

Abstract—Analysis of 32 years of standardized survey catches (1967–98) indicated differential distribution patterns for the longfin inshore squid (*Loligo pealeii*) over the northwest Atlantic U.S. continental shelf, by geographic region, depth, season, and time of day. Catches were greatest in the Mid-Atlantic Bight, where there were significantly greater catches in deep water during winter and spring, and in shallow water during autumn. Body size generally increased with depth in all seasons. Large catches of juveniles in shallow waters off southern New England during autumn resulted from inshore spawning observed during late spring and summer; large proportions of juveniles in the Mid-Atlantic Bight during spring suggest that substantial winter spawning also occurs. Few mature squid were caught in survey samples in any season; the majority of these mature squid were captured south of Cape Hatteras during spring. Spawning occurs inshore from late spring to summer and the data suggest that winter spawning occurs primarily south of Cape Hatteras.

Geographic and temporal patterns in size and maturity of the longfin inshore squid (*Loligo pealeii*) off the northeastern United States

Emma M.C. Hatfield

Steven X. Cadrin

Northeast Fisheries Science Center
National Marine Fisheries Service, NOAA
166 Water Street
Woods Hole, Massachusetts 02543

Present address (for E.M.C. Hatfield): FRS Marine Laboratory
Victoria Road
Aberdeen AB11 9DB
Scotland, United Kingdom

E-mail address (for E. M. C. Hatfield): e.hatfield@marlab.ac.uk

The longfin inshore squid, *Loligo pealeii*, is distributed in the northwest Atlantic from Canada to the Caribbean (Cohen, 1976). Within its range of commercial exploitation (from southern Georges Bank to Cape Hatteras) the population is considered to be a unit stock (NEFC¹), although heterogeneous subpopulations may exist (Garthwaite et al., 1989).

North of Cape Hatteras, *L. pealeii* migrate seasonally. The migration has been described as a movement offshore during late autumn (so that the species can overwinter in warmer waters along the edge of the continental shelf) and a return movement inshore during the spring and early summer (Summers, 1969; Serchuk and Rathjen, 1974; Tibbetts, 1977). Murawski (1993) defined *L. pealeii* as a member of a migratory, warm-water group of species, centered primarily in mid-Atlantic waters (particularly in the spring), that make inshore and northward migrations in the spring and offshore and southward migrations in late autumn.

Geographic patterns in Northeast Fisheries Science Center (NEFSC) survey catches, from the Gulf of Maine to Cape Hatteras, show that *L. pealeii* are distributed over the entire continental shelf (from inshore to offshore) in the autumn, are concentrated at the edge of the continental shelf and at the southern end of the survey area during winter and spring, and are concentrated inshore in summer (Sum-

mers, 1967; 1969; Serchuk and Rathjen, 1974; Vovk, 1978; Lange, 1980; Whitaker, 1980; Lange and Waring, 1992).

Analyses of survey catches indicate that depth, time of day, and temperature all influence cross-shelf distribution patterns (Summers, 1969; Serchuk and Rathjen, 1974; Lange and Waring, 1992; Murawski, 1993; Brodziak and Hendrickson, 1999). Diel correction factors have been applied to survey indices in various studies to adjust nighttime bottom trawl catches to daytime equivalents (daytime catches are higher when squid are concentrated close to the bottom) (Lange and Sissenwine 1983; Lange and Sissenwine²). Research by Lange and Waring (1992) and Brodziak and Hendrickson (1999) demonstrated that the diel differences were size specific and that further consideration of these differences in correction factors was warranted.

Until recently, *L. pealeii* was thought to have a life span of up to three years, and the stock was assessed accordingly (Sissenwine and Tibbetts, 1977; Lange, 1981; Lange and Sissenwine,

¹ NEFC (Northeast Fisheries Center). 1986. Report of the second NEFC stock assessment workshop. NEFC Lab. Ref. Doc. 88-02, 114 p. [Available from NEFSC, 166 Water Street, Woods Hole, MA 02543.]

² Lange, A. M. T., and M. P. Sissenwine. 1977. *Loligo pealeii* stock status. Northeast Fisheries Science Center Lab. Ref. Doc. 77-28, 9 p. [Available from NEFSC, 166 Water Street, Woods Hole, MA 02543.]

1983; Lange³; Lange et al.⁴). Recent advances in the use of statoliths for age determination of squid (see reviews in Rodhouse and Hatfield, 1990; Jereb et al., 1991; Jackson, 1994) have enabled new estimates of life span to be derived for *L. pealeii* (Macy, 1995; Brodziak and Macy, 1996; Macy⁵), which indicate that the life span of *L. pealeii* can be less than nine months. Back-calculations of hatching date from age data revealed that there is more than just a spring-summer spawning component of the population (Brodziak and Macy, 1996; Macy⁵), with a small proportion of squid hatching during winter. This winter spawning is presumed to occur offshore (Brodziak and Macy, 1996), in the vicinity of the submarine canyons along the edge of the northeastern U.S. continental shelf, from Hudson Canyon up to Georges Bank (Fig. 1). The possibility of winter spawning was raised initially by Summers (1969), based on length-frequency data, but squid were not presumed to spawn until their second year because their growth was assumed to be too slow to allow spawning during their first summer.

Our study reports on two studies: 1) an analysis of survey data from spring and autumn NEFSC surveys from 1967 to 1998, and from winter NEFSC surveys from 1992 to 1998, to describe gross distribution patterns of *L. pealeii* over the northwest Atlantic continental shelf from Cape Hatteras to the Gulf of Maine; 2) some results of a field study initiated in 1997 to investigate geographic and seasonal patterns of growth and maturity to determine if the winter spawning component off the northeastern United States can be defined by time and area.

Materials and methods

Survey analysis

Length-frequency data for *L. pealeii* were analyzed from NEFSC bottom-trawl surveys conducted in the autumn (generally from mid-September to late October) from 1967 to 1997; in the spring (generally from March to early April) from 1968 to 1998; and in the winter (generally in February) from 1992 to 1998. Data collection and processing and archiving methods are described by Azarovitz (1981). In

³ Lange, A. M. T. 1984. An assessment of the long-finned squid resource off the northeastern United States. Northeast Fisheries Science Center (NEFSC) Lab. Ref. Doc. 84-37, 24 p. [Available from NEFSC, 166 Water St. Woods Hole, MA 02543.]

⁴ Lange, A. M. T., M. P. Sissenwine, and E. D. Anderson. 1984. Yield analysis of long-finned squid, *Loligo pealei* (LeSueur). Northwest Atlantic Fisheries Organization (NAFO) SCR Doc. 84/IX/97, 29 p.

⁵ Macy W. K. 1995. Recruitment of long-finned squid in New England (USA) waters. ICES CM 1995/K:35, 18 p. [Available from W. K. Macy, Graduate School of Oceanography, Univ. Rhode Island, South Ferry Road, Narragansett, RI 02882].

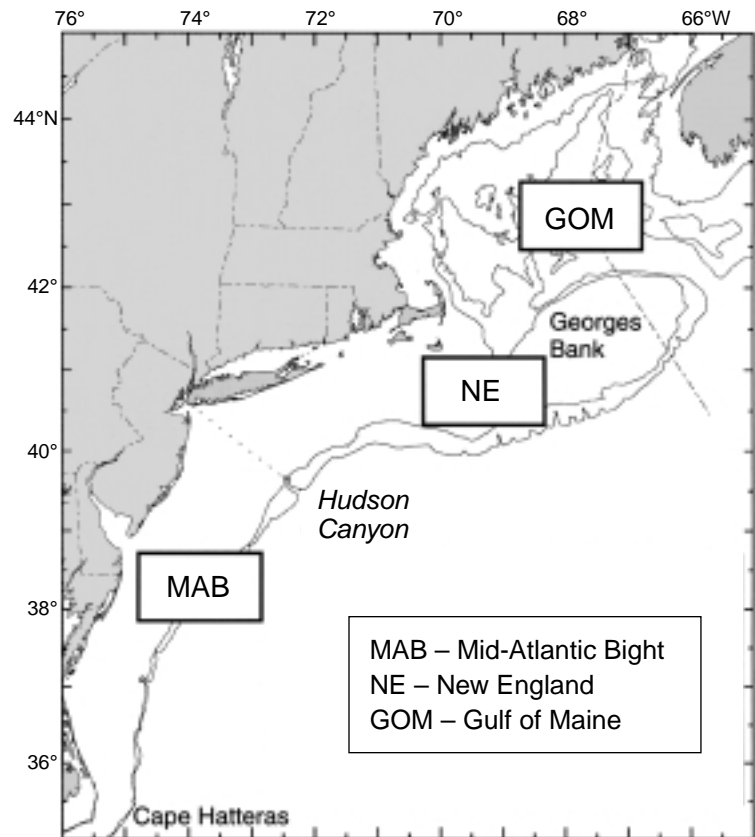


Figure 1

Map of the survey areas for longfin inshore squid off the northeastern coast of the United States (1967–98).

the autumn and spring surveys the same trawl-sampling gear (Yankee-36 trawl) has been used since 1967, except during 1973–81, when a Yankee-41 (high rising) trawl was substituted in the spring surveys. In the winter surveys the trawl gear was larger and the Gulf of Maine was not sampled.

The NEFSC survey area was divided into two geographic regions (the region north of Hudson Canyon to the Gulf of Maine [designated New England, NE] and the region south of Hudson Canyon to Cape Hatteras (designated Mid-Atlantic Bight [MAB]) and into four bottom depth zones (27–55 m, 56–110 m, 111–185 m, and 186–366 m [Fig. 1]). The 1–26 m depth zone was not sampled in NEFSC offshore surveys, but "inshore" strata were added to the survey in 1972.

For the spring and winter surveys, the combined effects of annual abundance (numbers of squid per standardized trawl haul), survey stratum, and time of day (night, 20:00–03:59; dawn and dusk, 04:00–07:59, 16:00–19:59; and day, 08:00–15:59), as described by Brodziak and Hendrickson (1999) for the autumn survey, were analyzed to determine adjustment factors for diel differences in log-transformed survey catches of prerecruit squid (≤ 80 mm dorsal mantle length [ML], the minimum size in commercial catches) and recruits (> 80 mm ML). The derived factors were then used to adjust all survey catches to

their daytime equivalent. The size groups (≤ 80 mm ML, > 80 mm ML) were chosen to allow comparisons with results from previous studies (e.g. Lange, 1980; 1981; Lange and Sissenwine, 1983; Brodziak and Hendrickson, 1999; NEFC¹; Lange and Sissenwine²; Lange³). Alternative analyses were performed for different size groups (≤ 50 mm ML, > 50 mm ML and ≤ 100 mm ML, > 100 mm ML) to assess the sensitivity of the results to the choice of size groups. The combined effects of geographic region (NE and MAB), depth zone, and year on survey catches were tested by using generalized linear models (GLM) to derive main effects and coefficients for each survey. Pairwise comparisons were tested by using a *t*-test with Bonferroni adjustments (Sokal and Rohlf, 1995) to compare specific regions, seasons, and depth zones. All tests were analyzed at the 5% significance level. Differences between seasons and regions were tested between autumn and spring surveys for the years 1968 to 1997, between autumn and winter for 1992 to 1997, and between spring and winter surveys from 1992 to 1998. Proportion of catches ≤ 50 mm ML were analyzed to evaluate the relative distribution of juvenile *L. pealeii*.

Biological analysis

Subsamples of 50–100 individuals were obtained from five different survey time series: NEFSC autumn (September–October 1997), winter (February 1998), and spring (March 1998), inshore Massachusetts (Howe⁶) (October 1997), and Connecticut (Johnson⁷) (Long Island Sound, May 1998). The samples were analyzed from each of five depth zones (1–26 m, 27–55 m, 56–100 m, 111–185 m, 186–366 m), within each of three geographic regions (Gulf of Maine [GOM]; Georges Bank–Southern New England, north of Hudson Canyon [SNE]; and Mid-Atlantic Bight, see above [MAB]). A fourth region, south of Cape Hatteras (SOH) was added later. Each sample comprised a nonrandom selection of lengths to represent the size range present in a tow. In total, 2156 individuals were subsampled from 53 survey tows. Sexes were determined and specimens were measured to enable the morphometric maturity analyses of Macy (1982); each individual squid was also weighed on a top-loading balance to 0.1 g. The morphometric method uses a suite of length measurements for female and male squid to determine maturity stage (measured on a scale of 1 to 4, where 1 is immature and 4 is fully mature). Opportunistic commercial samples from early winter (December 1998 and January 1999) were also analyzed (118 individuals) to bridge the temporal gap in survey coverage.

Data on dorsal mantle length (ML, mm) and total body mass (BM, g) for each maturity stage were used to estimate proportions for each maturity stage across the length

and weight range. These proportions were used to determine the sizes at which squid of both sexes changed from one maturity stage to the next.

Maturity-at-length data were weighted by diurnally adjusted catch-at-length data for each depth zone and region to provide population-weighted maturity patterns, assuming that survey length distributions accurately represent relative proportions of population components. Catch-weighted data were analyzed to derive 1) the patterns of maturity for each sex at different times of the year; 2) estimates of proportions of each maturity stage sampled by survey; 3) mean length for each maturity stage of each survey; 4) mean length for each region of each survey; and 5) mean length for each depth stratum of each survey. A small proportion (8.4%) of survey catches ≤ 50 mm ML were not subsampled; these were assigned to the juvenile stage. Catches at larger sizes, which were not subsampled (6.8% of survey catches), were removed from the analysis because sex or maturity stage could not be assigned with any degree of certainty. Individual squid, or size classes of squid, were not weighed during NEFSC surveys; therefore the maturity data from the biological analysis could only be catch-weighted by length because length was measured on a random subsample of squid caught at each station in NEFSC surveys.

Results

Survey analysis

Patterns of diurnal distribution were different among seasons surveyed (Table 1). In winter surveys, from 1992 to 1998, prerecruit (i.e. ≤ 80 mm ML) catch was lower at night and during dawn and dusk than during daylight hours (65% and 81% of daytime catch, respectively). However, for recruits (i.e. > 80 mm ML), catch was higher both at night and at dawn and dusk than during the day (131% and 115% of daytime catch respectively) in winter surveys. In autumn and spring surveys, from 1968 to 1998, both prerecruits and recruits showed a lower catch at night and during dawn and dusk than by day; recruits showed a lesser diurnal variation than prerecruits. Results from analyses with different size groups (≤ 50 mm ML, > 50 mm ML and ≤ 100 mm ML, > 100 mm ML) were very similar, suggesting that the interaction of size and time of day is gradual.

Catch rates varied significantly by season (Table 2). During winter and spring, survey catches were greater in the MAB by a factor of approximately four (Fig. 2). However, there was no significant difference in survey catches between geographic regions in autumn (Fig. 2). Pairwise comparisons showed that mean number-per-tow was significantly greater in autumn than in spring within both geographic regions and was greater in autumn than in winter in the NE. There were no significant differences between autumn and winter means in the MAB nor between spring and winter means in either the MAB or the NE.

Catch by depth, pooled over the MAB and NE, varied by season (Table 3). Pairwise comparisons of each depth for each season showed that winter and spring survey catches were lowest in the shallowest stratum (27–55 m), in-

⁶ Howe, A. B. 1989. State of Massachusetts inshore bottom trawl survey. Atlantic States Marine Fisheries Commission (ASMFC) Spec. Rep. 17:33–38. [Available from ASMFC, 1444 Eye Street, N.W., sixth floor, Washington, DC 20005.]

⁷ Johnson, M. 1994. State of Connecticut marine finfish trawl survey. Atlantic States Marine Fisheries Commission (ASMFC) Spec Rep. 35:24–26. [Available from ASMFC, 1444 Eye Street, N.W., sixth floor, Washington, DC 20005.]

Table 1

Relative catch rates for small (≤ 80 mm dorsal mantle length (ML)) and large (> 80 mm ML) *Loligo pealeii* in three seasonal NEFSC bottom-trawl surveys, 1967–98, by time of day (in relation to catch rates during daytime).

Time of day	Winter		Spring		Autumn	
	≤ 80 mm	> 80 mm	≤ 80 mm	> 80 mm	≤ 80 mm	> 80 mm
Night	0.65	1.30	0.51	0.72	0.09	0.34
Dawn and dusk	0.81	1.14	0.79	0.92	0.46	0.83
Day	1.00	1.00	1.00	1.00	1.00	1.00

Table 2

Results of generalized linear model (GLM) of survey mean numbers-per-tow by year, depth zone, and geographic region (df=degrees of freedom; SS=sum of squares; F = F -statistic; P =probability), for *Loligo pealeii* off the northeast United States, based on NEFSC bottom-trawl survey data, 1967–98.

Season and effect	df	Type III SS	Mean square	F	P
Winter					
year	6	42.51	7.09	2.71	0.0133
depth	3	339.62	113.21	43.36	0.0001
region	1	233.73	233.73	89.53	0.0001
Spring					
year	30	409.47	13.64	4.44	0.0001
depth	3	1696.53	565.51	183.79	0.0001
region	1	983.51	983.51	319.64	0.0001
Autumn					
year	30	557.85	18.59	5.17	0.0001
depth	3	1134.09	378.03	105.20	0.0001
region	1	9.12	9.12	2.54	0.1113

Table 3

Diurnally adjusted, mean numbers-per-tow of *Loligo pealeii* from the three annual NEFSC bottom-trawl surveys, 1967–98, by season.

	Depth zone (m)			
	27–55	56–110	111–185	186–366
Winter	42.9	103.1	215.5	30.3
Spring	42.6	90.7	342.5	91.9
Autumn	853.3	352.8	377.2	66.5

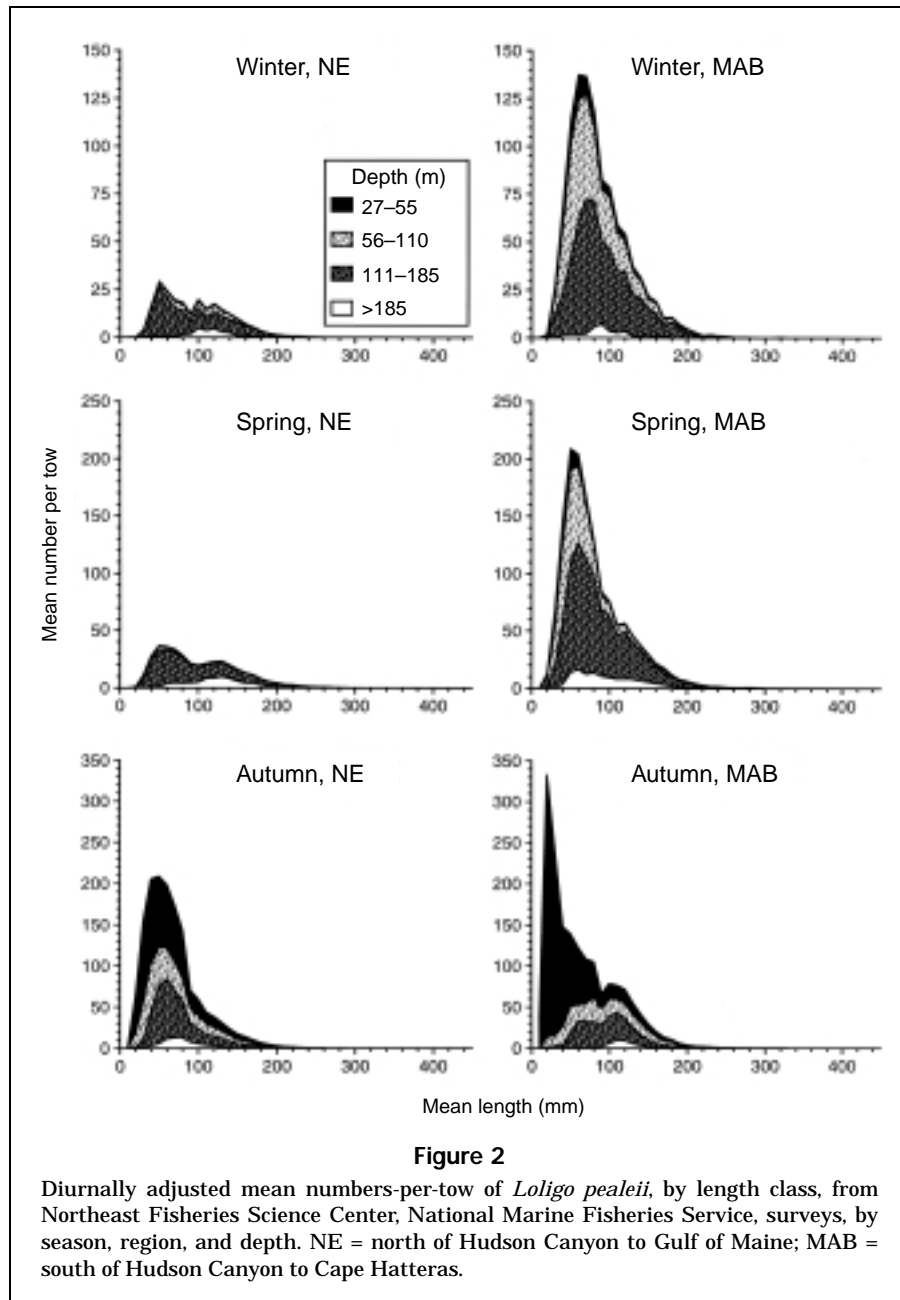
creased to peak values in deeper strata (111–185 m, greater than 10 times the catches in the shallowest strata), and were low in the deepest stratum (> 185 m). Conversely, autumn survey catches were highest in the shallowest stratum (27–55 m) and lowest in the deepest stratum (> 185 m). These patterns were also generally significant within both geographic regions (Table 4).

Table 4

Diurnally adjusted, mean numbers-per-tow of *Loligo pealeii* from the three annual NEFSC bottom-trawl surveys, 1967–98, by area (NE=north of Hudson Canyon to the Gulf of Maine; MAB=south of Hudson Canyon to Cape Hatteras).

	Depth zone (m)			
	27–55	56–110	111–185	186–366
Winter NE	6.0	38.9	160.4	28.7
Winter MAB	83.5	396.2	510.7	36.0
Spring NE	2.3	24.7	259.5	81.4
Spring MAB	86.8	392.3	787.3	129.7
Autumn NE	644.2	365.9	392.8	72.4
Autumn MAB	1082.5	293.1	293.7	45.5

In the pairwise comparisons of the winter and spring surveys, catches were significantly greater at 111–185 m than in other depth zones. In the 27–55 m depth zone, au-



tumn catches were considerably higher than in winter or spring. For all other depth zones and survey comparisons, the differences were not significant.

In the autumn survey, the proportion of small squid (≤ 50 mm ML) was highest at 27–55 m depths (over 50% of the sampled squid in that depth zone in the NE and almost 75% of the squid in that depth zone in the MAB, Table 5). Proportions of small squid at greater depths were considerably lower. These patterns show higher relative recruitment into the population in the shallow waters of the continental shelf in the autumn.

Similarly in the MAB during winter and spring, small squid form a higher proportion of squid sampled in the two

shallowest depth zones than at greater depths. A higher percentage of small squid was present in spring than in winter, with over 60% of squid sampled in the MAB from 27–55 m being ≤ 50 mm ML. However, the highest proportion of small squid in the NE during winter and spring was at intermediate depths.

Biological analysis

The raw data of numbers sampled for each sex, length, and maturity stage are given in Table 6. For all seasons combined, the ML at 50% maturity during 1997–98 was approximately 200 mm ML for females and males (Table 7,

Table 5

The percentage of *Loligo pealeii* <50 mm ML in each depth zone, for each region and survey, and for the number of years for which these data were available (NE=north of Hudson Canyon to the Gulf of Maine; MAB=south of Hudson Canyon to Cape Hatteras).

Depth zone (m)	Winter		Spring		Autumn		Winter		Spring		Autumn	
	NE	(No. of years)	NE	(No. of years)	NE	(No. of years)	MAB	(No. of years)	MAB	(No. of years)	MAB	(No. of years)
27-55	3	6	17	20	51	31	33	7	64	30	73	31
56-110	11	7	40	31	19	31	27	7	48	31	27	31
111-185	27	7	24	31	31	31	14	7	22	31	9	31
186-366	7	3	2	31	14	30	10	3	14	31	2	31

Table 6

Numbers of *Loligo pealeii* measured, for each sex and maturity stage, from samples taken for biological analysis in 1997-99. Maturity was based on a four-stage scale for sexual maturity for each sex where 1 was immature and 4 was fully mature. ML = mantle length.

ML (mm)	Females					Males				
	Stage 1	Stage 2	Stage 3	Stage 4	Total ♀	Stage 1	Stage 2	Stage 3	Stage 4	Total ♂
30	1				1					
40	5				5	2				2
50	31	1			32	18				18
60	59	3	1		63	30	5		1	36
70	73	17	1		91	32	22	2	1	57
80	57	30	1	1	89	27	37	12	1	77
90	51	45	5		101	10	45	16	4	75
100	27	51	2	3	83	2	50	17	2	71
110	10	62	5	6	83	2	35	30	8	75
120	8	86	14	4	112	1	32	40	4	77
130	3	79	6	4	92		24	37	11	72
140	3	71	10	8	92		14	39	10	63
150	2	38	16	14	70		14	43	10	67
160		25	6	7	38		14	28	8	50
170		13	2	7	22		12	31	7	50
180		7	2	3	12		6	18	7	31
190		9	1	2	12		3	19	9	31
200		1		5	6			5	9	14
210		1	1	1	3		1	2	8	11
220			1	3	4		1	4	7	12
230							1		5	6
240							1	1	5	7
250							1	1	3	5
260									1	1
270				1	1				3	3
280									1	1
290									1	1
Total	330	539	74	69	1012	124	318	345	126	913

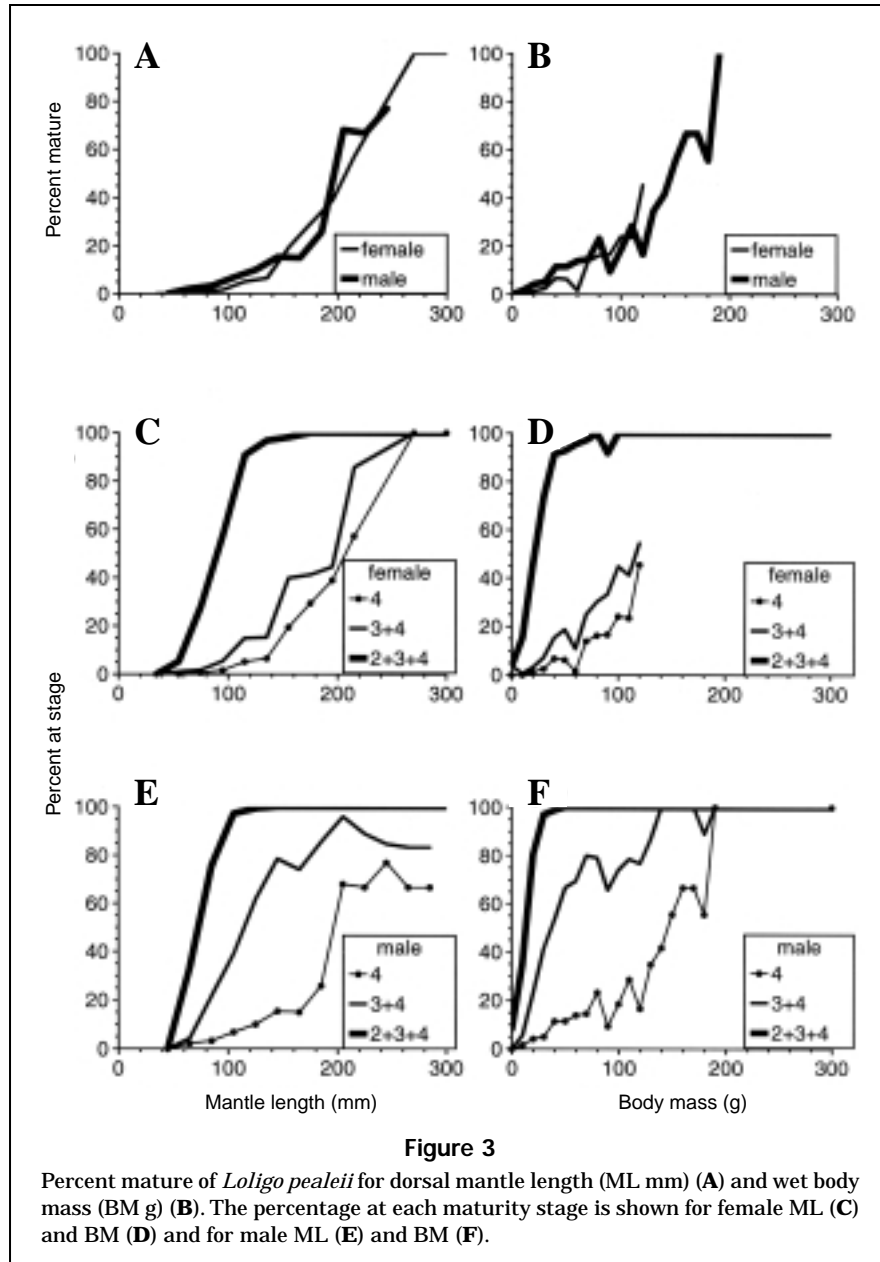


Table 7

Size at maturity for *Loligo pealeii* in mantle length (ML, mm) and body mass (BM, g), by sex. (— denotes a missing value).

Proportion mature	Female		Male	
	ML	BM	ML	BM
25%	166	111	184	113
50%	207	—	196	146
75%	238	—	241	184

Fig. 3, A and B). In terms of body mass, the size at 50% maturity for males was approximately 150 g, but, according to our samples, female maturity did not seem to be as closely associated with body mass (e.g. even squid in the heaviest size class were less than 50% mature).

In females, maturity stage 2 was reached at a relatively small size (Fig. 3, C and D). To reach stage 3 requires a considerable increase in length or body mass, whereas females in stage 4 are neither much longer, nor heavier than stage-3 females. Thus the transition from stage 3 to stage 4 (full maturity) takes place over a lesser period of somatic growth (and therefore possibly a shorter time period) than the transition from stage 2 to stage 3. In Macy's (1982) maturity stage notation, stage-3 females have no mature

Table 8

Diurnally adjusted, catch-weighted mean numbers-per-tow of *Loligo pealeii* sampled in each maturity stage. Maturity stages correspond to unsexed juveniles and a four-stage scale for sexual maturity for each sex where 1 was immature and 4 was fully mature (SOH: south of Cape Hatteras).

	Female					Male				Totals
	Juvenile	Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3	Stage 4	
Autumn	240.0	94.0	16.0	0.0	2.0	64.0	49.0	4.0	3.0	472.0
Winter	5.0	13.9	10.9	0.4	0.2	4.8	6.1	6.2	1.1	48.6
Spring plus SOH	26.3	12.7	10.0	2.3	1.4	5.4	5.0	5.0	2.4	70.5
Long Island Sound	436.0	0.0	52.0	378.0	176.0	161.0	0.0	196.0	144.0	1543.0
Commercial	0.0	5.0	155.0	0.0	0.0	8.0	198.0	331.0	15.0	712.0
Totals	707.3	125.6	243.9	380.7	179.6	243.2	258.1	542.2	165.5	2846.1

Table 9

Maturity patterns in *Loligo pealeii* (percentage of sample at each sex and stage derived from diurnally adjusted, catch-weighted mean numbers-per-tow. Maturity stages correspond to unsexed juveniles and a four stage scale for sexual maturity for each sex where 1 was immature and 4 was fully mature (SOH: south of Cape Hatteras).

	Female					Male			
	% juvenile	% stage 1	% stage 2	% stage 3	% stage 4	% stage 1	% stage 2	% stage 3	% stage 4
Autumn	50.7	20.0	3.4	0	0.5	13.6	10.3	0.9	0.6
Winter	10.3	28.7	22.4	0.7	0.4	9.8	12.5	12.7	2.2
Spring plus SOH	37.3	18.0	14.2	3.2	1.9	7.7	7.0	7.1	3.5
Long Island Sound	28.3	0	3.4	24.5	11.4	10.4	0	12.7	9.3
Commercial	0	0.7	21.8	0	0	1.1	27.8	46.5	2.1

oocytes (therefore they would not be considered to be close to maturity) and stage-4 females are fully mature.

In comparison, the transition of male squid (Fig. 3, E–F) from stage 2, to stage 3, to stage 4, seems more evenly spaced, with a more gradual development seen over the course of the maturation process. If anything, there seems to be a greater transition from stage 3 to stage 4, than from stage 2 to stage 3. The difference between stage-2 and stage-3 males is measured only as elongation of the testis in conjunction with a reduction in the ratio of mantle circumference to mantle length. In stage-4 males “elongate mature spermatophores are visible both in the Needham’s sac and the penis.” In subjective terms, stage 2 represents definitely immature, stage 3, maturing, and stage 4, fully mature males. Thus the rate at which full maturity is approached is very different between the sexes.

The raw data (numbers sampled in each size class, sex, and maturity stage) were then catch-weighted to be representative of the squid sampled in the different surveys and from commercial data. Catch-weighted proportions of female and male *L. pealeii* at each maturity stage are shown in Tables 8 and 9. In the autumn and spring surveys, and in the May Long Island Sound (LIS) samples, juvenile squid

were the most abundant stage within the sampled population. In winter surveys the juveniles were one of the least abundant stages. Mature squid were never abundant in the NEFSC survey subsamples, nor in the inshore autumn (October) Massachusetts survey (combined with NEFSC data for autumn surveys). Most mature squid were seen in the LIS samples. In NEFSC surveys, the majority of both sexes were immature and stages 1 and 2. In LIS samples more squid were either stage 3 or 4 than immature. No mature females were observed in the commercial samples, although a small proportion of males were mature.

The catch-weighted mean ML for each maturity stage, by season, is given in Table 10. There was little difference between the size of juvenile squid between seasons. For both sexes, squid at stages 1, 2, and 3 were all longest in the autumn samples and shortest in the spring and LIS samples. Conversely, mature squid of both sexes (stage 4) were considerably larger in the spring than in autumn. In the LIS samples, mature female squid were the same size as in spring survey samples; mature male squid, on the other hand, were smaller than in the spring survey but larger than the autumn survey samples. Commercial samples showed a larger size for each maturity stage sampled.

Table 10

Mean dorsal mantle length (ML, mm) of *Loligo pealeii* for each sex and maturity stage (corresponding to unsexed juveniles and a four stage scale for sexual maturity for each sex where 1 was immature and 4 was fully mature), from diurnally adjusted, catch-weighted mean numbers-per-tow data (SOH: south of Cape Hatteras).

	Female					Male			
	Juvenile	Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3	Stage 4
Autumn	34	77	133		115	70	105	161	94
Winter	41	71	122	166	164	54	93	131	169
Spring plus SOH	37	58	90	122	139	61	83	114	143
Long Island Sound	47		90	79	138	70		83	109
Commercial		83	160			79	150	169	180

Table 11

Mean dorsal mantle length (ML, mm) and percentage of each sex for each sample of *Loligo pealeii* by depth stratum per survey. Derived from diurnally adjusted, catch-weighted tow data.

	Depth zone		Depth zone		Depth zone		Depth zone		Depth zone	
	<27 m	%	27–55 m	%	56–110 m	%	111–185 m	%	186–366 m	%
Autumn juvenile ML	32	73	29	72	47	58	48	5		0
Autumn female ML	67	13	87	13	95	25	92	21	123	68
Autumn male ML	67	14	105	15	111	17	80	74	118	27
Winter juvenile ML			42	10	39	4	39	5	46	5
Winter female ML			100	68	84	63	97	47	111	47
Winter male ML			105	22	93	33	97	48	131	48
Spring juvenile ML	35	42	43	3	37	54	40	3	43	1
Spring female ML	60	32	113	61	78	26	100	47	123	48
Spring male ML	59	25	129	36	90	18	104	49	136	51
Long Island Sound juvenile ML	47	28								
Long Island Sound female ML	97	39								
Long Island Sound male ML	86	33								
Commercial female ML							158	23		
Commercial male ML							161	78		

The distribution of the catch-weighted mean ML, by sex, by depth zone, for each season separately is shown in Table 11. For juvenile *L. pealeii*, in autumn, at 1–55 m depth, there was little difference in size at depth. In the 56–110 m depth zone, juveniles in autumn were considerably larger than at shallower depths. In winter, there was evidence for a slight increase in the size of juveniles with increasing depth. In spring survey samples, juveniles were similar in size across the depth range sampled.

Female and male *L. pealeii* were generally smaller in the shallowest depth zone (1–26 m, only sampled in autumn and spring surveys), and much larger at depths greater than 185 m, for each survey. There was no clear pattern for intermediate depths. In autumn surveys, squid were generally smaller at 27–55 m depth than in deeper

water. In winter and spring, however, squid at this depth were longer than at 56–185 m. The LIS samples showed larger mean sizes for each group at <27 m depth than in autumn and spring samples.

In the autumn survey, squid of all maturity stages (except juveniles) were generally largest in the south (MAB) and smallest in the north (SNE and GOM, Table 12). Some of this distribution may have been an artifact of the sampling design because no squid were sampled in the MAB region in the 1–26 m depth zone, whereas this zone was sampled in the SNE, and was the only zone for which data were available for the GOM region.

In the winter survey, the general pattern was the reverse of that seen in the autumn. In this survey squid were generally smaller in the south (MAB) than in the

Table 12

Mean dorsal mantle length (ML, mm) by sex and maturity stage (corresponding to unsexed juveniles and a four-stage scale for sexual maturity for each sex, where 1 was immature and 4 was fully mature) of *Loligo pealeii* by region per survey. Derived from diurnally adjusted, catch-weighted mean numbers-per-tow data. MAB = Mid-Atlantic Bight; SNE = Georges Bank–Southern New England, north of Hudson Canyon; GOM = Gulf of Mexico; SOH = South of Cape Hatteras.

	Female					Male			
	Juvenile	Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3	Stage 4
Autumn MAB	23	98	132		162	69	120	172	170
Autumn SNE	38	71	130		85	69	102	147	96
Autumn GOM	33	68				65	69		71
Winter MAB	42	67	116	186	180	59	94	128	151
Winter SNE	50	80	127	148	159	52	94	134	171
Spring MAB	37	62	93	127	154	66	82	110	150
Spring SNE	41	51	95	132	151	54	88	125	183
Spring SOH		56	70	77	137	54	81	98	162
Long Island SNE	47		90	79	138	70		83	109
Commercial SNE		83	160			79	150	169	180

north (SNE only, no GOM samples were taken in the winter survey). The exception in winter were the few stage-3 and stage-4 females sampled.

In the spring survey, the same pattern as in the winter survey was observed; squid in the south were smaller than in the north. In the spring survey, samples available from south of Cape Hatteras (the limit of the MAB samples) followed the same trend because the observed mean sizes were smaller than the MAB samples. The exception to this were maturity-stage-1 squid.

Discussion

Survey analysis

The high proportion of small squid (≤ 50 mm ML) in the winter and spring surveys corroborated the occurrence of an early winter hatching event, documented from age data determined by squid statolith analysis (Brodziak and Macy, 1996; Macy⁵).

Mean numbers-per-tow of juvenile squid in the MAB were considerably higher than in the NE in all seasons surveyed. Recruitment of squid into the population was highest in autumn, but juvenile squid were distributed more widely over the continental shelf in the spring. Perhaps the MAB component of the *L. pealeii* stock was larger because it is more stable—a result of the higher proportion of squid recruited into the area each winter, spring, and autumn.

Murawski (1993) inferred a centering of the population in the MAB subject to the issue that portions of the stock are outside the area of the NEFSC surveys. Our data suggested that the area south of Cape Hatteras may play an important role in reproductive dynamics and recruitment to the population, suggesting that a considerable portion

of the stock is south of the surveyed area, particularly during winter and spring. South of Cape Hatteras a second loliginid species, *L. plei*, is abundant (Roper et al., 1984). In our study, all *Loligo* specimens were examined carefully to ensure that only *L. pealeii* were measured and included in the biological analyses.

Diel differences in catches of *L. pealeii* have been observed in a number of studies (Summers, 1969; Serchuk and Rathjen, 1974; Roper and Young, 1975; Sissenwine and Bowman, 1978; Lange and Sissenwine, 1983; Lange and Waring, 1992), where catches were consistently higher in daytime than at night. To account for diel effects on minimum swept-area estimates of *L. pealeii* biomass and stock size, nighttime catches were adjusted to daytime equivalents by using the diel correction factors of Lange and Sissenwine (1983). However, these correction factors were not size specific. Brodziak and Hendrickson (1999) applied size-specific diel correction factors to squid from the autumn survey (1967–94), splitting the data into pre-recruits (≤ 80 mm ML) and recruits (> 80 mm ML). In the autumn surveys the nighttime catch of prerecruits was only 8.7% of the daytime catch. The nighttime catch of recruits was 34% of the daytime catch. These differences were attributed to the different feeding behavior of juvenile and adult squid, in that juvenile squid might need to undertake more vertical migrations at night to meet their higher metabolic requirements. In our present study, pre-recruit nighttime catch differed to a lesser degree from the daytime catch in the winter and spring (65% in the winter surveys, and 51% in the spring surveys) than in the autumn. In the winter surveys, nighttime catches of recruits exceeded daytime catches by 31%. In spring, nighttime tows showed a lower catch of recruits, 72% of daytime values, than in winter. Patterns of diel differences reported in another study by Lange and Waring (1992) for spring catches were similar to those in our study. Their

reported autumn catches (Lange and Waring, 1992) were higher at night than in our study, but still lower than daytime catches.

The behavior of squid at both prerecruit and recruit sizes therefore appears to be different in the winter and spring than in the autumn. The prerecruit nighttime catch in winter and spring was half, or more than half of daytime catches, as opposed to 9% in autumn. For recruits, there was an even greater difference among seasons. In winter, almost 1.5 times as many squid were caught at night, than by day. In spring the nighttime catch was 72% of the daytime catch, twice the proportion of the autumn catch. Vovk (1978; 1985) and Maurer and Bowman (1985) have documented large changes in the diet of squid in different seasons, relating these changes in feeding activity and dietary preference to changes in the size composition of the squid population, movements of squid in search of food concentrations, seasonal abundance of prey, and environmental conditions that affect both prey and predator. Vovk (1985) noted that in autumn *L. pealeii* are daytime predators and do not feed extensively at night when they occur at shallow depths. In autumn, squid are more abundant near the seafloor by day (Brodziak and Hendrickson, 1999). Vovk (1985) also noted that feeding activity was generally low from December to April and related this to possible prey abundance. Perhaps the different diel behavior patterns of *L. pealeii* in winter and spring, when they appear to be more available to capture by bottom-trawls, are related to a lower prey abundance and a requirement for more time to be spent searching for prey. Some of these differences might be temperature related as well. In the autumn, with strong vertical stratification of the water column, there may be some physiological benefit for squid to move off the bottom at night into warmer waters. In winter and spring when there is no vertical stratification, no advantage is conferred by a strong diel migration as seen in the autumn.

Comparisons in performance and catchability of the two trawl nets used in the spring and autumn surveys (Yankee 36 and Yankee 41) have been conducted (Sissenwine and Bowman, 1978), but any differences in catchability were confounded by diel and vessel differences. In our study, we corrected for diel differences, and vessel differences were not found to be significant (NEFSC⁸).

Squid catches are more abundant in the autumn surveys than in winter and spring (Serchuk and Rathjen, 1974; Lange and Waring, 1992; Lange and Sissenwine²). This difference may be related to the recruitment of large numbers of small squid, present in shallow water, in autumn. Temperature, however, is a major factor limiting distribution. In winter and spring much of the continental shelf water is below the preferred temperature minimum for the species (ca. 8°C) (Summers, 1969; Serchuk and Rathjen, 1974; Murawski, 1993); therefore squid are apparently less abundant than in the autumn surveys when

temperature is not a limiting factor. The greatest differences between autumn and spring or winter surveys are most apparent in the NE, where a large portion of the stock may be outside the surveyed area owing to temperature limits (e.g. off the shelf or south of Cape Hatteras). In the MAB there are few differences in catches between spring and autumn at depths deeper than 27–55 m. Spring numbers are higher than autumn numbers from 111 to 185 m. The patterns between autumn and winter catches are similar to each other at that depth. Catches are always lower in winter than in autumn, but the differences are only significant from 27–110 m depth.

In winter and spring surveys, catches were highest from 111 to 185 m, both in the NE and the MAB. Catches were higher, in both surveys, in the MAB than in the NE. These patterns also were observed for *L. pealeii* in survey analyses from 1967 to 1971 (Summers, 1969; Serchuk and Rathjen, 1974), from 1970 to 1977 (Lange, 1980), and from 1975 to 1986 (Lange and Waring, 1992). This finding may imply that geographic distribution is relatively stable for *L. pealeii*, during February and March, at least within the areas surveyed. In autumn surveys, Serchuk and Rathjen (1974), Lange (1980), and Lange and Waring (1992) also reported highest catches in the MAB. However, Serchuk and Rathjen (1974) showed a relatively higher abundance of squid taken from 56–110 m depth than that observed in our study, where mean numbers per tow in the depth zone 27–55 m were greater than three times higher than those in the zones 56–110 m and 111–185 m. The difference between the 27–55 m zone and deeper strata was less noticeable in the NE, although mean numbers-per-tow were almost twice as high in the 27–55 m zone. The differences may result from diurnal adjustments, or from the inclusion of more years of data in the survey database. Lange (1980) found mean numbers-per-tow in the NE autumn to be highest from 111 to 185 m depths.

Biological analysis

We found that squid mature at greater lengths than previously reported for *L. pealeii* (NEFSC⁸). Figure 3 (C–F) shows that using stage 3 or greater to indicate maturity may be an adequate proxy for females. For example, the size at which 50% of females are mature is 198 mm with stages 3 and 4, and 207 mm with only stage 4 (Fig. 3C). Such a proxy may be valuable for samples with few observations of stage-4 females (e.g. the body mass at 50% maturity is 120 g with stages 3 and 4 [Fig. 3D]).

For males, however, the size difference between stage 3 and stage 4 is considerable, and substantial somatic growth is required to develop from stage 3 to stage 4. Combining the two maturity stages in males is therefore unsupported biologically, and the combined data would underestimate size at 50% maturity.

That mature squid are largest in winter and smallest in autumn samples (and intermediate in size in the early [NEFSC] and late [LIS] spring) has been noted previously (Summers, 1971; Lange, 1980; Macy, 1980). Prior to the availability of age data for the species, the size differences at maturity were ascribed to different year class-

⁸ NEFSC (Northeast Fisheries Science Center). 1996. Report of the 21st Northeast Regional Stock Assessment Workshop (SAW 21). Center Reference Document 90-05, 200 p. [Available from NEFSC, 166 Water St., Woods Hole, MA 02543.]

es (Summers, 1971; Lange, 1980; Macy 1980). The observation that immature squid are larger in autumn than in winter and spring was documented by Lange (1980) but not interpreted. Some of this variability might be explained as a function of temperature. If *L. pealeii* have a life-span of 9–12 months (Brodziak and Macy, 1996), then females that are mature in September–October samples would have hatched between November and January. Females that are mature in March would have hatched around May or June. Brodziak and Macy (1996) showed that squid hatched between November and April had a lower growth rate than those that hatched between May and October. Recent laboratory studies on small *L. pealeii* have indicated that squid grow significantly faster at higher temperatures (Hatfield et al., 2001), in accord with results described for other cephalopod species (*Octopus bimaculoides*—Forsythe and Hanlon, 1988; *L. forbesi*—Forsythe and Hanlon, 1989; *Sepia officinalis*—Forsythe et al., 1994). These laboratory studies also found that the effect of temperature on growth is most pronounced during the early life cycle of these cephalopods, nominally the first three months. If temperatures experienced by *L. pealeii* hatching in May and June are warmer than temperatures experienced by squid hatching from November to January, then the growth potential will be lower for winter-hatching squid (seen as mature squid in autumn surveys), resulting in the observed lower size at maturity in autumn versus winter and spring. The same phenomenon would explain the size differences of immature squid among seasons. The large immature squid caught in the autumn survey are probably the same squid that become the large, mature squid in the winter, spring, and LIS samples. The small immature squid in the spring are probably those squid which become the small mature squid seen in autumn survey samples. If the winter-hatching squid are from southern spawning events, then the temperature difference between winter-spawned and summer-spawned squid may not be very large. However, age data for *L. pealeii* show that growth rates are generally slower for winter hatched squid. Also, growth studies on *L. forbesi* have shown that a temperature difference of just 1°C can change growth rates of squid by 2% body weight/day and produce a threefold difference in weight at 90 days after hatching (Forsythe and Hanlon, 1989).

The high numbers of juvenile squid in the autumn survey were from protracted spawning in inshore waters some 4–5 months previously (documented since Verrill [1882] first reported inshore spawning). The high proportion in spring therefore reflects a period of spawning, possibly also some 4–5 months earlier, around September or October of the previous year. Juvenile squid in winter and spring survey samples denote the presence of a hatching component other than the main inshore autumn component. The high proportion observed in LIS (May) samples probably reflects an extended winter–spring spawning period because squid of the size found in Long Island Sound in May could not have been the result of that season's inshore spawning. The inshore spawning season does not usually begin until late April and incubation time may require up to 4 weeks at the temperatures at that time

of year (27 days at 12°C, McMahon and Summers, 1971). Brodziak and Macy (1996) showed a pattern of year-round hatching, which is consistent with the patterns suggested by our data.

Summers (1969), Serchuk and Rathjen (1974), and Brodziak and Hendrickson (1999) all reported an increase in size of *L. pealeii* with increasing depth. We found the smallest squid in the shallowest water and the largest squid in the deepest water, confirming that nearshore waters of the continental shelf are a preferred habitat for juvenile *L. pealeii* during the autumn (as described by Brodziak and Hendrickson [1999]). The pattern of ontogenetic descent exhibited by other loliginid species (*L. vulgaris*—Worms, 1983; *L. gahi*—Hatfield et al., 1990; *L. vulgaris reynaudii*—Augustyn et al., 1992) is consistent in *L. pealeii*, but less marked at intermediate depths.

In winter and spring, mean length is generally higher in the NE and lower in the MAB. In autumn, mean length is generally lower in the NE and higher in the MAB. Lange (1980) showed a similar pattern for immature females from the autumn survey. Males, however, showed the opposite pattern. Lange's (1980) winter and spring survey data showed the same pattern as our study for immature females and all males, except the fully mature squid.

Commercial samples from early winter (December and January) contained no mature female squid that might produce the winter hatching component evident from age data and aggregated survey length-frequency distributions. Egg masses are only found consistently in one small offshore area (off Chesapeake Bay) by commercial fishermen in the early winter (see Fig. 4). However, the commercial samples were from the southern edge of Georges Bank, and the survey data suggest that the winter recruitment originates from the southern part of the MAB. The scarcity of mature squid in NEFSC survey samples suggests that sampling did not occur consistently in the right areas or seasons to identify major spawning peaks. Whitaker (1978) documented that about 40% of males were fully mature in January and February in the region south of Cape Hatteras, off the coast of South Carolina. There was a large proportion of mature squid in samples from March and April, with 74% of females and 56% of males fully mature. There is evidence for both spawning and hatching in the SNE from March to April; as in 1999, egg masses were caught incidentally from northeast of Hudson Canyon and up towards the southern flank of Georges Bank, at depths of about 200 m, from mid-March to late April (Stommell⁹). In the 1998 Massachusetts spring survey, in mid-May, a high abundance of small squid, about 30 mm ML, were caught south of Martha's Vineyard, at depths of <27 m (senior author, personal obs.). These observations suggest that spawning is probably protracted, from early to late winter, and early winter spawning is more dominant in the southern end of the U.S. continental shelf. Thus, the available fishery-dependent samples may not be indicative of the population. The information on age and maturity in Brodziak and Macy (1996) was derived from

⁹ Stommell, M. 1999. Personal. commun. FV Nobska, Woods Hole, MA 02543.

data collected from the winter fishery, most of which occurs north of the MAB region. A more structured design is required to address some of these issues. The entire size and maturity stage range needs to be sampled across the geographic range of each survey and these data should be augmented with opportunistic sampling outside the area or time frame in which the surveys are carried out.

In summary, results from these two studies complement each other to reveal patterns of reproductive dynamics for *L. pealeii* that have been suggested previously in other studies but that have never thoroughly been investigated. The high frequency of small squid present in spring survey catches indicates that winter spawning is indeed an important component of reproduction for the population, and biological analyses suggest that this winter spawning occurs primarily south of Cape Hatteras, rather than in the vicinity of the offshore submarine canyons along the edge of the northeastern U.S. continental shelf, from Hudson Canyon up to Georges Bank.

Acknowledgments

We would like to extend our thanks to John Galbraith of NEFSC, Arnie Howe of the Massachusetts Division of Marine Fisheries, Dave Simpson of the State of Connecticut Marine Division, for coordinated field sampling from surveys; Glenn Goodwin and Gier Mosen of Seafreeze and Joe Mantineo of Ruggiero Seafoods for commercial samples. Lars Axelson, Glenn Goodwin, and Jim Ruhle shared their observations on spawning grounds of *Loligo pealeii* with us. Chad Keith and Lynette Suslowicz provided technical help in the cutting room, Jon Brodziak provided the code for, and assistance with, the diel correction analyses. We would like to thank John Boreman, Steve Murawski, and Fred Serchuk for their thoughtful and instructive reviews of this manuscript. EMCH would like especially to acknowledge Steve Murawski's guidance and help throughout the course of her Research Associateship with NMFS. We also thank other scientific personnel on NEFSC, MA, and CT bottom-trawl surveys and last, but most definitely not least, the thousands of squid that have sacrificed their lives for the advancement of science! Funding for EMCH was provided through the National Research Council Research Associateship program.

Literature cited

Augustyn, C. J., M. R. Lipinski, and W. H. H. Sauer.
1992. Can the *Loligo* squid fishery be managed effectively? A synthesis of research on *Loligo vulgaris reynaudii*. In Benguela trophic functioning (A. I. L. Payne, K. H. Brink, K. H. Mann, and R. Hilborn, eds.), p. 903-918. S. Afr. J. Mar. Sci. 12.

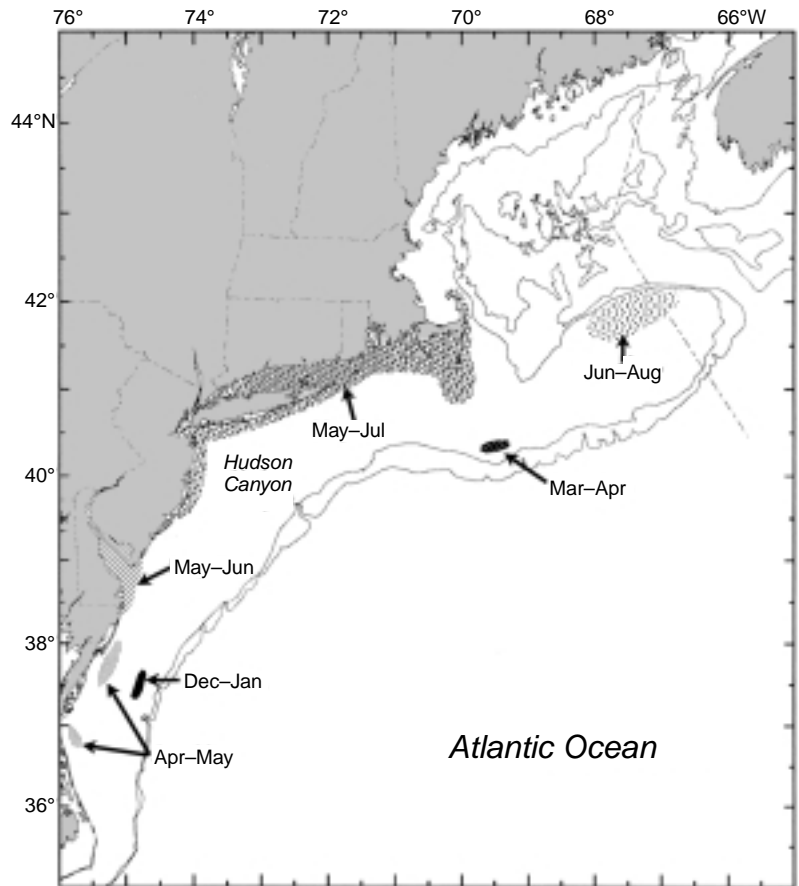


Figure 4

Persistent spawning areas and seasons for *Loligo pealeii*, as indicated from incidental catches of eggs in commercial squid trawls.

- Azarovitz, T. R.
1981. A brief historical review of the Woods Hole Laboratory trawl survey time series. Can. Spec. Publ. Fish. Aquat. Sci. 58:62-67.
- Brodziak, J. K. T., and L. C. Hendrickson.
1999. An analysis of environmental effects on survey catches of squids, *Loligo pealeii* and *Illex illecebrosus* in the northwest Atlantic. Fish. Bull. 97:9-24.
- Brodziak, J. K. T., and W. K. Macy III.
1996. Growth of the long-finned squid, *Loligo pealei*, in the northwest Atlantic. Fish. Bull. 94:212-236.
- Cohen, A. C.
1976. The systematics and distribution of *Loligo* (Cephalopoda, Myopsida) in the western North Atlantic, with descriptions of two new species. Malacologia 15:299-67.
- Forsythe, J. W., and R. T. Hanlon.
1988. Effect of temperature on laboratory growth, reproduction and life span of *Octopus bimaculoides*. Mar. Biol. 98:369-379.
1989. Growth of the Eastern Atlantic squid, *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda). Aquaculture Fish. Manag. 20:1-4.
- Forsythe, J. W., R. H. DeRusha, and R. T. Hanlon.
1994. Growth, reproduction and life span of *Sepia officinalis* (Cephalopoda: Mollusca) cultured through seven consecutive generations. J. Zool. 233:175-192.

- Garthwaite, R. L., C. J. Berg, and J. Harrigan.
1989. Population genetics of the common squid *Loligo pealei* LeSueur, 1821, from Cape Cod to Cape Hatteras. *Biol. Bull.* 177:287–294.
- Hatfield, E. M. C., R. T. Hanlon, J. W. Forsythe, and E. P. M. Grist.
2001. Laboratory testing of a growth hypothesis for juvenile squid *Loligo pealeii* (Cephalopoda: Loliginidae). *Can. J. Fish. Aquat. Sci.* 58:845–857.
- Hatfield, E. M. C., P. G. Rodhouse, and J. Porebski.
1990. Demography and distribution of the Patagonian squid (*Loligo gahi*, d'Orbigny) during the austral winter. *J. Cons. Int. Explor. Mer* 46:306–312.
- Jackson, G. D.
1994. Application and future potential of statolith increment analysis in squids and sepioids. *Can. J. Fish. Aquat. Sci.* 51:2612–2625.
- Jereb, P. S., S. Ragonese, and S. von Boletzky.
1991. Squid age determination using statoliths: proceedings of the international workshop held in the Istituto di Tecnologia della Pesca e del Pescato (ITPP-CNR), Mazara del Vallo, Italy, 9–14 October 1989. N.T.R.-I.T.P.P. (Note Tecniche e Reprints dell'Istituto di Tecnologia della Pesca e del Pescato) special publication 1, 128 p.
- Lange, A. M. T.
1980. The population dynamics of the squids (*Loligo pealei* and *Illex illecebrosus*) from the northwest Atlantic. M.S. thesis, Univ. Washington, Seattle, Wa, 178 p.
1981. Yield-per-recruit analyses for squid, *Loligo pealei* and *Illex illecebrosus*, from the Northwest Atlantic. *J. Shellfish Res.* 1:197–207.
- Lange, A. M. T., and M. P. Sissenwine.
1983. Squid resources of the northwest Atlantic. *In* Advances in assessment of world cephalopod resources. FAO Fish. Tech. Pap. 231:21–54.
- Lange, A. M., and G. T. Waring.
1992. Fishery interactions between long-finned squid (*Loligo pealei*) and butterfish (*Peprilus triacanthus*) off the northeast USA. *J. Northwest Atl. Fish. Sci.* 12:49–62.
- Macy, W. K.
1980. The ecology of the common squid, *Loligo pealei* LeSueur, 1821, in Rhode Island waters. Ph.D. diss., Univ. Rhode Island, Narragansett, RI, 249 p.
1982. Development and application of an objective method for classifying long-finned squid, *Loligo pealei*, into sexual maturity stages. *Fish. Bull.* 80:449–459.
1995. The application of digital image processing to the aging of long-finned squid, *Loligo pealei*, using the statolith. *In* Recent developments in fish otolith research (D. H. Secor, J. M. Dean, and S. E. Campana, eds.), p. 283–302. Univ. South Carolina Press, Columbia, SC.
- Maurer, R. O., and R. E. Bowman.
1985. Food consumption of squids (*Illex illecebrosus* and *Loligo pealei*) off the northeastern United States. NAFO (Northwest Atlantic Fisheries Organization) Sci. Coun. Studies 9:117–124.
- McMahon, J., and W. C. Summers.
1971. Temperature effects on the developmental rate of squid (*Loligo pealei*) embryos. *Biol. Bull.* 141:561–567.
- Murawski, S. A.
1993. Climate change and marine fish distributions: forecasting from historical analogy. *Trans. Am. Fish. Soc.* 122:647–658.
- Rodhouse, P. G., and E. M. C. Hatfield.
1990. Age determination in squid using statolith growth increments. *Fish. Res.* 8:323–334.
- Roper, C. F. E., M. J. Sweeney, and C. E. Nauen.
1984. FAO species catalogue. Vol. 3. Cephalopods of the world. An annotated and illustrated catalogue of species to interest to fisheries. FAO Fish. Synop. (125) Vol. 3, 277 p.
- Roper, C. F. E., and R. E. Young.
1975. Vertical distribution of pelagic cephalopods. *Smithsonian Contributions to Zoology* 209, 51 p.
- Serchuk, F. M., and W. F. Rathjen.
1974. Aspects of the distribution and abundance of long-finned squid, *Loligo pealei*, between Cape Hatteras and Georges Bank. *Mar. Fish. Rev.* 36:10–17.
- Sissenwine, M. P., and E. W. Bowman.
1978. An analysis of some factors affecting the catchability of fish by bottom trawls. ICNAF (Int. Comm. for the Northwest Atlantic Fisheries) Res. Bull. 13:81–87.
- Sissenwine, M. P., and A. M. Tibbetts.
1977. Simulating the effect of fishing on squid (*Loligo* and *Illex*) populations off the northeastern United States. ICNAF (Int. Comm. for the Northwest Atlantic Fisheries) Sel. Pap. 2:71–74.
- Sokal, R. R. and F. J. Rohlf.
1995. Biometry, the principles and practice of statistics in biological research. W. H. Freeman and Company, New York, NY, 887 p.
- Summers, W. C.
1967. Winter distribution of *Loligo pealei* determined by exploratory trawling. *Biol. Bull.* 133:489.
1969. Winter population of *Loligo pealei* in the mid-Atlantic bight. *Biol. Bull.* 137:202–216.
1971. Age and growth of *Loligo pealei*, a population study of the common Atlantic coast squid. *Biol. Bull.* 141:189–201.
- Tibbetts, A. M.
1977. Squid fisheries (*Loligo pealei* and *Illex illecebrosus*) off the northeastern coast of the United States of America, 1963–1974. ICNAF (Int. Comm. for the Northwest Atlantic Fisheries) Sel. Paps. 2:85–109.
- Verrill, A. E.
1882. Report on the cephalopods of the northeastern coast of America. U.S. Comm. Fish and Fish., part 7, Rep. Comm. 1879:211–450.
- Vovk, A. N.
1978. Peculiarities of the seasonal distribution of the North American squid *Loligo pealei* (Lesueur 1821). *Malac. Rev.* 11:130.
1985. Feeding spectrum of Longfin squid (*Loligo pealei*) in the northwest Atlantic and its position in the ecosystem. NAFO (Northwest Atlantic Fisheries Organization) Sci. Coun. Studies 8:33–38.
- Whitaker, J. D.
1978. A contribution to the biology of *Loligo pealei* and *Loligo plei* (Cephalopoda, Myopsida) off the southeastern coast of the United States. M.S. thesis, College of Charleston, Charleston, SC, 165 p.
1980. Squid catches resulting from trawl surveys off the Southeastern United States. *Mar. Fish. Rev.* 42:39–43.
- Worms, J.
1983. *Loligo vulgaris*. *In* Cephalopod life cycles, vol. I, species accounts. Academic Press, London, 475 p.