

Population biology of northern shortfin squid (*Illex illecebrosus*) in the Northwest Atlantic Ocean and initial documentation of a spawning area

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Growth, maturity, and age structure of the northern shortfin squid (*Illex illecebrosus*) population were characterized from samples collected during a stratified, random bottom-trawl survey conducted in May 2000. The survey was conducted on the continental shelf of the east coast of the US and utilized a commercial squid fishing vessel and standardized sampling protocols and gear. Statolith increment counts of 391 individuals, representing the full maturity spectrum from juveniles to mated females (34–250 mm), ranged in age from 69 to 215 d. Substantial variability in the precision of individual age estimates was encountered. The population consisted of a predominant winter cohort of maturing and mature squid (hatched during October–February, with a peak in January) and a spring cohort of juveniles (hatched during February and March, with a peak in March). Recruitment patterns to northern and southern fishing grounds are discussed. The first evidence of a spawning area, located on the continental shelf in the Mid-Atlantic Bight, is presented. Growth in length and weight was best described by a Gompertz model and a power model, respectively. The age range of mated females (115–215 d) indicated a shorter lifespan than expected based on maturity and age information for Newfoundland squid. A latitudinal cline in female size-at-maturity was evident, whereby maturity stages of squid in the southern part of the survey area were more advanced than those in the northern part. Also, females from US waters reach maturity and spawn at smaller sizes and younger ages than females from Newfoundland waters. The results suggest that females from the Mid-Atlantic Bight may exhibit faster rates of growth and maturation, and possibly a shorter lifespan, than their Newfoundland counterparts.

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Introduction

The northern shortfin squid, *Illex illecebrosus* (Lesueur, 1821), is a highly migratory ommastrephid that inhabits the continental shelf and slope waters of the Northwest Atlantic Ocean, between Iceland and the east coast of Florida (29°30'N–66°N; Roper *et al.*, 1998), and is considered to constitute a single stock throughout its range (Dawe and Hendrickson, 1998).

The onset and duration of the *Illex* fisheries reflect the timing of squid availability on the fishing grounds. Bottom-trawl fisheries occur on the US continental shelf, primarily in the Mid-Atlantic Bight, and have historically occurred on the Scotian Shelf off Canada during June through late autumn (Hendrickson *et al.*, 2002). An inshore jig fishery

exists later in the year, generally during August through late autumn, in waters off Newfoundland (Hurley, 1980; Dawe, 1981). Migration patterns between US and Canadian fishing grounds are unknown. However, long-term annual trends in relative biomass indices and mean body size are similar for the Scotian Shelf and US shelf stock components (Hendrickson *et al.*, 2002) and indicate that a period of high productivity (1976–1981) occurred between two low-productivity periods (1970–1975 and since 1982).

Most squid species are highly migratory, have a lifespan of less than one year (Rodhouse and Hatfield, 1990; Jereb *et al.*, 1991; Jackson, 1994), and exhibit protracted spawning (Jackson, 1994). Recruitment is continuous with overlapping “microcohorts” entering the population over a wide geographic area and exhibiting variable growth rates

(Caddy, 1991). Consequently, age estimates rather than tracking of length frequency modes are preferred for cohort identification and growth-rate estimation (Amaratunga, 1983; Pierce and Guerra, 1994; Jackson *et al.*, 1997). Age can be estimated from statolith increment counts provided that daily increment formation has been validated (Jackson, 1994), such as for *I. illecebrosus* (Dawe *et al.*, 1985; Hurley *et al.*, 1985). However, few studies have addressed the precision of age estimates.

Population structure and seasonal growth rates have been characterized based on Newfoundland jig fishery samples (Dawe and Beck, 1997). Recruitment occurred throughout the fishing season and monthly cohorts were replaced every two to three months by younger squid. Growth rates, in length and body weight, were described as linear and increased with month of hatching for both sexes. However, juveniles and mature females were not present in these samples. Winter cohorts were considered to be the primary source of recruitment to this fishery based on the seasonal distribution of paralarvae (Lu and Roper, 1979; Dawe and Beck, 1985; Dawe and Warren, 1993), length compositions (Squires, 1967; Coelho *et al.*, 1994), and male maturation data (Mercer, 1973). However, this hypothesis was not confirmed by ageing studies of squid sampled from the Newfoundland fishery during 1982 (Dawe *et al.*, 1985) and 1990 (Dawe and Beck, 1997). Squid caught during July–November were predominantly hatched during spring (March–May) rather than winter.

Statolith-based age analyses and growth and maturity data are lacking for squid from the US shelf and for the population prior to the start of the fisheries. These data are not collected during ongoing spring and autumn research surveys, in part because squid availability is highly variable owing to migrations on and off the US shelf.

Spawning areas have not been identified. Despite intensive survey efforts during the 1970s and 1980s, little is known about the early and late stages of the life cycle because few juveniles and mature females have ever been captured (O'Dor and Dawe, 1998). Only seven mature females, distributed sporadically between Newfoundland and Cape Hatteras, North Carolina (Dawe and Drew, 1981), and two mated females have been recorded (O'Dor and Dawe, 1998). The neutrally buoyant, gelatinous egg balloons have never been found in nature (O'Dor and Balch, 1985). Nevertheless, a winter spawning site located off the east coast of Florida has been inferred because (1) squid in all fishing areas migrate offshore and southward during late autumn, (2) winter water temperatures south of Cape Hatteras meet conditions for successful embryonic development ($> 12.5^{\circ}$; O'Dor *et al.*, 1982; Trites, 1983; Rowell and Trites, 1985), and (3) *Illex* sp. paralarvae have been collected along the north wall of the Gulf Stream during February and March (Dawe and Beck, 1985; Rowell *et al.*, 1985; Vecchione and Roper, 1986; O'Dor and Coelho, 1993).

Based on observations of females spawning in captivity, *I. illecebrosus* is classified as a terminal spawner. Females are

capable of releasing multiple egg balloons (Durward *et al.*, 1979b), but only during a single spawning period that occurs shortly after mating and they die within days thereafter (O'Dor *et al.*, 1980). Back-calculations of hatch dates from statolith increment counts indicate that spawning occurs during December through June (Dawe and Beck, 1997). A secondary summer spawning peak has been inferred from size composition data collected during autumn bottom-trawl surveys of the US shelf (Lange and Sissenwine, 1981).

The objectives are to characterize population structure, growth, and maturity based on fishery-independent samples collected prior to the start of the fishing season. Statolith-based age data are used for cohort identification and estimation of growth rates and median age-at-maturity. Ageing precision is also addressed.

Materials and methods

Sampling

Samples were collected during a bottom-trawl survey conducted by the commercial freezer trawler FV "Relentless" (length overall 39 m) during 20–27 May 2000. The survey area extended from Georges Bank ($40^{\circ}50'N$ $66^{\circ}50'W$) to Nag's Head, North Carolina ($35^{\circ}50'N$, $75^{\circ}W$), encompassing the fishing grounds of the US *Illex* fishery. Sampling was conducted at 40 stations located in a subset of 16 survey strata sampled seasonally by the Northeast Fisheries Science Center (Figure 1), utilizing the random station selection protocol described in Azarovitz (1981). The vessel was rigged with a high-opening (headrope height = 26 m) commercial squid bottom trawl with a fishing circle of 100 meshes of 3.2-m stretched mesh and a 25-mm diamond-mesh codend liner. Tows were standardized at 30 min (time between winch lock and re-engage) and a speed of 3.5 knots. Sampling was restricted to the period between sunrise and sunset (05:00–19:00 EST), when squid are on or near the bottom and are available to bottom-trawl gear (Roper and Young, 1975; Brodziak and Hendrickson, 1999). Headrope height, door spread, depth, and bottom temperature were recorded throughout each tow by SCANMAR sensors. Surface temperature was recorded at the beginning and end of each tow by a hull-mounted thermistor located at a depth of 3.7 m.

Data were collected from fresh samples. At each station, total *Illex* catch was weighed to the nearest 0.02 kg with a motion-compensated electronic scale (Marel M-2000 M60). All squid < 70 mm dorsal mantle length (DML) were sampled because they were caught in low numbers ($n = 123$). For larger squid, a maximum random subsample of 250 individuals was obtained from the catch at each station. Body weight (0.1 g) and DML (nearest millimetre) were recorded for 2575 females and 2676 males. The length frequency distribution of the population was obtained by multiplying the length frequency distribution of each subsample by the ratio of catch weight to subsample weight at each station.

Maturity stage was determined for a maximum random subsample of 100 squid per station ($n = 1448$ males and 1398

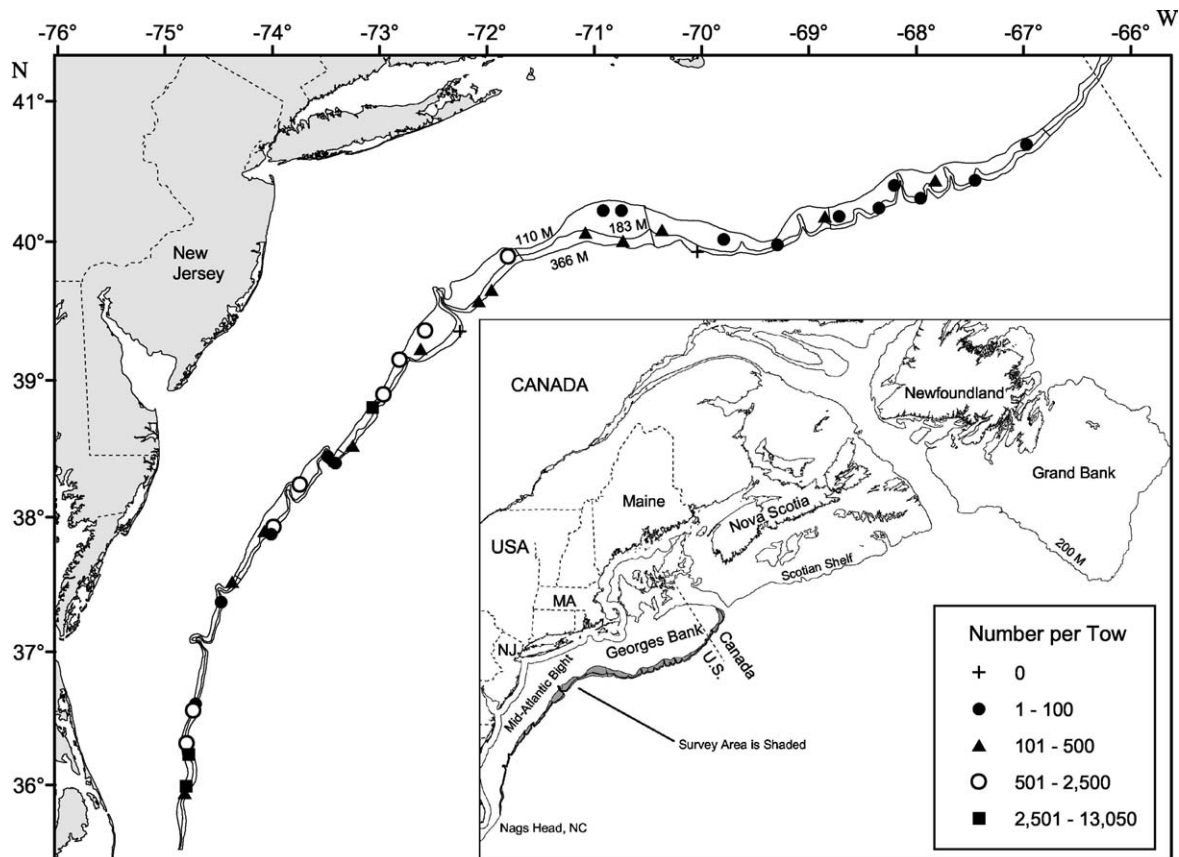


Figure 1. Sampling strata and relative abundance (number per tow) of *I. illecebrosus* caught in a bottom-trawl survey of the eastern US continental shelf during May 2000. Inset shows the survey area in relation to fishing grounds on the Scotian Shelf and inshore Newfoundland.

females). Squid were examined for the presence of gonads visible to the naked eye, and if lacking, were classified as juveniles of indeterminate sex. Male maturity stages were determined macroscopically using four gonadal development stages: 1, immature; 2, maturing stage I; 3, maturing stage II; and 4, mature (Mercer, 1973). Five female maturity stages were assessed based on the nidamental gland length to DML ratio (Durward *et al.*, 1979a). These classification scales allow comparisons with previous maturity studies. To ensure classification consistency, all determinations were made by the same scientist. Squid samples were labelled individually and stored in the freezer.

Length–weight relationships ($W = aDML^b$) were estimated, by sex and for sexes combined, by least-squares linear regression of log-transformed total weight (W) vs. log-transformed DML. Analysis of covariance (ANCOVA) was used to test the effects of sex, latitude, and depth on the length–weight relationship.

Age determination

After thawing, statolith pairs were extracted from approximately 10% of the individuals sampled for sexual maturity

at each station and in proportion to sex. Overall, ages were determined from 391 squid (153 males, 218 females, and 20 juveniles). The age frequency distribution of the population, in weeks, was obtained by scaling the length-at-age distribution of each age subsample to the length frequency distribution of the catch at each station.

Statoliths were mounted and ground in accordance with the method of Dawe and Beck (1997) and then viewed on a high-resolution monochrome screen at $400\times$ with an Olympus CH30 microscope equipped with a JAI CV-M50 monochrome camera and polarizing filter. Growth increments were counted by eye (and tallied using a hand counter) along the statolith radius, primarily on the dorsal dome surface, but also from the rostral end. In some cases, determining the number of peripheral increments required extrapolation (Jackson and Choat, 1992). One reader, with expertise in ageing various species of squid, conducted all increment counts. The age of an individual, in days, was defined as the mean of two consecutive increment counts.

Precision was determined using two methods. A single-blind ageing experiment was conducted and involved one reader who unknowingly read both statoliths from 20

randomly selected squid. One statolith from each pair was read twice (replicates) on different days. Linear regression of the mean increment counts of statolith 1 vs. statolith 2, for each pair, was used to measure precision. The standard deviation of the residuals around the regression line measured the variability of age determinations around an estimate of their “true” value. A nested ANOVA was also conducted to partition the sums of squares associated with age estimation into variances among statoliths within and between squid. The model treated the mean increment count of both statoliths from each pair as the dependent variable, individual squid as the main effect, and unique statolith as a variable nested within the individual. In addition, coefficients of variation (CVs) for replicate increment counts and their standard errors (s.e.) were used to assess age precision.

Spatial distribution

ArcView 8.2 (ESRI, 2002) was used to map relative abundance (number per tow) and the distribution of mature and mated females. Relative abundance was computed by multiplying the number at length in each station subsample by the ratio of total catch weight to the sum of the subsampled weights by sex.

Maps of catch rates from seasonal bottom-trawl surveys (depth range: 9–366 m) conducted by the Northeast Fisheries Science Center (Azarovitz, 1981) were also prepared. Mean number per tow, by stratum, was mapped (excluding strata with zero catches) for the survey periods of winter (December–January, 1993–2001), spring (March–April, 1968–2001), summer (June–July, 1977–1980), and autumn (September–October, 1967–2001). Surveys were conducted from Georges Bank to Cape Hatteras during winter and from the Gulf of Maine to either North Carolina or South Carolina during other seasons.

The spawning area was defined as the strata within which the majority (98%) of the mated females were caught because spawning occurs shortly after mating (O’Dor *et al.*, 1980). The catch-weighted proportions of females ($F/[M + F]$) in the spawning area vs. more northerly stations (non-spawning area) were compared. The proportion of females in the total catch from the non-spawning area ($\bar{P}_{\text{non-sp}}$) was estimated as the weighted average:

$$\bar{P}_{\text{non-sp}} = \sum_{s=1}^{19} w_s p_s,$$

where p_s is the fraction of females in a random sample of the catch at station s , and w_s is the fraction of the total squid catch in the non-spawning area taken at station s . Ignoring variance in the weights w_s , the variance of $\bar{P}_{\text{non-sp}}$ is:

$$\text{Var}(\bar{P}_{\text{non-sp}}) = \sum_{s=1}^{19} w_s^2 \text{Var}(p_s),$$

where $\text{Var}(p_s) = p_s(1 - p_s)/n_s$ is the variance of the females at station s based on the random sample of n_s

squid. By the central limit theorem, the distributions of $\bar{P}_{\text{non-sp}}$ and \bar{P}_{sp} should be approximately normal.

Growth and maturity

Exponential, linear, power, and Gompertz functions were fit to length-at-age and weight-at-age data to estimate relative growth rates at the beginning of the fishing season. Exploratory models were fit, by sex, to pooled data with and without the inclusion of juveniles and to data from the predominant hatch month (January) to determine the best model fit. Relative growth rates were also estimated for sexes combined because fishery samples are generally not separated by sex.

The relationship between length and age was modelled using the PROC NLIN procedure (SAS Institute Inc., 1985) to obtain least-squares estimates of parameters of the integrated form of the Gompertz growth model (Ratkowsky, 1983). A multiplicative lognormal error term was used based on the observation that variability in length-at-age increased with age.

The relationship between weight and age was modelled as a power function and estimated by least-squares linear regression of log-transformed values. ANCOVA was used to test the effects of sex and maturity stage.

Median length (L_{50}) and age (A_{50}) at maturity, by sex, were estimated by fitting a logistic regression (SAS Institute Inc., 1985) to the proportions mature at length and age, respectively. Female maturity Stages 4 and 5 were categorized as mature (Stages 1–3 as immature) based on the close relationship between histological observations of oogenesis and the maturity index (Coelho *et al.*, 1982). Male maturity Stages 3 and 4, characterized by the presence of spermatophores in Needham’s sac, were categorized as mature (Stages 1 and 2 as immature).

Results

Spatial distribution

Squid were more abundant in strata located south of 40°N (Figure 1). For comparison, the seasonal bottom-trawl surveys (Figure 2) indicate that abundance on the US shelf is low during winter and an on-shelf migration begins during March and April along the entire shelf edge, with high densities of squid emanating from the southernmost strata. During June and July, squid are distributed further inshore (to 27 m) and throughout most of the shelf south of Georges Bank. In late autumn, an off-shelf migration is evident in nearly all strata based on the increase in density with depth.

During the May survey, squid were distributed along a density gradient that increased in a southerly direction. Relative abundance was negatively correlated with latitude ($p < 0.01$) and positively correlated with surface temperature ($p < 0.01$), reflecting a significant ($p < 0.001$) inverse correlation between surface temperature and latitude. Surface temperatures throughout the survey area ranged

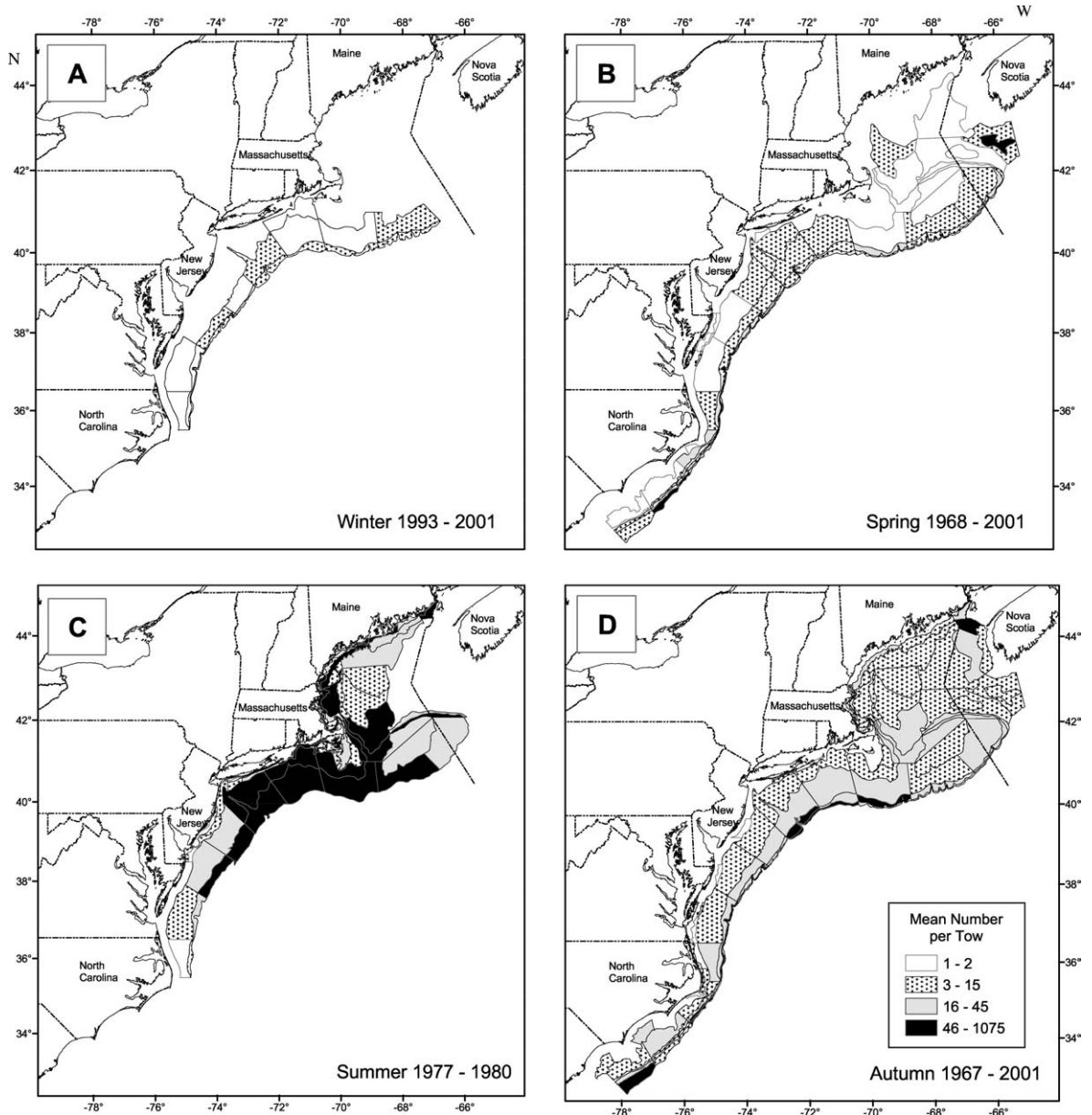


Figure 2. Distribution of *I. illecebrosus* (mean number per tow by stratum) on the eastern US continental shelf during winter (A), spring (B), summer (C), and autumn (D).

between 10.6 and 20.1°C. Bottom temperatures were generally more constant, ranging between 9.9 and 13.5°C, and were not correlated with latitude. However, bottom temperatures at shelf edge stations south of 36.5°N were much higher (16.4–21.4°C). In this region, the seaward movement of shelf water into the Gulf Stream is a common occurrence that results in abrupt increases in bottom temperature at frontal boundaries (Churchill and Berger, 1998).

Juveniles tended to be spatially segregated from adults and were associated with large catches of euphausiids and myctophids. They were predominantly caught in deep water

(140–260 m) at the two northernmost stations, on the south-east edge of Georges Bank, where adult abundance was low and surface (10.6°C) and bottom temperatures (9.9°C) were lowest. Juveniles comprised the entire catch at one station.

Size composition

Overall, squid ranged in DML from 34 to 250 mm with a mode at 160 mm (Figure 3). Length modes at 40, 140, and 160 mm represented juveniles, males, and females, respectively. Squid > 160 mm were predominately (70%) females.

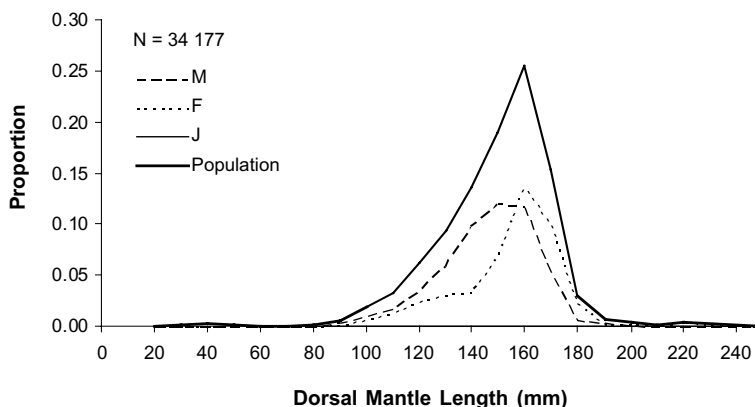


Figure 3. Length frequency distributions of the *I. illecebrosus* population, and by sex, during May 2000.

The ranges recorded for DML were 64–211 and 74–250 mm for males and females, respectively (for body weights 5–246 g and 10–350 g, respectively). The slopes of the length–weight relationship for males ($W = 0.000012\text{DML}^{3.085}$, $r^2 = 0.92$) and females ($W = 0.000013\text{DML}^{3.062}$, $r^2 = 0.96$) were not significantly different ($p > 0.05$). The relationship for sexes combined was $W = 0.00001\text{DML}^{3.045}$ ($r^2 = 0.94$). Average squid size (DML) decreased significantly ($p < 0.01$) with latitude ($r^2 = 0.30$). Average size was not affected by catch size (in numbers) and the interaction effect between latitude and catch was not significant ($p > 0.05$).

DML of juveniles ranged between 34 and 68 mm (mean = 46 mm) and body weight ranged between 1.0 and 5.7 g (mean = 2.4 g). A separate length–weight relationship was fit ($W = 0.0004\text{DML}^{2.263}$, $r^2 = 0.77$).

Age analyses

The estimated age distribution (range: 69–215 d) of the population sampled (Figure 4) showed a juvenile mode of 11 wk (range: 69–108 d; mean = 80 d), a female mode of 18 wk (range: 92–215 d; mean = 141, s.d. = 1.3), and a male mode of 20 wk (range: 70–176 d; mean = 136, s.d. = 1.2). The age distribution of Stage 5 females was broad, extending from 18 to 24 wk (mean = 153 d). The oldest individual (215 d), a mated female, was also the largest (DML = 250 mm; weight = 350 g). The age range of mated females was 115–215 d. Average age decreased significantly ($p < 0.01$) with latitude ($r^2 = 0.36$). Average age was not affected by catch size (in numbers) and the interaction effect between latitude and catch was not significant.

Most (63%) of the population was hatched during January (Figure 4). Individuals hatched during October and November were Stage 5 females, but most were hatched during December (47%) and January (37%). Juveniles were hatched primarily during February (33%) and March (70%).

The means of the two increment counts for each statolith pair were not significantly different ($p > 0.05$) for 60% of the pairs included in the single-blind ageing precision

study. There was a significant linear relationship between the means ($p = 0.05$) with a slope near 1 ($b = 0.96$, s.e. = 0.03) and no apparent trend in the residuals (s.d. = 18 d). Results from a nested ANOVA indicated that 17% of the variance was attributable to age estimation error (Table 1), of which 83% was attributable to increment count differences between statoliths 1 and 2 and the remainder (17%) to differences between replicate counts of the same statolith (equating to 2.9% of the total model error).

CVs for replicate counts ranged from 0 to 13% and were $< 9\%$ for 90% of the 391 statoliths. Results from a one-way ANOVA ($p = 0.0001$, $r^2 = 0.96$) with mean increment count as the dependent variable indicated that 3.8% of the variance was attributable to differences between replicate counts of the same statolith. The s.d. of the residuals (no apparent trend) for the linear regression of replicate counts 1 vs. 2 ($r^2 = 0.85$) was 8.6 d.

Maturity

Sex could be determined macroscopically beginning at 64 mm for males and 74 mm for females. Maturity Stages 1 (50% males and 18% females) and 2 (12% males and 39% females) were predominant in both sexes. The percentage of Stage 4 males (21%) was twice as high as the percentage of Stage 5 females (10%).

For both sexes, length frequency distributions by maturity stage showed considerable overlap (Figure 5). However, both sexes exhibited significant ($p \leq 0.05$) differences in mean size between early and advanced maturity stages (Figure 6), with no significant increase in mean size after Stage 2 (males) or Stage 3 (females). Patterns in body weight with maturity stage were similar to those in DML.

Both sexes exhibited significant ($p \leq 0.05$) differences in mean age between maturity stages. Stages 1 through 3 females were significantly younger than Stage 5 females and Stage 1 males were significantly younger than Stages 2 through 4 (Figure 6).

Males attained 50% maturity at a smaller size ($L_{50} = 162$ mm) than females ($L_{50} = 182$ mm), but the differences

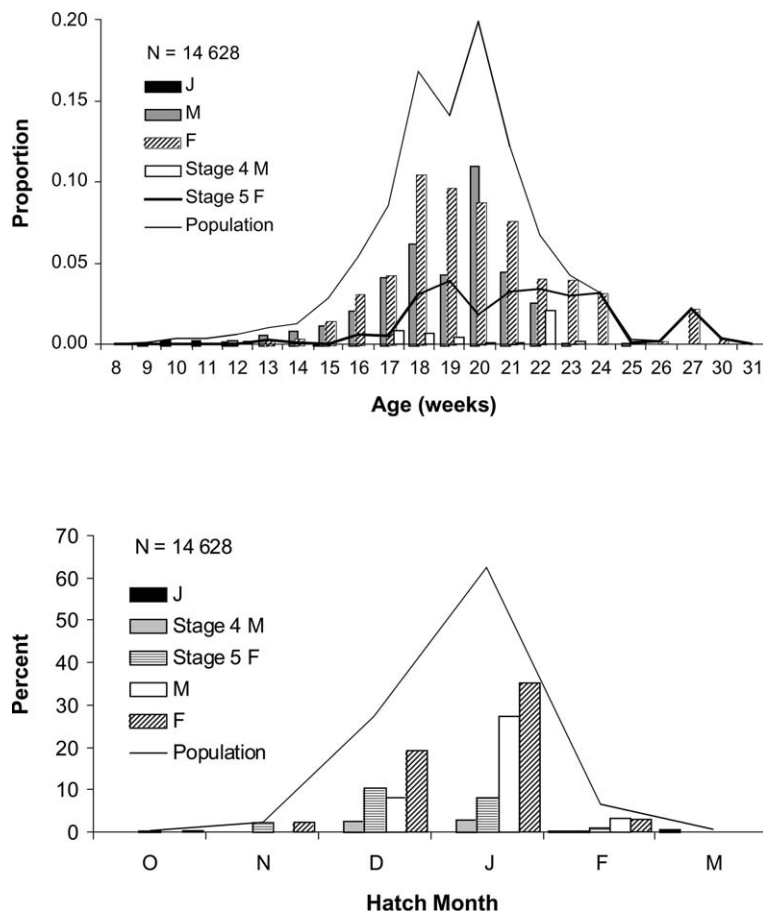


Figure 4. Statolith-derived age distributions (top panel) and percent composition by hatch month (lower panel) for various components of the *I. illecebrosus* population during May 2000.

were not significant because parameter estimates for a and b were within one standard error of each other (Table 2). Minimum lengths at maturity were 110 and 118 mm, respectively. Small percentages of females (4.5%) and males (2.3%) > 170 mm were immature. However, the mean ages of mature vs. immature squid from this size group were not significantly different ($p > 0.05$) for either sex. Minimum age-at-maturity was 88 d for males and 92 d for females. Females attained 50% maturity at a younger age ($A_{50} =$

144 d) than males ($A_{50} = 154$ d), but this difference was not significant (Table 2).

Latitude and surface temperature were highly significant covariates ($p < 0.001$ and $p < 0.01$, respectively) in the female length-at-maturity model. Predicted L_{50} values increased with latitude and with decreasing surface temperature.

Spawning and sex ratio

The presence of spermatophore bundles attached either to the inner wall of the mantle cavity or at the base of the gills near the oviducal gland indicated that 31% (24 individuals) of the Stage 5 females in the subsamples had mated. Approximately 42% (ten individuals) of these individuals had mated more than once (as evidenced by the presence of two or three spermatophore bundles; Figure 7). Spent females were absent in the samples.

Stage 5 females were caught at half (55%) of the stations, but most (97%) were caught south of $39^{\circ} 10' N$. Most of the mated females (98%) were also caught in this area (Figure 8), at depths of 113–377 m. These latitudinal

Table 1. Results of a nested ANOVA for partitioning the variance in statolith increment counts among squid, between paired statoliths, and within statoliths.

Source	d.f.	SS	%	MS	F	p
Among squid	19	29 881	82.7	1 573	60.8	<0.0001
Between paired statoliths	20	5 195	14.4	260	10.0	<0.0001
Within statolith	40	1 035	2.9	26		
Total	79	36 111				

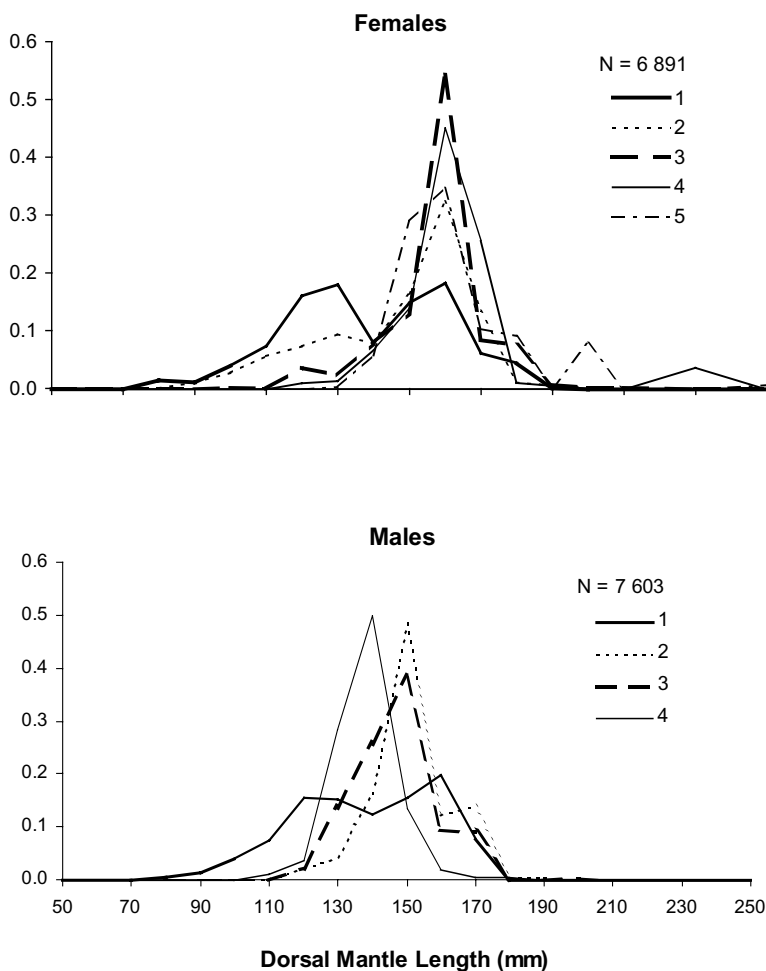


Figure 5. Length frequency distributions of *I. illecebrosus* males and females by maturity stage during May 2000.

ranges, characterized by surface temperatures of 13.4–20.1°C and bottom temperatures of 11.4–20.3°C, comprise the known spawning area.

Catch-weighted percentages of females in the spawning (47%; 95% confidence interval: 42–52%) vs. non-spawning area (51%; 48–54%) were not significantly different.

Growth

The highest r^2 values for the weight-at-age and length-at-age models resulted from a power model and a Gompertz model, respectively. Juveniles were included in all models because their inclusion explained a greater portion (55–66%) of the total variance than their exclusion (<28%). Data were pooled across hatch months because exploratory models explained less of the total variance (<18%) when fit to data grouped by predominant hatch month.

Both sexes exhibited substantial variability in size-at-age. Weight-at-age data were more variable, particularly for females, than length-at-age data (Figure 9). The Gompertz model fitted the length-at-age data equally well

for males and females, but the fit was not as good for sexes combined (Table 3). The estimated asymptotic DML of females (176 mm) was greater than for males (156 mm).

The power model also fit male and female weight-at-age data equally well, and again a lower r^2 value was obtained for sexes combined (Table 3). Slopes and intercepts were significantly different ($p = 0.0001$) between sexes, females weighing more than males at any given age, and also among females of different maturity stages ($p < 0.0001$).

Discussion

The results address some of the remaining questions concerning the life history and population structure of *I. illecebrosus*, such as spawning location, lifespan, growth, maturity, and population structure prior to the start of the directed fisheries.

The distribution of mated females indicates that northern shortfin squid spawn along the edge of the continental shelf in the Mid-Atlantic Bight. It is unknown where squid spawn

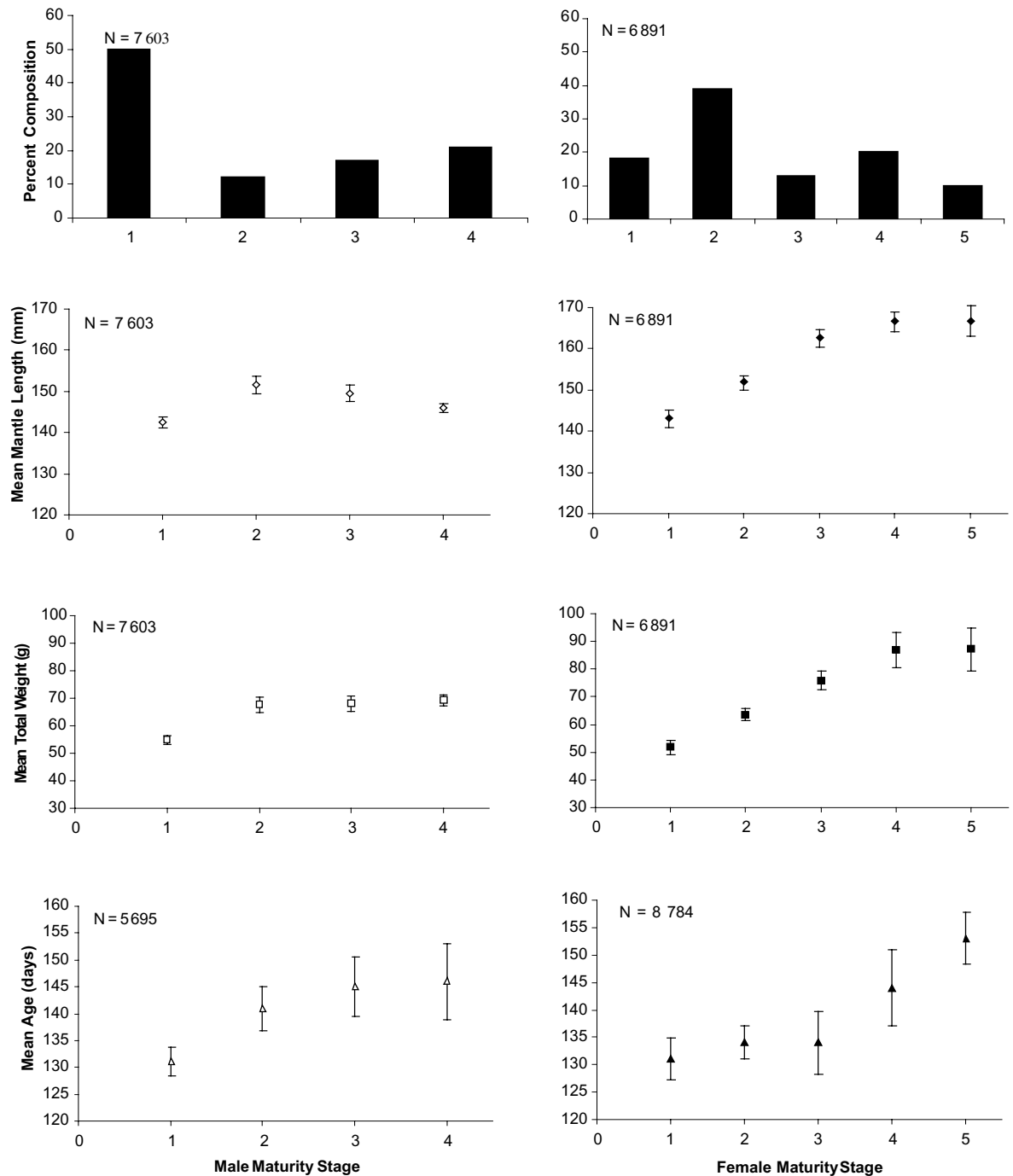


Figure 6. Percentage composition, mean dorsal mantle length (mm), mean total weight (g), and mean age of *I. illecebrosus* by sex and maturity stage during May 2000 (vertical bars: 95% confidence limits of the means).

within the water column. Spawning has only been documented in captive females and both demersal (Bradbury and Aldrich, 1969) and midwater (O'Dor and Balch, 1985) spawning have been observed. During the survey, mated females were caught within 26 m of the seabed

where temperatures throughout the water column were above 12.5°C, the minimum required for normal embryonic development (O'Dor *et al.*, 1982). However, thermal stratification normally occurs in the Mid-Atlantic Bight during the period that squid are present on the US shelf

Table 2. Median lengths (L_{50} , mm) and ages (A_{50} , d) at maturity and parameter estimates (a and b; with s.e. in brackets) for logistic regressions of fraction mature on DML and age, by sex (juveniles included with each sex).

Sex		L_{50}/A_{50}	n	a	b	p
M	DML	162	1591	-7.17 (0.50)	0.0442 (0.0035)	<0.0001
	Age	154	173	-9.78 (2.00)	0.0636 (0.0146)	<0.0001
F	DML	182	1541	-7.93 (0.54)	0.0435 (0.0034)	<0.0001
	Age	144	238	-8.02 (1.24)	0.0558 (0.0090)	<0.0001

(May through October) and bottom temperatures generally do not exceed 12°C (Mountain and Holzwarth, 1989) at the depth range sampled. This suggests that spawning occurs in midwater. Bottom and midwater temperatures above 12°C are not generally present on the Scotian Shelf and further north (Drinkwater and Trites, 1987). The lack of observations of mated females and presence of few mature females in samples from more northerly waters (Dawe and Drew, 1981; O'Dor and Dawe, 1998) suggest that the Mid-Atlantic Bight serves as the primary spawning ground for the stock during part of the year. The spawning area overlaps spatially with the fishing grounds of the directed bottom-trawl fishery (Hendrickson *et al.*, 2002), but maturity analyses of fishery samples will be required to determine whether spawners are captured in the fishery.

Previously, the lifespan was largely unknown because few mated squid had been captured. The new information about the age range of mated females (115–215 d) can be used as a proxy for lifespan because a sperm storage receptacle is lacking and spawning and death occur within several days of mating (O'Dor *et al.*, 1980). Thus, the lifespan of the winter

cohort is about four to seven months (mean = 5 months). This is shorter than expected from extrapolation of the age range (110–250 d) of Stage 1–3 females caught in Newfoundland waters (Dawe and Beck, 1997). Such differences are not likely to be attributable to age estimation error, because both studies utilized the same ageing method and maturation index. The selectivity of jigs for larger squid (Lipinski, 1994) may have contributed to the differences between the two studies, but it seems more likely that they represent real lifespan differences.

Lifespan may vary with latitude owing to differences in growth and maturation rates. The species is distributed throughout a broad latitudinal range and migrates between subtropical, temperate, and boreal regimes during its life cycle. Embryonic growth rates increase with temperature up to some maximum (O'Dor *et al.*, 1982) and maturation of some squid species is affected by temperature, food availability, and photoperiod (Mangold, 1987). Surface temperature was inversely correlated with latitude and both factors were significant covariates in the female size-at-maturity model: size-at-maturity was reduced with increasing temperature and more females had reached the final maturity stage in the southern part of the survey area. A difference of 33 mm was predicted for L_{50} values of females captured at latitudes of 40.5°N vs. 39°N. Surface temperatures observed during the survey at these latitudes (12.3 and 13.2°C, respectively) closely bracket the minimum water temperature (12.5°C) required for successful embryonic development. During the survey, females reached maturity and even spawned at smaller sizes and younger ages than females in less advanced stages from Newfoundland waters (Dawe and Beck, 1997). Similarly, males caught on the Scotian Shelf reached maturity two months earlier than those

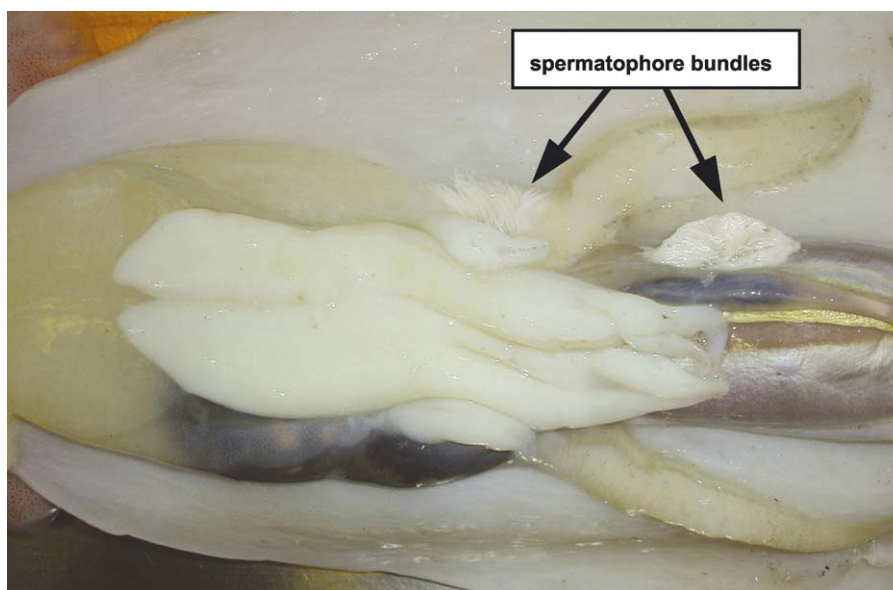


Figure 7. Ventral view of the mantle cavity of a Stage 5 female *I. illecebrosus* that has mated twice.

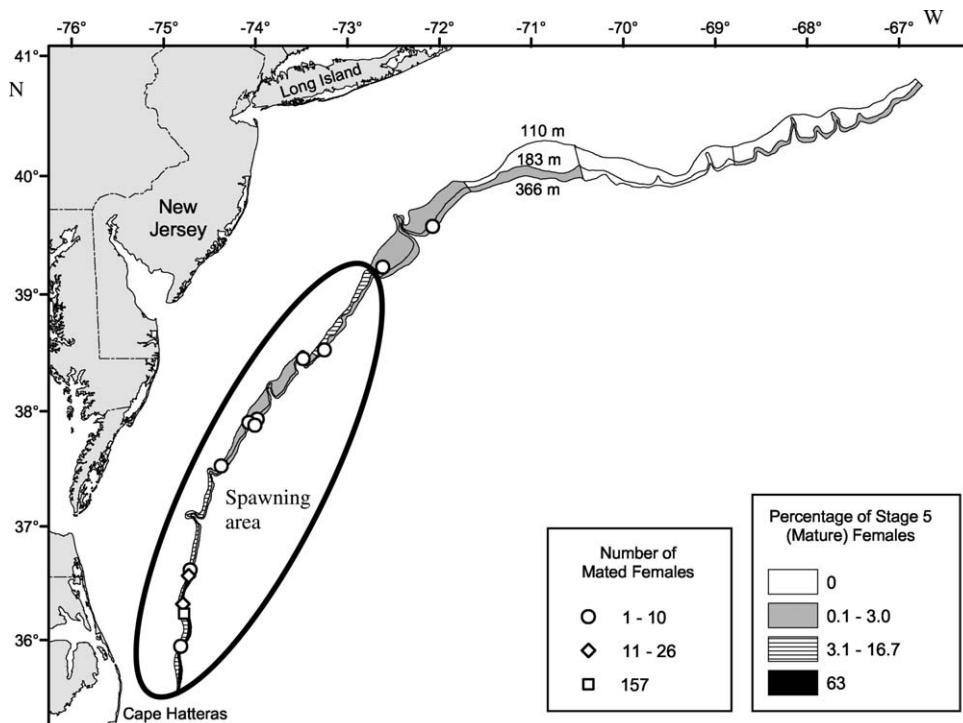


Figure 8. Percentage of Stage 5 females by stratum and number of mated females used to define the *I. illecebrosus* spawning area (encircled strata) in the Mid-Atlantic Bight.

caught further north (Coelho and O'Dor, 1993). Collectively, these findings suggest that squid from warmer waters of the Mid-Atlantic Bight exhibit faster rates of growth and maturation, and possibly a shorter lifespan, than their northern counterparts.

Latitude (or temperature) explained a large part of the variance in average squid size, confirming the results of previous surveys conducted between the Scotian Shelf and the Mid-Atlantic Bight (Lange and Johnson, 1981). Lange and Johnson (1981) also found that females were larger than males. While mean lengths and length-at-age were not significantly different between sexes in the May samples, growth in body weight was significantly different, whereby females weighed slightly more than males at any given age. The difference is attributable to an increase in the weight of females as they mature according to the changes observed in the weight-at-age relationship for consecutive maturity stages. A similar relationship was not evident for males.

Length and age-at-maturity relationships were not significantly different between sexes, but both sexes exhibited significant differences in mean size between early and advanced maturity stages. This suggests that squid stop growing after maturation starts or that maturation takes place rapidly. Rapid maturation appears possible because immature females held in captivity became mature within 40 to 60 d (O'Dor *et al.*, 1977). Only a small percentage (10%) of the winter cohort was ready for spawning in May. In contrast

to mass spawning events of some loliginid squids (Hanlon and Messenger, 1996), a strategy of continuous spawning by a small fraction of the population would spread out the risk of recruitment failure over time.

The presence of a latitudinal cline in size-at-maturity is consistent with the hypothesis that *Illex* in Newfoundland require a larger body size (associated with delayed maturity) to complete the long-distance autumn spawning migration (O'Dor and Coelho, 1993). Unlike males, females do not reach maturity in Newfoundland waters prior to their autumn migration (Squires, 1967; Mercer, 1973). In addition to aiding in migration, a larger body size may provide a reproductive benefit as postulated for *I. argentinus*, for which fecundity has been shown to increase with mantle length (Laptikhovskiy and Nigmatullin, 1993).

Age, size, and maturity characteristics may be used to determine recruitment patterns in each fishing area. The onset of the annual migration onto the fishing grounds occurs along a latitudinal cline from south to north and squid arrive inshore in Newfoundland approximately one month later than on the US shelf, during July (Hendrickson *et al.*, 2002). During some years, small squid have been caught in the inshore waters of Newfoundland during November, but only in the southern areas (Squires, 1957). It is likely that these individuals originated from more southerly areas, because there is no evidence that squid spawn in these northern waters.

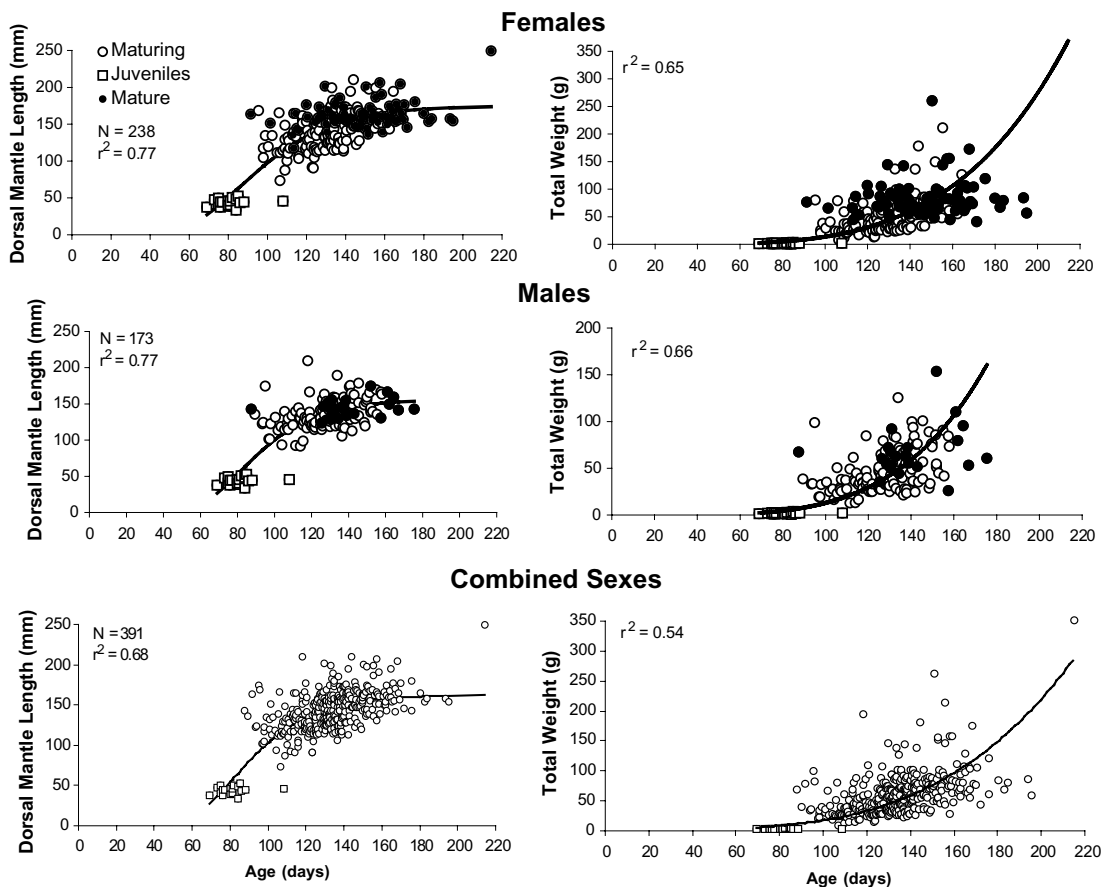


Figure 9. Observed lengths-at-age and derived Gompertz growth curves (left panels) and observed weights-at-age and derived power growth curves (right panels), by sex and for sexes combined, for *I. illecebrosus* during May 2000.

The hatch-month distribution from the May survey may not be directly comparable with the one from the 1990 Newfoundland study (Dawe and Beck, 1997) owing to interannual differences in growth rates and gear selectivity. However, with these potential differences aside, the data suggest the following hypothetical patterns of recruitment to northern and southern fishing grounds. The winter cohort, hatched primarily in January and predominant in the May survey, provides most of the recruits for the squid fishery on the US shelf starting in June. Few squid from this cohort were caught in the Newfoundland jig fishery during July through November (Dawe and Beck, 1997), suggesting that few survive long enough to migrate all the way to Newfoundland. Instead, jig fishery catches from July through September were dominated by squid hatched during March, corresponding to the hatching period of juveniles caught on the US shelf in May. During October and November, April/May-hatched squid dominated the jig fishery catches (Dawe and Beck, 1997), corresponding to progeny of the spawners present on the US shelf during May. Large numbers of squid hatched during October and November were not present in

the May survey samples, which supports the lifespan estimate from the age analysis. If growth rates increase during the summer (Dawe and Beck, 1997), the spring cohort present on the US shelf in May (at three months of age) could presumably recruit to the US, Scotian Shelf, and Newfoundland fisheries as early as July. Based on a lifespan of seven months, these squid would spawn in September. Progeny of the spawners present in the Mid-Atlantic Bight in May would presumably recruit to all three fishing areas in autumn, but squid from Newfoundland must return south to spawn in warmer waters. Confirmation of these hypothetical recruitment patterns will require age analyses of squid collected concurrently from the different fishing grounds throughout the fishing season.

Curvilinear models have been used to describe squid growth throughout the life cycle because growth may follow different patterns between paralarval and adult stages. In addition, individual growth rates show a high degree of plasticity (Jackson, 1994). Mantle length growth of *Illex* sp. is exponential during the paralarval stage (Balch *et al.*, 1988) and linear during the maturing stages (Dawe

Table 3. Parameter estimates (with s.e. in brackets) from length-at-age data (DML in mm; A in d) fit to a Gompertz growth model ($DML = \alpha \exp[-\exp\{\beta - \gamma A\}]$) and a power model according to least-squares linear regressions of log-transformed total body weight (W in g) vs. log-transformed age ($W = \epsilon A^\phi$; with results from an ANCOVA test for equality of slopes and intercepts) by sex and for sexes combined (juveniles included with each sex).

	F	M	Sexes combined	
n	238	173	391	
Gompertz model				
α	176 (6)	156 (6)	163 (4)	
β	3.2 (0.2)	3.6 (0.4)	3.6 (0.2)	
γ	0.037 (0.003)	0.044 (0.005)	0.043 (0.003)	
r^2	0.77	0.77	0.68	
Power model				
ϵ	-16.96 (0.99)	-16.96 (1.20)	-13.70 (0.83)	
ϕ	4.26 (0.20)	4.25 (0.25)	3.60 (0.17)	
r^2	0.65	0.63	0.54	
ANCOVA				
Source	d.f.	Type III SS	F	p
Age	1	111.4	347.5	0.0001
Sex	1	12.3	38.4	0.0001
Age \times sex	1	11.9	37.0	0.0001

and Beck, 1997). The distinct gap observed in the May length composition around 70 mm occurs just prior to sexual differentiation and coincides with the transition from exponential to linear growth as well as the habitat shift from warmer offshore waters to colder shelf waters (Perez *et al.*, 1996). The inclusion of juveniles and mature individuals in the age analyses confirmed that the overall growth pattern throughout the life cycle is sigmoidal, as has been described for *I. coindetti* from the Strait of Sicily (Arkhipkin *et al.*, 2000) and *I. argentinus* from the Patagonian Shelf (Uozumi and Shiba, 1993).

The precision of statolith-based age estimates is an important aspect when evaluating growth parameter estimates and recruitment patterns. Age estimation error for a single reader may be attributable to differences in preparation methods (e.g., mounting, grinding), increment enumeration methods (e.g., type of viewer, viewing magnification, increment interpretation) or both factors. For *I. illecebrosus* statoliths, the use of image analysis resulted in a systematic bias by underestimating ages of young squid and overestimating ages of old squid compared to a light microscopy method (Gonzalez *et al.*, 2000). The bias was attributed to differences in increment interpretation and resulted in a doubling of growth-rate estimates. Gonzalez *et al.* (2000) also suggested that increased growth rates for squid grouped by hatch month were an artifact of age estimation error, owing to methodological differences between statolith-based vs. gladius-based estimates. However, substantial variability in the precision of statolith-based age

estimates may also occur when conducted by a single reader using exactly the same methodology. For example, approximately 11.5% of the observed ageing error was attributable to statolith preparation method (i.e., degree of grinding) and 2.9% was attributable to increment interpretation. The 95% confidence interval for ages derived from two independent increment counts was 34 d, which implies that assigning squid to monthly cohorts may be overly optimistic.

Representative sampling is particularly important for characterization of the age, size, and maturity structure of squid populations given their high rates of natural mortality and growth, seasonal migrations, and overlapping microcohorts (Caddy, 1991). Fishery samples may not be representative of the entire population owing to inherent spatial and temporal biases in fishing effort and catchability differences between sampling units. The use of a commercial squid fishing vessel and gear offered the advantage of improved catchability in conjunction with a standardized, random sampling design. In addition, sampling the population prior to the start of the fisheries reduced potential sampling biases resulting from size-selective fishery removals.

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