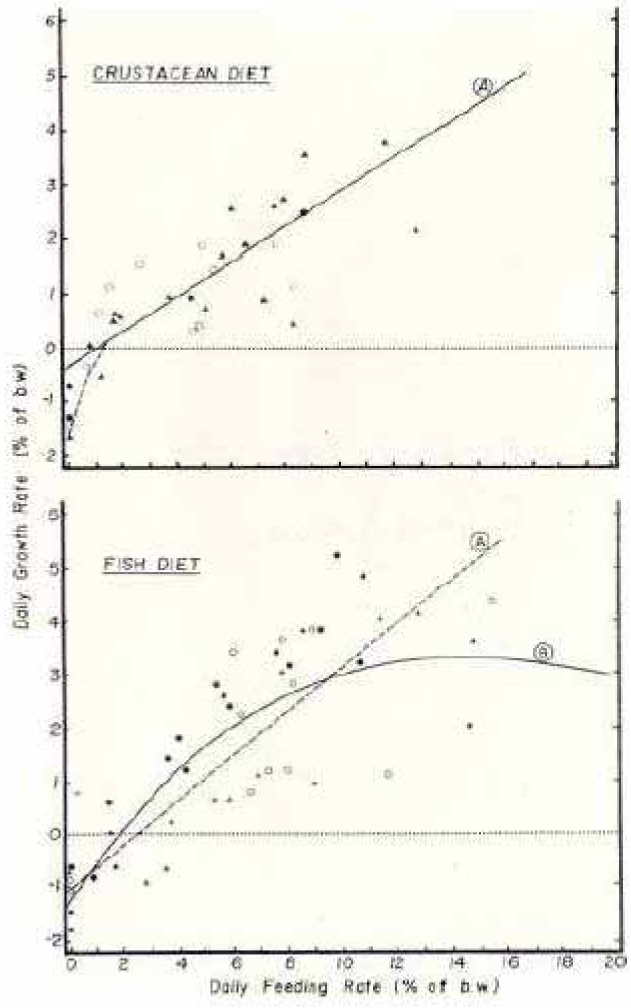


Figure 5.6. Daily growth and feeding rates for individual, tagged squid in a school fed *ad libitum* twice daily on either crustaceans (*Crangon* sp.) or fish (*Fundulus* sp.); squid were weighed and diets alternated at 3 d intervals; • = 75–89 g squid, º = 90–99 g, ▲ = > 100 g. Crustacean diet (A) fitted regression (DGR = 0.32 .DFR –0.37, r = 0.79, n = 40); fish diet A: linear regression for all observations (DGR = 0.39' DFR – 0.99, r = 0.79, n = 60); (B) DGR = 0.86 .DFR 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 with permission *J. Shellfish Res.*)

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, *see Chapter 7*). 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 (*see Chapter 8*).

5 Bathymetric movements and energetics

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 that allows them to feed continuously at the level where biomass is peakine;. 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, 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 *et al.* 1979, 1980b, Amaratunga 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 2 000 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 *et al.* 1980a, Amaratunga 1981a). As deep Gulf Stream countercurrents provide a push towards suitable areas on the southern shelf (Trites 1983, Pickart 1994), this scenario would return them to suitable spawning sites at > 12°C and is substantiated by concentrations in deep slope waters (Rathjen 1981).

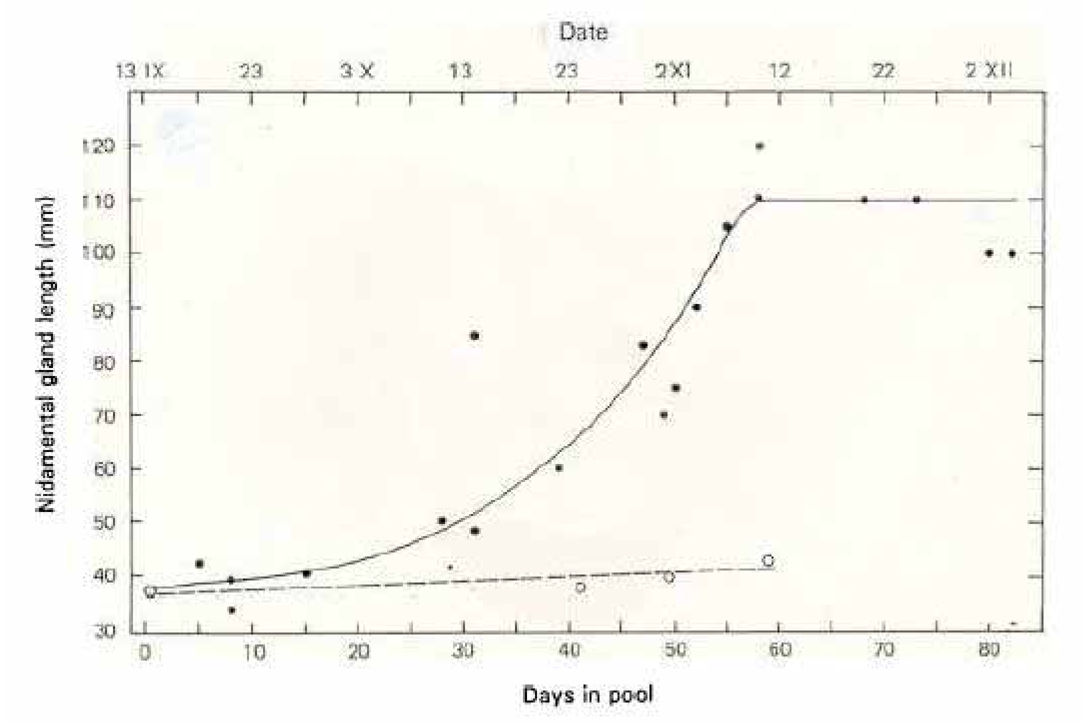


Figure 5.7. A comparison of maturity, as indicated by nidamental gland length, of wild-caught Nova Scotian inshore female squid (open circles) with captives (closed circles) held over the same period (from O'Dor *et al.* 1977 with permission *Biol. Bull.*); originally presented as evidence for precocious maturation of captives, these data are now interpreted as evidence for population turnover and provide an estimate of natural maturation rates.

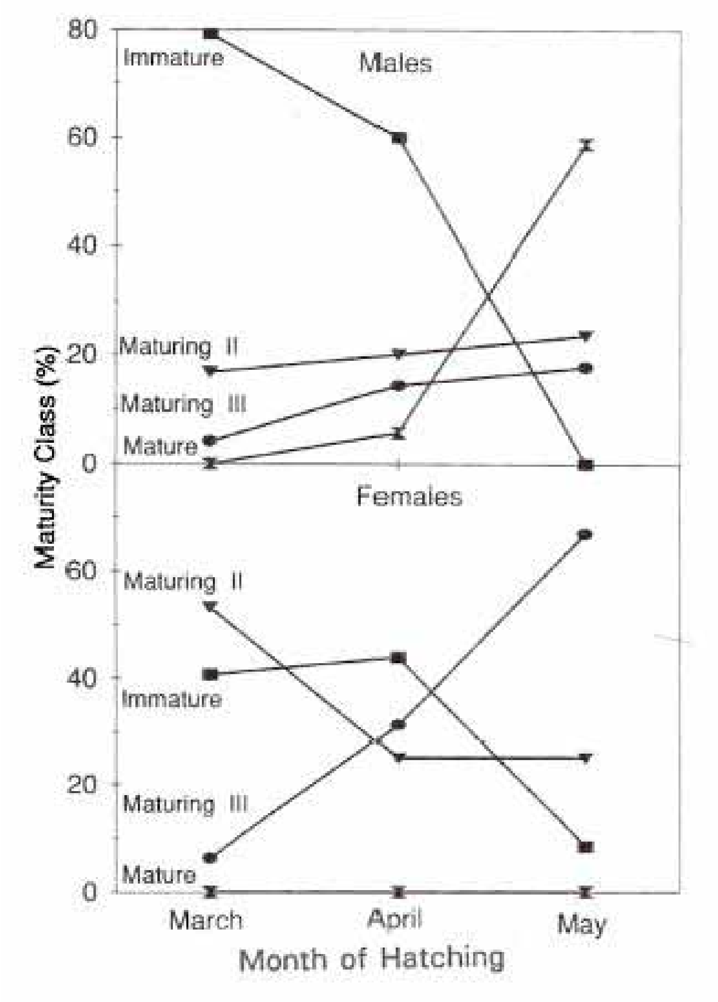


Figure 5.8. Maturity stages of *Illex illecebrosus* in Newfoundland waters in 1990 for individuals hatched in different months; late hatching leads to accelerated maturation, since ages at capture typically differ by only a few days. (from Dawe and Beck 1992)

Limited data indicate a possible nocturnal ascent of juveniles (Dawe *et al*. 1981b). During the night, 75 percent of the catch in the first 500 m occurs in the first 100 m while in the day the figure drops to 40 percent (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 percent of that at night, so that differences may reflect net avoidance. The low proportion of juveniles taken with gut contents (13 percent, 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*).

6 Reproduction

6.1 Maturation, sex ratio 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

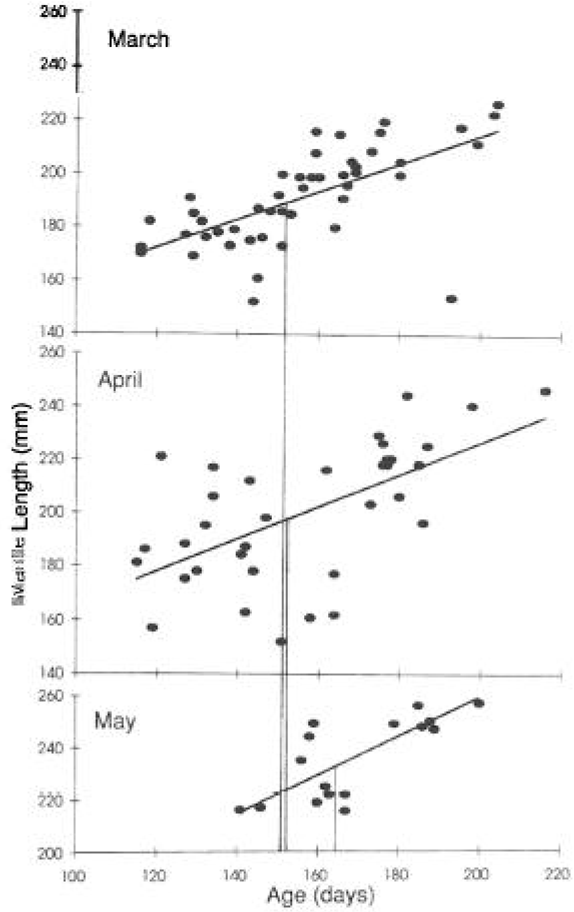


Figure 5.9. Mantle length-at-age for male *lllex illecebrosus* in Newfoundland waters in 1990; linear regressions indicate trends for animals hatched in the three principal months. Although hatching dates advanced by 60 d, median ages at capture (marked by lines dropping to the axis) advanced by only 12 d and the predicted size at this age increased from 190 to 235 mrn. (adapted from Dawe and Beck 1992

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 (Schuldt 1979, *see Chapter 3*), has been examined (Coelho *et al.* 1985), but no satisfactory relationship has yet been found.

Female *I. illecebrosus* emigrate from fishing areas before maturing, thus many details of maturation are known only from studies of captives, which advance to maturity in 2 to 3 months (Fig. 5.7). 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. 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 (Fig. 5.8, Dawe and Beck 1992), it now seems likely that the rapid lIlaturation rate of captives is normal.

Although the age structure at a particular locale remains relatively constant throughout the season, as indicated by the median ages in Fig. 5.4, Fig. 5.8 shows that the animals increase their maturity at a given age 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 maturity in nature probably reflects the exposure of each 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 Fig. 5.9.

The maturation process in females is summarized in Table 5.2, which relates easily observed morphological features to gametogenesis observed histologically, 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 5.2 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 5.2 (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 (Fig. 5.10). Some inshore populations may be up to 95 percent female (O'Dor *et al*. 1980b). Males may predominate (c. 60 percent) offshore early in the season, but their proportion may drop to as little as 26 percent in November (Amaratunga 1980a). Both the segregation and the shifting ratios may be accounted for by the cannibalistic tendencies of large females. 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.

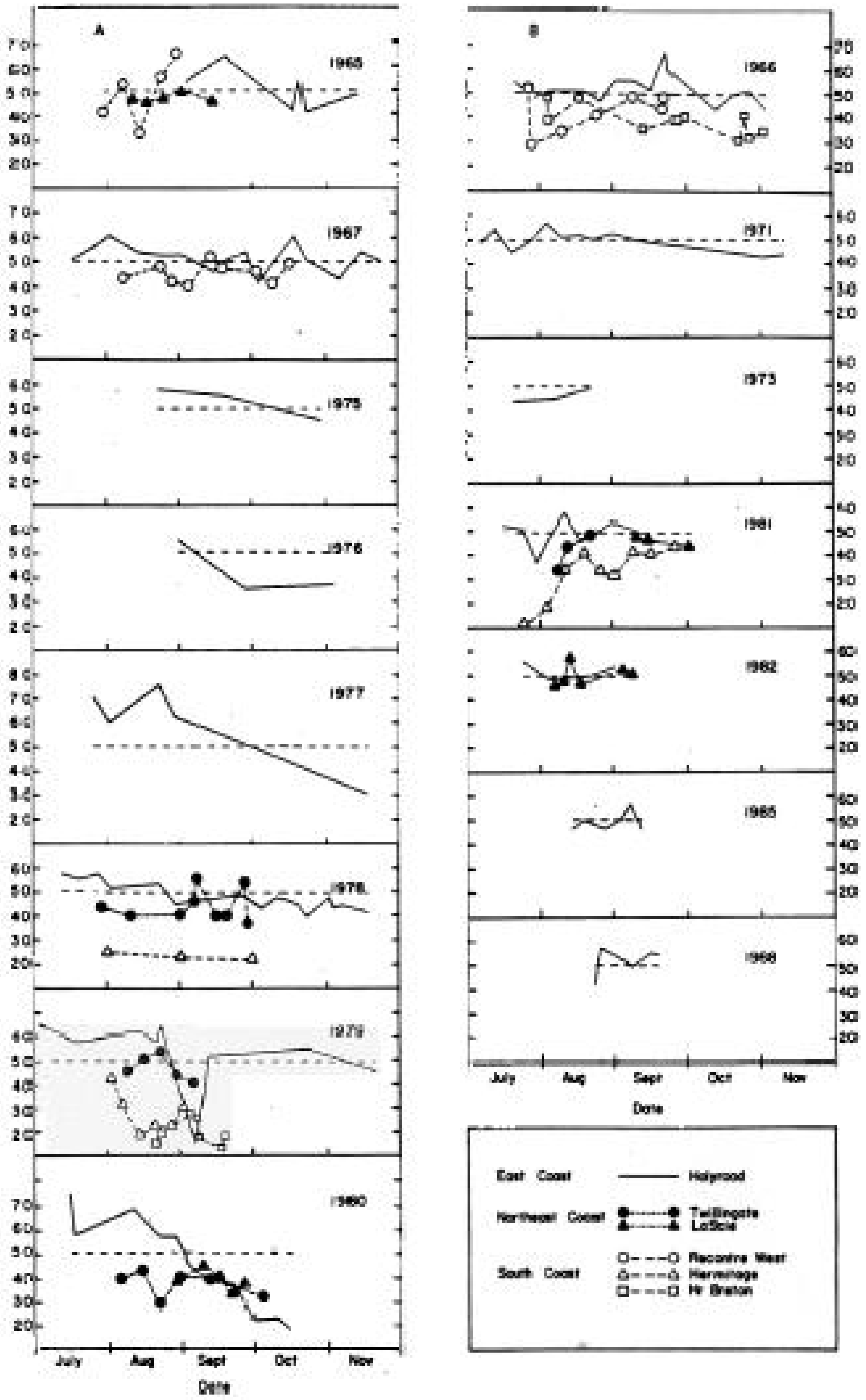
Egg numbers are the most commonly used estimator of fecundity, but this is valid only if the fertilization rate is high. Both the changing sex ratio and laboratory records of low fertilization rates suggest that males are potentially limiting in this species. Final egg size is independent of body size, but egg numbers are higher in larger squid. The oviducts of captive females held without males contained eggs amounting to 23 percent BW at death with little ovary remaining, equivalent to about 1 200 eggs per gram BW. When males are present, mating and spawning often occur before all of the ovarian eggs are matured. Females still 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.

6.2 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 5.11 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 N) and with only two exceptions they had oviducal eggs present (late state N or stage V). This selectivity may reflect an element of female receptivenessince 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 (Drew 1911, Arnold 1962, Fields 1965).

Spermatophores are transferred to the inside of the 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. Fig. 1, Plate 1 in Drew 1911), judging from the sucker scars on the dorsal mangle 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

Figure 5.10 (below). 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. (Dawe *unpubl. data*)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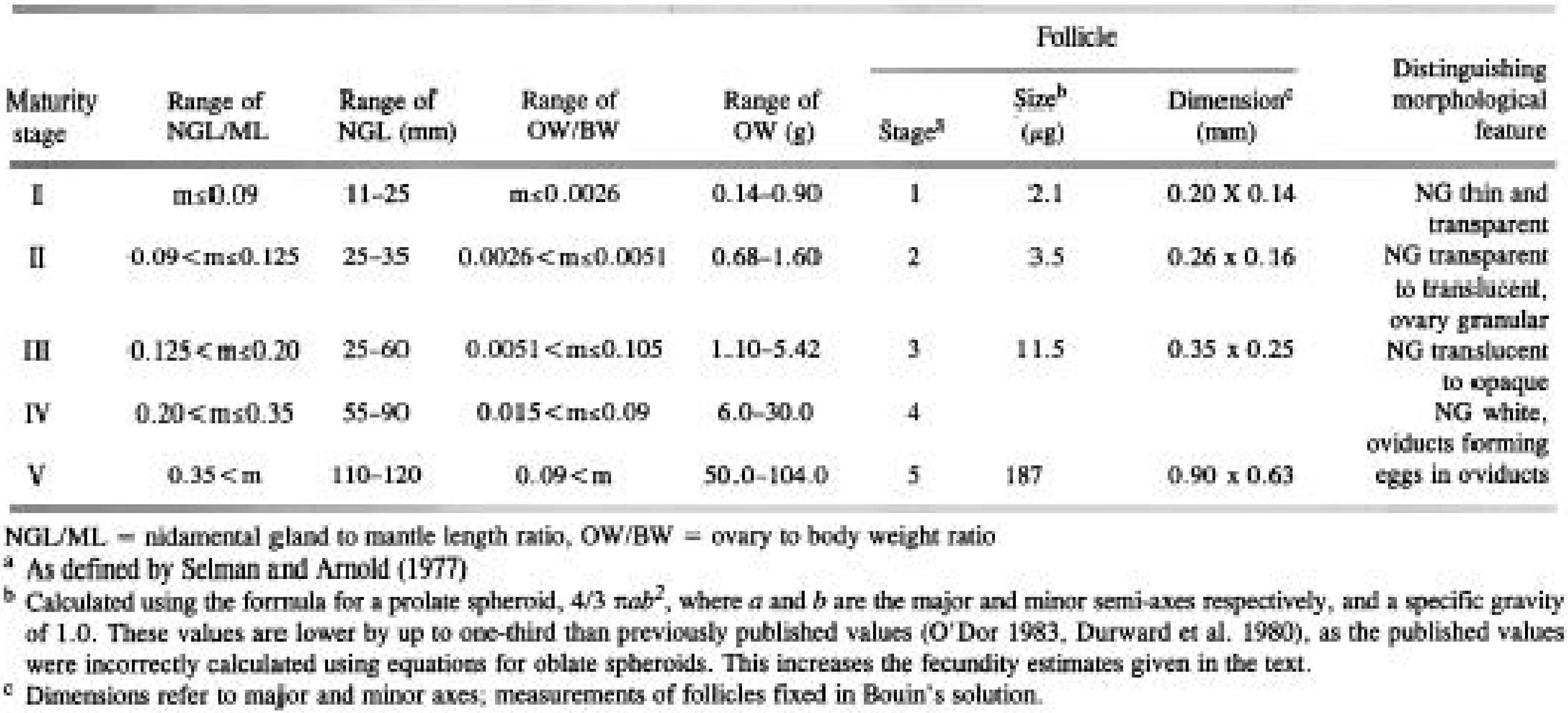
Oct
Nov
Date
East Coast
Holyrood
Northeast Coast
Twillingate
LaScie
South Coast
Recontre West
Hermitage
Hr Breton

Table 5.2. Characteristics of the maturation stages in female *Illex illecebrosus* (modified from Durward *et al*. 1980)



Maturity stage	Range of NGL/ML	Range of NGL (mm)	Range of OW/BW	Range of OW (g)	Follicle: Stage[a]	Follicle: Size[b] (μg)	Follicle: Dimension[c] (mm)	Distinguishing morphological feature
I	$m \le 0.09$	11–25	$m \le 0.0026$	0.14–0.90	1	2.1	0.20 X 0.14	NG thin and transparent
II	$0.09 < m \le 0.125$	25–35	$0.0026 < m \le 0.0051$	0.68–1.60	2	3.5	0.26 x 0.16	NG transparent to translucent, ovary granular
III	$0.125 < m \le 0.20$	25–60	$0.0051 < m \le 0.105$	1.10–5.42	3	11.5	0.35 x 0.25	NG translucent to opaque
IV	$0.20 < m \le 0.35$	55–90	$0.015 < m \le 0.09$	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 spheroid, $4/3\ \pi ab^2$, 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.

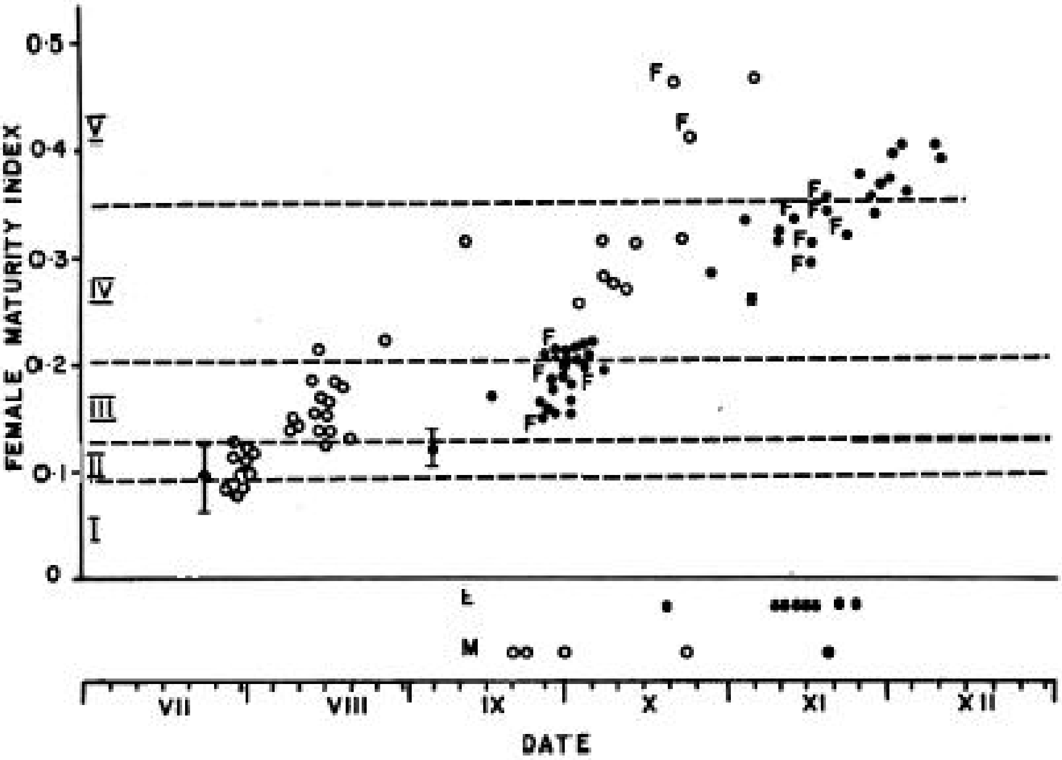


Figure 5.11. The progress of female sexual maturation and related events in two schools (open vs. closed circles) of *Illex illecebrosus* held in the same tank in 1979; the circles with bars indicate the initial means and standard deviations of the maturity indices (See Table 5.2, NGL/ML) at the time of capture; other circles are for individuals' measured at death. The letter P 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 with permission NAFO)

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 fm 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. This gel was pumped out between the arms to accumulate in front of the female as a large mass on bottom similar to those described by Hamabe (1963) for *Todarodes pacificus*. In captivity, single *I. illecebrosus* females produce several (6 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 1–2 min while hovering in midwater using rapid fm 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.

6.3 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. 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 (equal density) changes in both temperature and salinity. 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 Iliex from nature is of a large floating mass from the Mediterranean near Naples (Naef 1928) that was later identified as Iliex coindetii (Boletzky *et al.* 1973). The rarity of reports of floating squid masses in general (Clarke 1966) suggests 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, Fig. 5.12 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.

6.4 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,

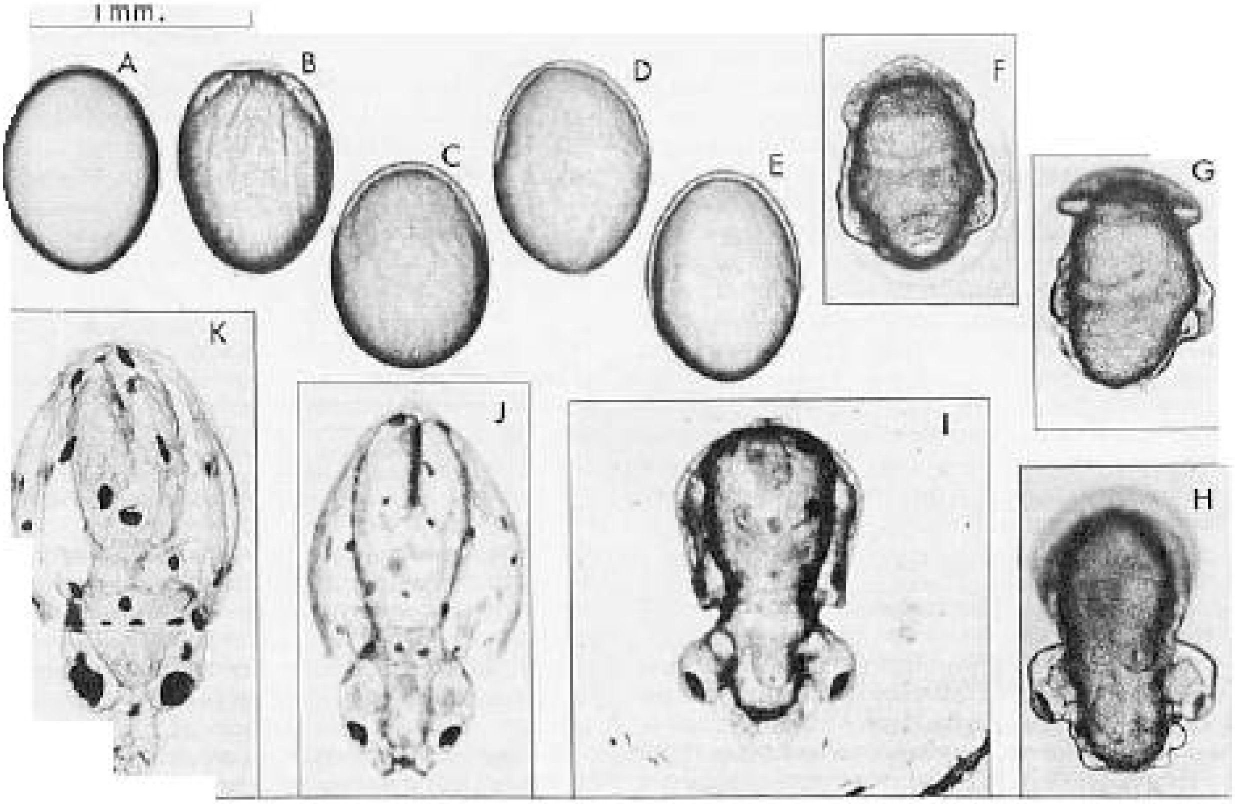


Figure 5.12. Egg development in IIiex iiiecebrosus at 22°C; (A) unfertilized egg; (B) fifth cleavage, 5 h; (C) stage III (Naef 1921–1923), trilaminar blastoderm, 1/3 cellulated, 24 h; (D) stage V, 1/2 cellulated, 2 d; (E) stage VII, cellulation nearly complete, eye and mouth placodes visibly thickened, 3 d; (P) 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 with permission NAFO)

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 (Trites 1983, Pickart 1994).

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 (Squires 1957, 1967, Lange 1981, Lu and Roper 1979, Dawe and Beck 1985, Hatanaka *et al.* 1985, Rowell *et al.* 1985b). 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 *et al.* 1985, Dawe and Beck 1992).

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 (Squires 1967, Mercer and Paulmier 1974, Lipinski 1979, 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 1 000 m zone during October and November (Rathjen 1981). From nature only two records of mated females exist (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).

If spawning occurs 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.

7 Population structure and life-history pattern

All available data suggest that longevity for this species is about one year (Squires 1967, Dawe *et al.* 1985, Dawe and Beck 1992), although this is probably somewhat variable (Squires 1967, Coelho *et al.* 1994). Maximum age estimated at Newfoundland in one limited study did not exceed 250 days (Dawe and Beck 1992), 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 northernmost 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, *see Chapter 11*).

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 (Lange 1981, Coelho *et al.* 1994). These seasonal peaks appear to be adaptively timed so that juveniles may avail of major seasonal productivity peaks in spring and autumn respectively (*see Chapter 11*). 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, *see Chapter 11*). 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 (*see Chapter 11*). 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). 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 1992) 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 lateseason 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 (Fig. 5.3), and observed age structure in one year showed no evidence of males emigrating before females (Dawe and Beck 1992).

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 1992) 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, perhaps more likely, to northward extension of the spawning area during the warmest season (Trites 1983).

8 Fisheries

8.1 Fishing areas and catch trends

Trends in *I. illecebrosus* fisheries in any of the three fishery areas (Fig. 5.2) have not been reviewed for more than a decade (Hurley 1980, Dawe 1981, Lange and Sissenwine 1983). 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 (Fig. 5.13) 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 (Squires 1957, Templeman 1966, Dawe 1981). 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 percent (5050 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, Fig. 5.13). 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 handoperated 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 (Fig. 5.1). This fishery developed in three stages, related primarily to market developments. Initially, squid were fished mainly for drying (Hurley 1980) and export to China (Fig. 5.1). 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 1970s 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 (Fig. 5.14) due to low abundance of squid. During

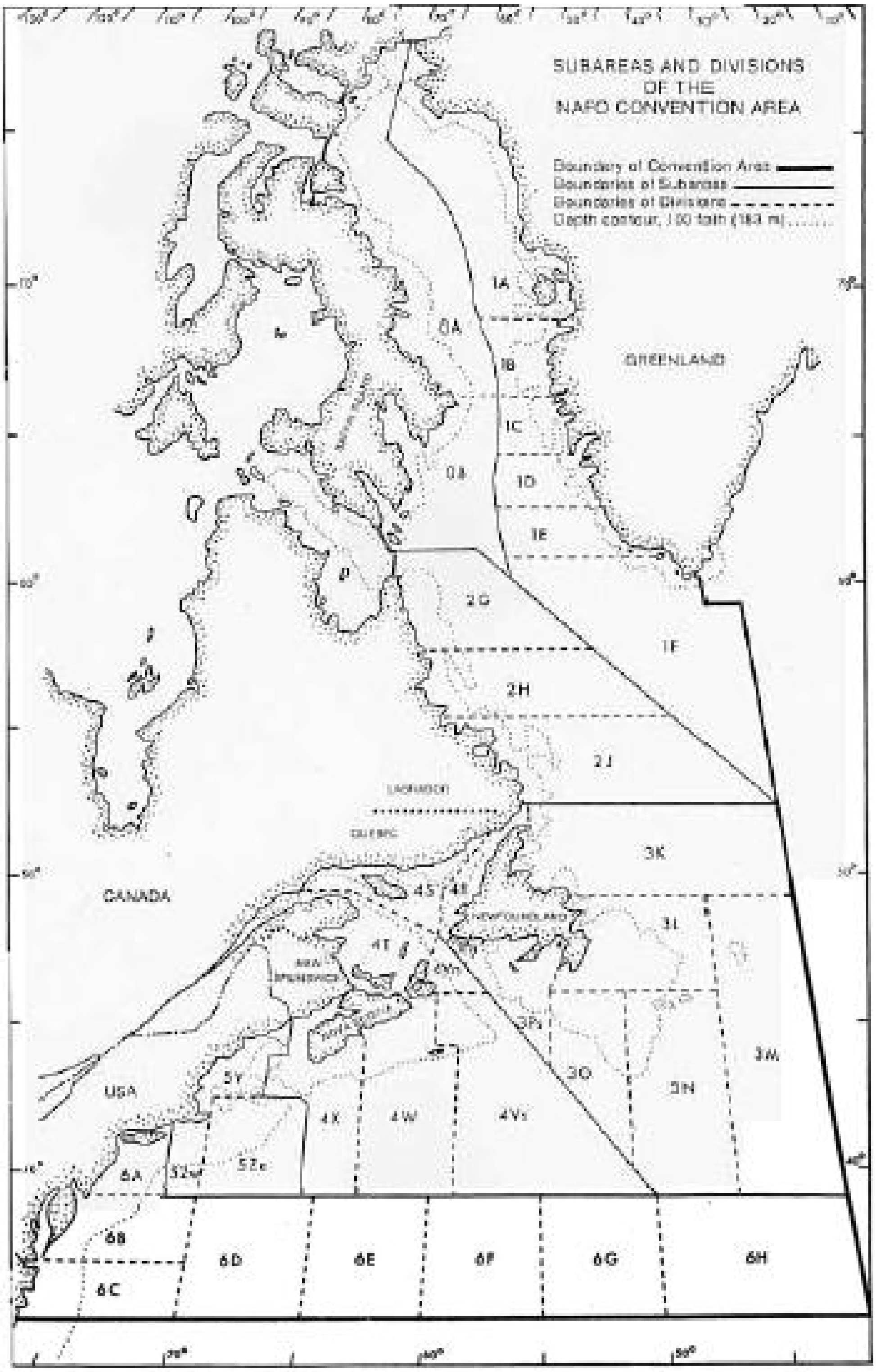


Figure 5.13. Map of the northwest Atlantic, showing NAFO (and ICNAF) subareas discussed in the text

1983–1993 abundance has remained generally low, peaking at only about 4 400 t in 1990. This 11–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. 5.1 and 5.14, Beck *et al*. 1994).

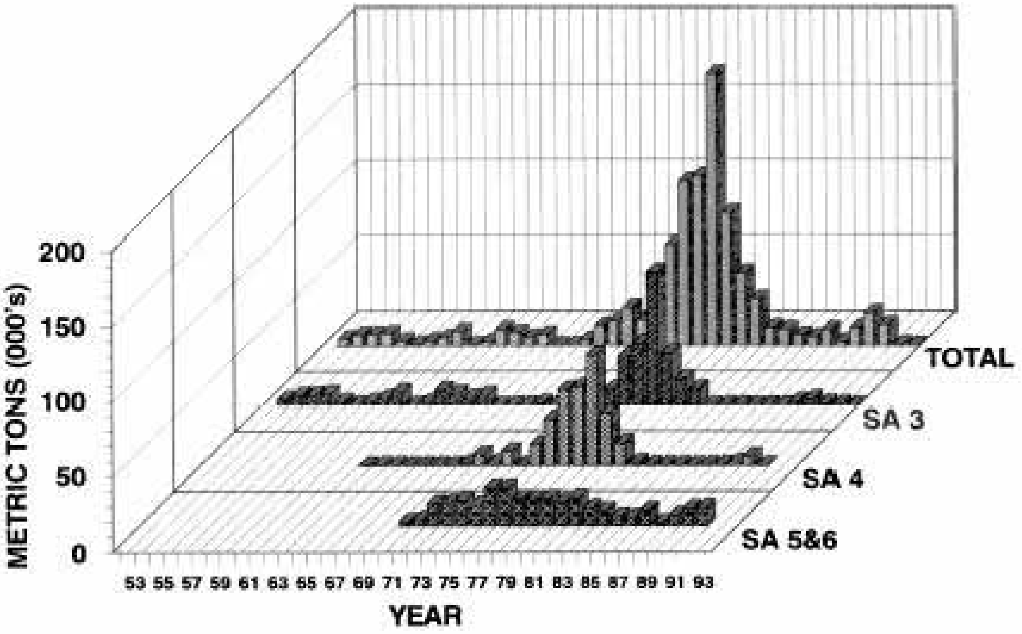


Figure 5.14. Recent catch statistics for *Illex illecebrosus* by NAFO region showing onset of the international fishery and the relative stability of the fishery in southern regions

In the two more southern fishery areas (Nova Scotia and northeastern USA) the squid fisheries have for more than two 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 (Mercer 1973a, Lange and Sissenwine 1983). 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 (Tibbetts 1977, Lange and Sissenwine 1983).

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 fell between 1 000 and 2 000 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 (Fig. 5.14) 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). 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 (Fig. 5.14). 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. Much of the Scotian Shelf squid catch is taken as by-catch in the smallmeshed 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 were 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 (Fig. 5.14), due to increasing participation by foreign fleets.lt increased from about 6 600 t in 1971, with five foreign fleets participating, to peak at about 25 000 tin 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 2000 tin 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.

The annual catch is generally taken throughout July to November at Newfoundland, with peak catches usually occurring in September or October (Mercer 1973a, Beck *et al*. 1994). Most of the catch is taken along the northeast coast of Newfoundland (NAFO Divisions 3L and 3K, Fig. 5.13), 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, Fig. 5.13). The fishery may extend from April through November. Peak catches occur earlier than at Newfoundland, with the 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* (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 reflect annual recruitment since about 1972. 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, *see Chapter 11*). 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). Especially evident is that uncommon prolonged periods of poor squid recruitment (1968–1974 and 1982–1993, Fig. 5.14) 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 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 (*see Chapter 7*).

8.2 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) and will be summarized and updated here. All northwest Atlantic squid resources were initially managed through ICNAF. Pre-emptive quotas, first established because of 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 tin 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.

In 1977, the USA lowered the Subarea 5+6 TAC for short-finned squid to 30 000 t. At that time it also established seasonal and spatial regulations (fishing "windows"). That TAC level and other regulations have remained in effect since then. 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 is advisable. Given the one-year life cycle of this species, the basis for an annual Subarea 5+6 TAC of 30 000 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 teach (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 42000 t and the TAC was established in 1980 (and annually since then) at 150 000 t (NAFO 1980).

In recent years the 150 000 t TAC has been partitioned among foreign fleets (with allocations by both NAFO and Canada), the Canadian offshore fleet (including an allocated by-catch from the Canadian silver hake fishery), inshore Subarea 4 and inshore Subarea 3. Besides these allocations, a portion of the TAC is held in reserve for mid-season reallocation in years of high squid recruitment. This practice guards against overexploitation in years of poor squid recruitment.

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 TACs 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 levels have been allocated in this manner annually. 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 to December 31, whereas the Canadian fishery (both inshore and offshore) is April 1–December 31.

Acknowledgements

We wish to thank Paul Beck, Joe Drew and Norval Balch who assisted in data collection, analysis and presentation as well as to Moira Hynes, who helped prepare the manuscript.

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