An analysis of environmental effects on survey catches of squids *Loligo pealei* and *Illex illecebrosus* in the northwest Atlantic

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Abstract.–An analysis of environmental effects on autumn survey catches of two commercially exploited squid species, *Loligo pealei* and *Illex illecebrosus*, was conducted. Research survey data collected during 1967–94 were used to determine the significance and relative importance of average depth of tow, time of day, bottom temperature, and surface temperature on bottom trawl catches of *L. pealei*, a neritic species, and *I. illecebrosus*, an oceanic species. We examined habitat associations of both species by using randomization methods and found that *L. pealei* was consistently associated with all of the environmental factors examined. In comparison with *L. pealei*, catches of *I. illecebrosus* were much lower and associations with environmental factors were inconsistent. We also examined whether environmental conditions affected catches of juvenile and adult squid differentially. Depth had an important effect on the magnitude of juvenile and adult *L. pealei* catches, with the ratio of juvenile to adult catches decreasing with depth. Depth had a similar, but less pronounced, effect on *I. illecebrosus* catches. Time of day also affected *L. pealei* and *I. illecebrosus* catches. Catches of both species were lowest at night and diel effects were more pronounced for juveniles than for adults. Bottom and surface temperatures had a substantial effect on catches of juvenile and adult *L. pealei* but had a variable influence on *I. illecebrosus* catches. The joint effects of depth stratification, time of day, and annual squid abundance on survey catches were also analyzed to determine correction factors for diel differences in catchability of juvenile and adult squid. Significant diel differences in catchability were detected for juvenile and adult *L. pealei* and for juvenile *I. illecebrosus* and diel correction factors were determined for survey catches of these size categories. In contrast, significant diel differences in catchability of adult *I. illecebrosus* were not detected.

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An analysis of environmental effects on survey catches of two commercially exploited squid species, *Loligo pealei* and *Illex illecebrosus*, was conducted for the continental shelf of the United States in the northwest Atlantic. Research survey data, collected during autumn, were used to determine the significance and relative importance of average depth of tow, time of day, bottom temperature, and surface temperature on bottom trawl catches of *L. pealei*, a neritic species, and *I. illecebrosus*, an oceanic species. Both squids grow rapidly (Brodziak and Macy, 1996; Dawe and Beck[1]), appear to live less than one year (Hurley et al., 1985; Macy, 1995; Brodziak and Macy, 1996; Dawe and Beck[1]), and undertake seasonal migrations in response to fluctuations in food availability, water temperature, and spawning (Lange and Sissenwine, 1983; Rowell et al., 1985a; O'Dor and Coelho, 1993). The rapid growth and short lifespan of these sympatric species suggest that environmental conditions were probably important determinants of their distribution and abundance on the continental shelf.

We investigated whether there was empirical evidence of habitat associations for both species by applying the habitat association method of Perry and Smith (1994). This randomization method accounted for the stratified random sampling design of the Northeast Fisheries Science Center (NEFSC) survey and tested whether catches within a year were associated with depth, time of day, surface temperature, and bottom temperature. Within-year associations that were consistent through time indicated which environmental conditions affected distribution and also provided a qualitative indication of habitat preferences.

We also examined whether environmental conditions affected catches of juvenile and adult squid differentially. Juveniles and adults of both species tend to differ in their food habits (Vovk, 1972; Vinogradov and Noskov, 1979; Macy, 1982; Maurer and Bowman, 1985) and, as a result, may use different habitats for feeding. We compared the effects of average depth of tow, time of day,

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[1] Dawe, E. G., and P. C. Beck. 1992. Population structure, growth, and sexual maturation of short-finned squid at Newfoundland, Canada, based on statolith analysis. ICES Council Meeting, Shellfish Committee/K, 33 p.

and surface and bottom temperature on survey catches to determine whether the habitat preferences of juveniles and adults overlap. Potential effects of different categories of depth, time of day, and surface temperature and bottom temperature on mean catch per tow were tested for juveniles and adults of both species, and the potential impacts on the ratio of juvenile to adult catches were also examined. These analyses also suggested whether environmental effects were similar for these sympatric species, because the degree of spatial overlap between their geographic distributions is at a maximum during autumn.

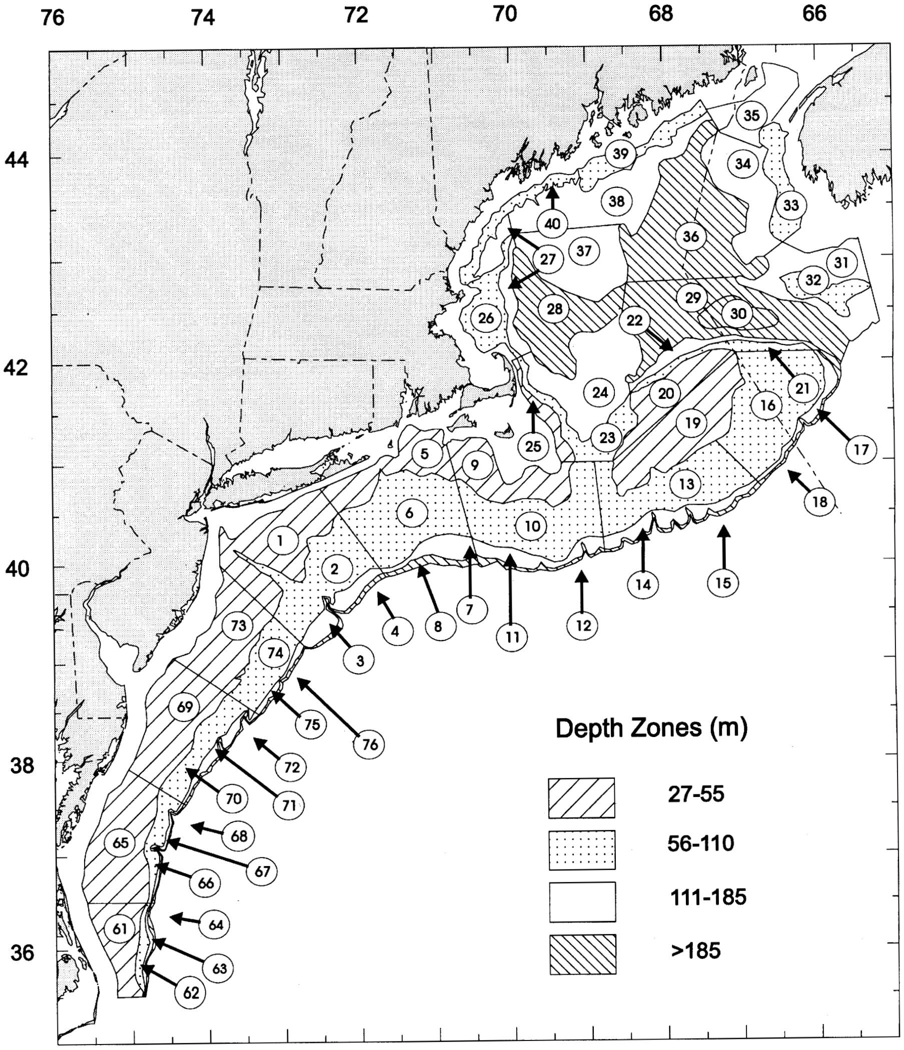

Figure 1

Offshore depth strata for autumn Northeast Fisheries Science Center bottom trawl surveys, 1963–94.

Last, we evaluated the relative magnitude of diel effects on juvenile and adult squid catches in relation to survey design and fluctuations in annual squid abundance. Previous bottom trawl studies have shown that diel effects on catches of *L. pealei* and *I. illecebrosus* can be important (Roper and Young, 1975; Sissenwine and Bowman, 1978; Lange and Sissenwine, 1983; Arkhipkin and Fedulov, 1986; Shepherd and Forrester[2]) because greater catchability occurs during the day. As a result of diel vertical migrations, night catches of these two species can be biased low in relation to day catches. To account for diel effects on minimum swept-area estimates of *L. pealei* biomass and stock size, diel correction factors have been used to adjust nighttime bottom trawl catches to daytime equivalents (Lange and Sissenwine, 1980; 1983). However, these correction factors were developed for total numbers of squid and were not size specific, even though Sissenwine and Bowman (1978) noted that a sixfold difference between the diel correction factor for weight and numbers of *L. pealei* suggested differential vertical migration by size. In this study, we applied a general linear model to determine size-specific diel correction factors for *L. pealei* and *I. illecebrosus* that accounted for potential effects of survey design and fluctuations in annual abundance. When diel effects were significant, correction factors were determined to standardize nighttime catches to daytime units.

Materials and methods

Survey data

Research survey data were analyzed from NEFSC autumn bottom trawl surveys conducted during 1967–94 between Cape Hatteras, North Carolina, and the Gulf of Maine. In general, autumn surveys were conducted from mid-September through mid-

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[2] Shepherd, G., and J. Forrester. 1987. Diurnal variation in catchability during bottom trawl surveys off the Northeastern United States. ICES Council Meeting 1987/B:44 (mimeo), 15 p.

October and along a similar cruise track each year. Standardized survey gear, procedures, and the stratified random sampling design are described in Azarovitz (1981). Offshore survey strata are defined by four depth zones; ranging between 27 m and 366 m. Strata numbers 1–30, 33–40, and 61–76 were included in our analyses (Fig. 1). Sampling was conducted 24 hours a day. Autumn survey data were used because only in autumn are both squid species distributed primarily within the survey sampling area. Survey data during 1963–66 could not be analyzed because catches of squid were not separated by species during these years.

At each randomly selected survey station, sampling was performed with a no. 36 Yankee otter trawl rigged with roller gear. Only standard tows, consisting of 20–30 minutes duration at a vessel speed of 3.5 knots, were included in the analyses. After each tow, the total weight of *L. pealei* and *I. illecebrosus* was measured to the nearest 0.1 kg, each species was enumerated, and length-frequency data (mantle length [ML] measured to the nearest cm) were collected. The following hydrographic and navigational data were recorded for each station: depth at the start and end of every tow (m), time of tow (h:m, Eastern Standard Time), bottom water temperature (°C), and surface water temperature (°C). Towing depth was computed as the average of depths recorded at the start and end of each tow. Surface water temperature was included in this analysis because the effect of surface temperature on the vertical distribution and catchability of these squids was unknown but was anecdotally important and potentially different from the effect of bottom temperature during autumn. In general, bottom and surface water temperatures within the survey region vary during autumn owing to the transition from a stratified water column, characteristic of summer, to a well-mixed condition typical of winter (Bowman, 1977). In particular, the relationship between surface and bottom water temperatures varied on an annual basis during the 1967–94 autumn surveys. Surface and bottom temperatures were not significantly correlated in 8 out of 28 years (29%), and exhibited a positive correlation ($\bar{\rho}=0.43$) in 19 out of 28 years (68%) during 1967–94.

When an environmental factor was not measured at a survey station, that station was excluded from the association test for that factor. Stations with missing environmental measurements occurred at random, with the exception of the Georges Bank portion of the autumn 1990 survey when no bottom temperature measurements were made. In total, 7177, 7179, 6105, and 6280 stations were available for the association tests of squid catch with depth, time of day, bottom temperature, and surface temperature, respectively.

Within-year associations

Perry and Smith (1994) developed a nonparametric test of association between an environmental factor and the quantity of catch during a stratified random survey. Their method uses the maximum absolute difference between the cumulative distribution function (CDF) of an environmental factor and the catch-weighted CDF of that environmental factor as a test statistic in a randomization procedure to evaluate whether a significant association exists. In particular, the test algorithm is as follows. First, the empirical CDF (*f*) of the environmental factor is computed as

$$f(t)=\sum_h \sum_i \frac{W_h}{n_h} I(x_{ih}), \tag{1}$$

where t = the value of the environmental factor;
h = an index for the survey strata;
i = an index for the tow in stratum h;
x_{ih} = the observed value of the environmental factor from the i^{th} tow in stratum h;
W_h = the proportion of the survey area in stratum h;
n_h = the number of tows in stratum h; and
$I(x)$= an indicator function with $I(x)=1$, when $x \le t$, and $I(x)=0$, when $x > t$.

Second, the empirical cumulative distribution of catch as a function of the environmental factor *(g)* is computed as

$$g(t)=\sum_h \sum_i \frac{W_h y_{ih}}{n_h \bar{y}_{st}} I(x_{ih}),$$

where

$$\bar{y}_{st}=\sum_h W_h \bar{y}_h, \tag{2}$$

and where y_{ih}= the catch from the i^{th} tow in stratum h;
$\bar{y}_h$ = the mean catch in stratum h; and
$\bar{y}_{st}$ = the stratified mean catch.

In Equation 2 above, the quotient $y_{ih}/\bar{y}_{st}$ expresses the relative catch under environmental condition x_{ih} in comparison with the stratified mean. The maximum absolute value of the difference between *f(t)* and *g(t)* over all values of the environmental factor is the observed test statistic (T) where

$$\mathrm{T}=\underset{\forall t}{MAX}\left|\sum_h \sum_i \frac{W_h}{n_h}\left(\frac{y_{ih}-\bar{y}_{st}}{\bar{y}_{st}}\right) I(x_{ih})\right|. \tag{3}$$

To evaluate whether the test statistic is significant, the observed environmental measurements (x_{ih}) are randomly sampled with replacement and assigned to observed catches with probability W_h / n_h under the hypothesis that the association between catch and the environmental factor is random. The value of the test statistic (T_R) is then computed for this random assignment. The randomization procedure of assigning environmental measurements to catches and of computing the value of T_R is repeated a large number of times to generate a distribution of test statistics for the null hypothesis of random association between catch and environmental factor. Last, the observed test statistic T is compared to the distribution of test statistics T_R from the randomization procedure to evaluate whether the null hypothesis of random association can be rejected.

We applied this test to *L. pealei* and *I. illecebrosus* catch, in numbers per tow, using four environmental factors: average depth of tow, time of tow, bottom water temperature, and surface water temperature. A total of 2000 randomizations were performed to provide an empirical distribution based on 2001 test statistics, including the original test statistic.

Size-specific environmental effects

Size-specific environmental effects on mean catches were evaluated separately for each species using tows that captured both juveniles and adults to ensure that comparisons were made under the same environmental conditions and that the ratio of juvenile to adult catch was well defined**.** Catch numbers of squid were separated into prerecruit (≤8 cm ML for *L. pealei* and ≤10 cm ML for *I. illecebrosus*) and recruit (>8 cm ML for *L. pealei* and >10 cm ML for *I. illecebrosus*) size categories, where prerecruits and recruits roughly corresponded to juvenile and adult squid. In what follows, prerecruit and recruit categories will sometimes be colloquially referred to as juveniles and adults, respectively. However, both *L. pealei* (Macy, 1980) and *I. illecebrosus* (Coelho and O'Dor, 1993) exhibit variability in sex-specific size at maturity, and for both species, an unmeasured fraction of smaller individuals within the recruit category were juveniles. The effect of depth on mean catch was evaluated first. Tow depth was categorized according to the depth zones used to define offshore strata of the NEFSC bottom trawl surveys: depth zone I (27–55 m), zone II (56–110 m), zone III (111–185 m), and zone IV (186–366 m). Similarly, time of tow was categorized into three time zones: zone I (night: 20:00–23:59 and 00:00 to 3:59), zone II (dawn and dusk: 4:00–7:59 and 16:00–19:59), and zone III (day: 8:00–15:59). Bottom and surface temperatures were grouped into three zones based on the 25th (P_{25}) and 75th (P_{75}) percentiles of the empirical temperature distribution of each of these two variables. Temperature zone I was P_0 to P_{25}, zone II was P_{25} to P_{75}, and zone III was P_{75} to P_{100}. Mean catches between zones were compared after applying a logarithmic transformation to stabilize the variance of number per tow. Similarly, mean ratios of juvenile to adult catches were compared between zones after applying a logarithmic transformation to the ratio. Mean $\log_{10}$-transformed catch per tow values of juveniles and adults and their ratios were tested at the 5% level of significance by using the GT-2 test which is appropriate for unplanned comparisons with unequal sample sizes (Sokal and Rohlf, 1981). Only the effects of individual environmental factors on juvenile and adult catches were evaluated in these univariate tests and the potentially important factors of interannual changes in abundance or of survey stratification were subsumed into random variation.

Diel correction factors

We analyzed the combined effects of survey design, time of day, and annual squid abundance to determine correction factors for diel differences in catchability of juvenile and adult squid. As in the evaluation of size-specific environmental effects, catches (C) from tows that captured both juveniles and adults were $\log_{10}$-transformed. A general linear model (Searle, 1987) was applied to estimate the effects of survey stratum (Fig. 1), time of day category, and year on $\log_{10}$-transformed catches. Time of day was categorized into three time zones: zone I (night: 20:00–23:59 and 00:00–3:59), zone II (dawn and dusk: 4:00–7:59 and 16:00–19:59), and zone III (day: 8:00–15:59) so that the time period effect (T) measured diel differences in mean catch. The year effect (Y) provided a measure of the effect of changes in relative annual abundance on mean catch whereas the survey stratum effect (S) accounted for the effects of geographic location and depth. The general linear model (GLM) was

$$\log C_{ijk} = \log U_R + \log T_i + \log Y_j + \log S_k + \varepsilon_{ijk}, \qquad (4)$$

where C_{ijk} = mean catch during the i^{th} time period (T_i) in the j^{th} year (Y_j) within the k^{th} stratum (S_k);
U_R = mean catch in a standard reference cell (where standard time period=day, year=1994, and survey stratum=1); and
ε_{ijk} = an independent and identically distributed normal random variable with zero mean and constant variance σ^2.

Parameters of the GLM model were estimated using ANOVA for both prerecruit and recruit catches of each species. The significance of time, year, and stratum effects were evaluated by using type-III sums of squares that do not depend on the order in which effects are added to the model (Searle, 1987). Because daytime was the reference time period, the diel coefficient for the daytime had the value 1. Point estimates and confidence intervals of time zone I (T_I) and II (T_{II}) coefficients in relation to the daytime coefficient were computed whenever the diel effect was significant. Given estimates of T_I and T_{II}, catches (y_{ih}) made during time zone I or II period can be corrected to daytime catch units by dividing them by the diel effects coefficient as y_{ih} / T_I and y_{ih} / T_{II}, respectively. Diel-standardized, stratified mean catches ($\bar{y}_{st}$*) can be expanded by the total number of sampling units within the survey region (N) to provide minimum swept-area estimates of juvenile or adult population size ($N\,\bar{y}_{st}$*) and variance ($N^2\ Var[\bar{y}_{st}$*]) within the survey region using stratified random sampling estimators (Cochran, 1977).

Results

Within-year associations

The neritic squid species exhibited different degrees of within-year habitat associations than those exhibited by the oceanic species. Results of the randomization tests of *L. pealei* catches with depth, time of day, bottom temperature, and surface temperature (Table 1) showed that *L. pealei* catch was consistently associated with each of these factors. Associations were significant (P<0.05) in all years for depth, bottom temperature, and surface temperature. For time of day, associations were significant in all years except 1980 (96%). In contrast, results of the randomization tests for *I. illecebrosus* (Table 2) indicated that catches of this species were inconsistently associated with only some of the factors. During the 28 years analyzed, a total of 15, 13, 7, and 12 associations were significant for depth, time of day, bottom temperature, and surface temperature, respectively. All four factors were significantly associated with *I. illecebrosus* catch during 1983; otherwise, there was no apparent pattern of annual associations. Overall, *L. pealei* exhibited consistent within-year associations, whereas *I. illecebrosus* exhibited variable within-year associations with the four environmental factors.

Table 1

Results of univariate randomization test of association between catches of *L. pealei* and depth, time of day, bottom temperature, and surface temperature, during the NEFSC autumn bottom trawl survey, 1967–94. Table entries are the probabilities of random association[1] between *L. pealei* catches and the environmental factor. The symbol "*" denotes probability values of 0.05 ≥ P > 0.01, and the symbol "**" denotes the probability values of 0.01 ≥ P.

	Environmental factor			
Year	Average depth	Time of day	Bottom temperature	Surface temperature
1967	0.00**	0.00**	0.00**	0.00**
1968	0.00**	0.00**	0.00**	0.00**
1969	0.00**	0.00**	0.00**	0.00**
1970	0.00**	0.00**	0.00**	0.00**
1971	0.03*	0.00**	0.00**	0.00**
1972	0.00**	0.00**	0.00**	0.00**
1973	0.04*	0.00**	0.00**	0.00**
1974	0.00**	0.00**	0.00**	0.00**
1975	0.00**	0.00**	0.00**	0.00**
1976	0.00**	0.00**	0.00**	0.00**
1977	0.00**	0.00**	0.00**	0.00**
1978	0.00**	0.00**	0.00**	0.00**
1979	0.00**	0.00**	0.00**	0.00**
1980	0.00**	0.07	0.00**	0.00**
1981	0.00**	0.00**	0.00**	0.00**
1982	0.01**	0.00**	0.03*	0.00**
1983	0.01**	0.00**	0.00**	0.00**
1984	0.00**	0.00**	0.00**	0.00**
1985	0.00**	0.00**	0.00**	0.00**
1986	0.01**	0.00**	0.00**	0.00**
1987	0.00**	0.00**	0.00**	0.00**
1988	0.00**	0.02*	0.00**	0.00**
1989	0.00**	0.00**	0.02*	0.00**
1990[1]	0.00**	0.00**	0.00**	0.00**
1991	0.00**	0.00**	0.00**	0.00**
1992	0.00**	0.00**	0.00**	0.00**
1993	0.02*	0.01**	0.00**	0.00**
1994	0.00**	0.00**	0.00**	0.00**

[1] No bottom temperature data were collected on Georges Bank during 1990.

We compared the interquartile range of the catch-weighted CDF of each factor to the interquartile range of its unweighted CDF to see how associations varied across years. For brevity, the term "midrange" denotes the "average interquartile range" in what follows. For depth, this comparison of CDFs showed whether *L. pealei* or *I. illecebrosus* preferred shallower or deeper water in relation to observed depths. The midranges of depth for *L. pealei* and *I. illecebrosus* catches were 37–75 m and 79–149 m (Fig. 2A), respectively, whereas the midrange of all observed depths was 51–166 m. For *L. pealei*, the average of the median catch-weighted depth was 50 m, about 35 m shallower than the average observed depth and equal to the P_{25} of the observed depths. In contrast, the average of the median catch-weighted depth for *I. illecebrosus* was 106 m, roughly 20 m deeper than the average observed depth. Overall, *L. pealei* was consistently associated with shallow depths (37–75 m), whereas *I. illecebrosus* was more common in deeper waters (79–149 m).

The comparison of midranges for time of day indicated whether *L. pealei* or *I. illecebrosus* catches were more prevalent during night or day. We measured time in relation to a reference time of day (6:00 AM EST) because this roughly corresponds to first light, during autumn, when diel effects on the behavior of squid might be expected to change. This choice did not affect the results of the habitat association test; however, median time of day was 18:00 EST, instead of 12:00 noon EST. The midranges for time of day for *L. pealei* and *I. illecebrosus* catches were 10:00–17:00 EST and 10:00–18:00 EST, respectively (Fig. 2B). In comparison, the midrange for time of day was 13:00–1:00 EST. For both *L. pealei* and *I. illecebrosus*, the average median catch-weighted time of day was 14:00 EST, roughly 4 hours earlier than the average median time of 18:00 EST, and roughly equal to P_{25} of the overall time distribution. Overall, both *L. pealei* and *I. illecebrosus* exhibited diel catchability because squid catches were consistently greater during day than at night.

Table 2

Results of univariate randomization test of association between catches of *I. illecebrosus* and depth, time of day, bottom temperature, surface temperature during the NEFSC autumn bottom trawl survey, 1967–94. Table entries are the probabilities of random association[1] between *I. illecebrosus* catches and the environmental factor. The symbol "*" denotes probability values of $0.05 \geq P > 0.01$, and the symbol "**" denotes the probability values of $0.01 \geq P$.

	Environmental factor			
Year	Average depth	Time of day	Bottom temperature	Surface temperature
1967	0.13	0.01**	0.01**	0.00**
1968	0.03*	0.24	0.05*	0.01**
1969	0.08	0.03*	0.26	0.33
1970	0.16	0.15	0.02*	0.02*
1971	0.01**	0.01**	0.00**	0.08
1972	0.24	0.30	0.12	0.03*
1973	0.04*	0.13	0.71	0.12
1974	0.52	0.03*	0.03*	0.23
1975	0.34	0.00**	0.77	0.00**
1976	0.02*	0.20	0.54	0.30
1977	0.04*	0.44	0.26	0.01**
1978	0.12	0.00**	0.87	0.03*
1979	0.00**	0.15	0.07	0.07
1980	0.01**	0.01**	0.24	0.25
1981	0.61	0.01**	0.51	0.25
1982	0.03*	0.00**	0.09	0.18
1983	0.03*	0.00**	0.01**	0.00**
1984	0.03*	0.47	0.42	0.00**
1985	0.00**	0.00**	0.24	0.12
1986	0.03*	0.51	0.60	0.31
1987	0.39	0.34	0.53	0.04*
1988	0.98	0.12	0.06	0.34
1989	0.69	0.10	0.32	0.58
1990[1]	0.00**	0.00**	0.27	0.09
1991	0.04*	0.36	0.11	0.48
1992	0.13	0.01**	0.00**	0.00**
1993	0.33	0.24	0.53	0.03*
1994	0.04*	0.18	0.09	0.39

[1] No bottom temperature data were collected on Georges Bank during 1990.

Potential effects of bottom temperature were also examined to see whether *L. pealei* or *I. illecebrosus* preferred warmer or cooler bottom temperatures. The midranges of bottom temperature for *L. pealei* and *I. illecebrosus* catches were 11–15°C and 9–13°C, respectively, and the midrange for bottom temperature was 8–13°C (Fig. 2C). For *L. pealei*, the average of the median catch-weighted bottom temperature was 13°C, about 3°C warmer than the average of the overall bottom temperature distribution. For *I. illecebrosus*, the average of the median catch-weighted bottom temperature was 11°C, which was nearly equal to the average of the observed bottom temperature distribution Although *L. pealei* was associated with warmer bottom temperatures, it did not appear that *I. illecebrosus* was closely associated with bottom temperature.

Effects of surface temperature were also examined to see whether *L. pealei* or *I. illecebrosus* preferred warmer or cooler surface temperatures. The midranges of surface temperature for *L. pealei* and *I. illecebrosus* catches were 17–20°C and 13–20°C (Fig. 2D), respectively, and the midrange for all surface temperatures was 11–19°C. For *L. pealei*, the average of the median catch-weighted surface temperature was 18°C; about 4°C warmer than the average overall surface temperature distribution. Similarly, the median catch-weighted surface temperature of 16°C for *I. illecebrosus* was 2°C warmer than this average. Overall, *L. pealei* was generally associated with warmer surface temperatures, whereas *I. illecebrosus* associations were more variable, and this species was less frequently associated with warmer surface temperatures.

Size-specific environmental effects

Mean catches of *L. pealei* prerecruits and recruits varied across depth zones (Fig. 3A) where combined sample sizes for depth zones I, II, III, and IV were 1234, 1012, 270, and 99 tows, respectively. Mean catches of prerecruits peaked in zone I and declined with depth, whereas mean catches of recruits peaked in zone III. The lowest mean catch of *L. pealei* prerecruits and recruits occurred in the deepest strata, zone IV. There was no significant difference between mean catches of prerecruits in depth zones II and III or recruits in zones I and II or zones II and III (Fig. 3A). The mean ratio of prerecruit to recruit catches was highest in depth zone I (Fig. 3B) and exhibited a declining trend with depth. However, the mean ratio was not significantly different in depth zones II, III, and IV. Overall, catches of *L. pealei* prerecruits decreased with depth, whereas recruit catches peaked at intermediate depths (111–185 m).

For *I. illecebrosus*, mean catches exhibited heterogeneity across depth zones (Fig, 3C), where sample sizes for depth zones I, II, III, and IV were 85, 283, 161, and 81 tows, respectively. Mean catches of recruits increased with depth and were highest in depth zone IV, whereas mean catches of prerecruits were relatively homogeneous across depths but were lowest in zone II. For prerecruits, mean catches were significantly different only between zones I and II (Fig. 3C). In contrast, mean catches of recruits were significantly different between all depth zones except zones III and IV and zones II and III. The mean ratio of prerecruit to recruit catches peaked in zone I, whereas the mean ratios in zones II, III, and IV were not significantly different (Fig. 3B). Overall, catches of *I. illecebrosus* prerecruits peaked in the shallowest depth zone (27–55 m) but were similar at greater depths. Similar to those of *L. pealei*, catches of *I. illecebrosus* recruits increased with depth as the ratio of prerecruit to recruit catch decreased with depth.

As expected, mean catch of *L. pealei* prerecruits and recruits peaked during day and were lowest at night (Fig. 4A). Sample sizes for time zones I, II, and III were 518, 968, and 1129 tows, respectively. For prerecruits, mean catch by time of day differed significantly for all three time zones (Fig. 4A), whereas mean catches of recruits were not significantly different between those for time zone II and zone III. The mean ratio of prerecruit to recruit catches peaked during day and was lowest at night (Fig. 4B), whereas the mean ratios for all time zones were significantly different (Fig. 4B). Overall, catches of both *L. pealei* prerecruits and recruits increased during day, although the difference between day and night catches was more pronounced for prerecruits.

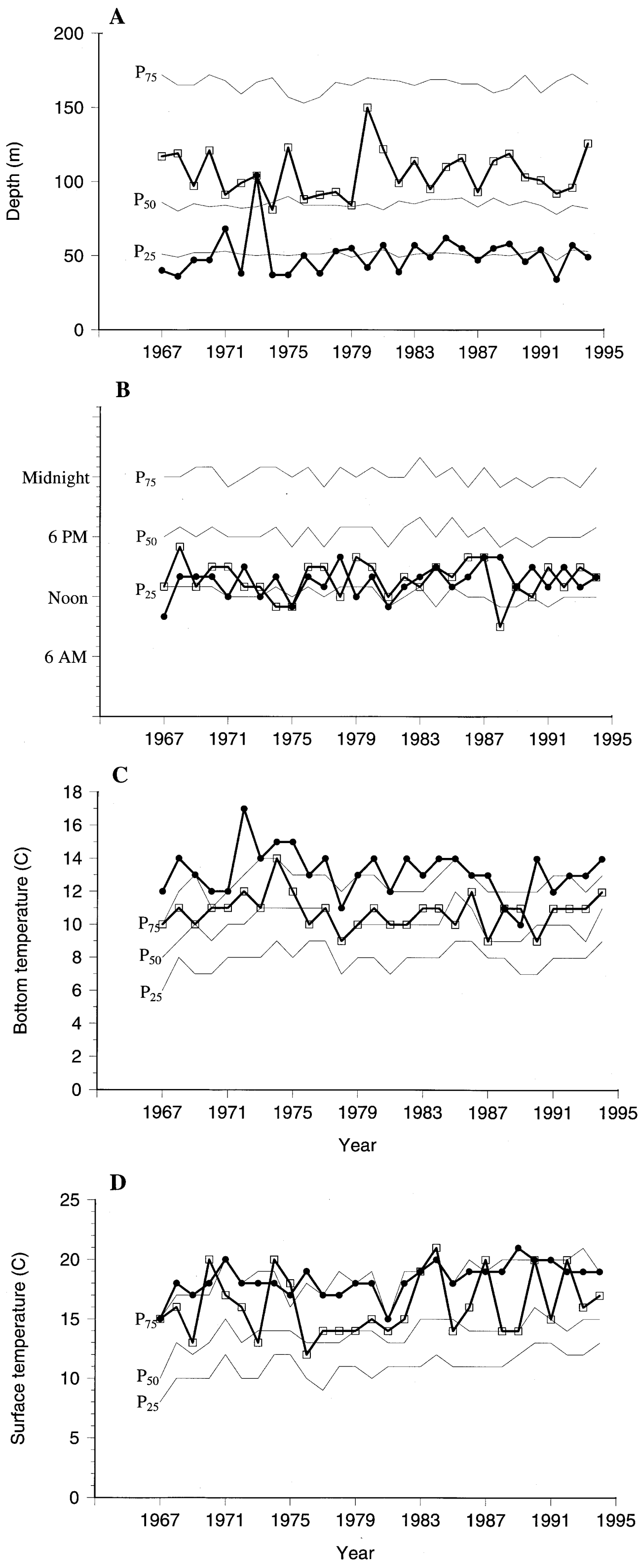

Figure 2

Catch-weighted averages of (**A**) depth (m), (**B**) time of day (h), (**C**) bottom temperature (°C), and (**D**) surface temperature (°C) by year for *L. pealei* (solid circle) and *I. illecebrosus* (open square). The 25th, 50th, and 75th percentiles (P_{25}, P_{50}, and P_{75} , thin solid lines) of the annual autumn distribution of each environmental factor are provided for comparison.

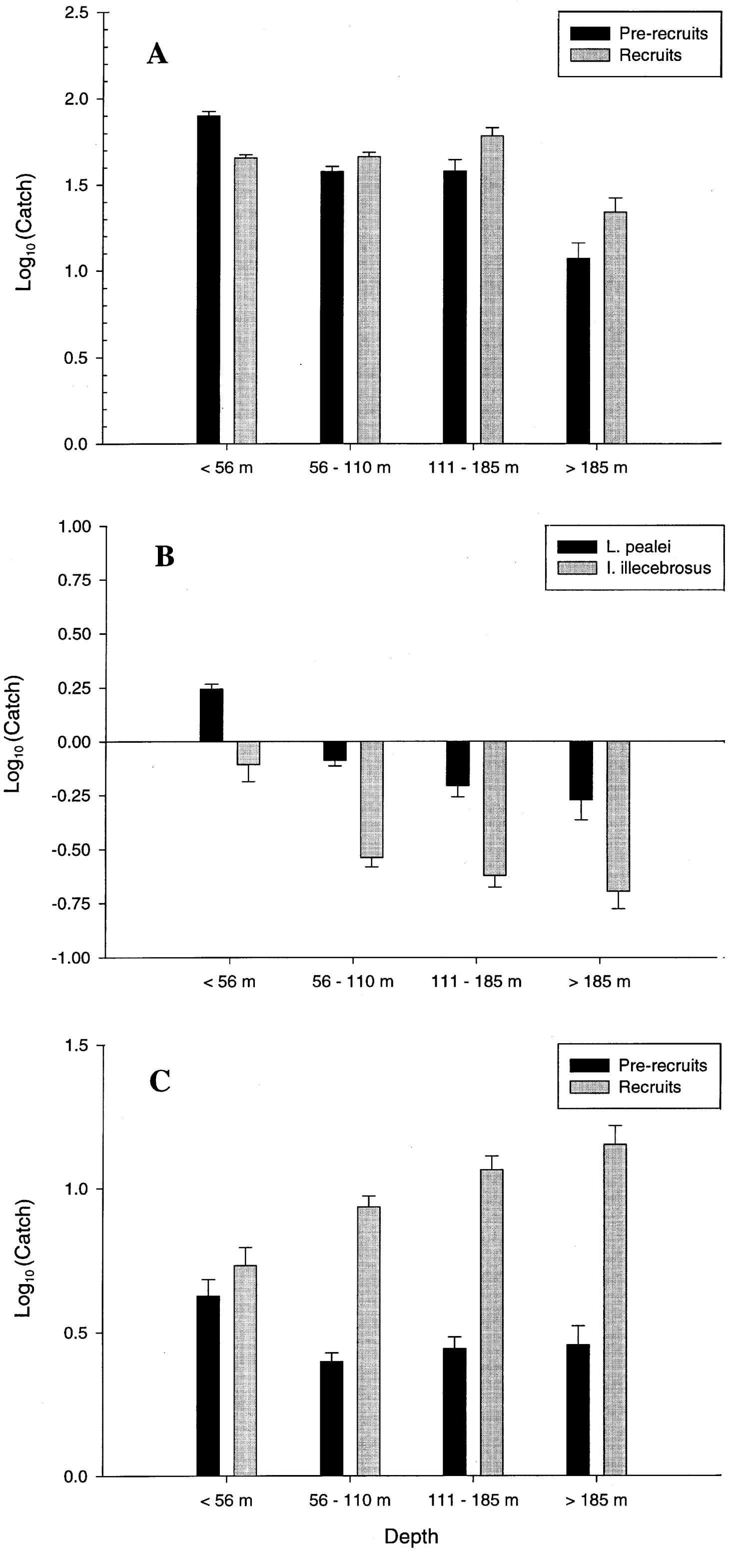

Figure 3

(**A**) Mean catch of *L. pealei*, (**B**) mean ratio of prerecruit to recruit catches, and (**C**) mean catch of *I. illecebrosus* by depth for positive catches of *L. pealei* and *I. illecebrosus* prerecruits and recruits.

For *I. illecebrosus*, the mean catch of prerecruits was highest during the day, whereas the mean catch of recruits peaked during dawn and dusk (Fig. 4C), where sample sizes for time zones I, II, and III were 86, 211, and 313 tows, respectively. Mean catches of prerecruits and recruits were lowest at night. For prerecruits, mean catches were not significantly different between time zones I and II (Fig. 4C). In contrast, mean catches of recruits were not significantly different between time zones II and III. Although the mean ratio of prerecruit to recruit catches peaked during the day (Fig. 4B), mean ratios were significantly different between time zones II and III. Similar to catches of *L. pealei*, catches of both size categories of *I. illecebrosus* were lowest at night.

Mean catches of *L. pealei* prerecruits and recruits differed by bottom temperature zone (Fig. 5A) where temperature zones I, II, and III were 5.5 to 10.9°C (n=604), 10.9 to 16.1°C (n=1,340), and 16.1 to 28.0°C (n=272), respectively. Mean catch of prerecruits increased with bottom temperature and peaked in the warmest zone, whereas mean catch of recruits was greatest in zones II and III. In contrast, the mean catches of both size categories were lowest in temperature zone I. Mean catches of prerecruits were significantly different between all bottom temperature zones (Fig. 5A), whereas mean catches of recruits were not significantly different between zones II and III. The mean ratio of prerecruit to recruit catch peaked in zone III (Fig. 5B), and the mean ratios were not significantly different between zones I and II. Overall, catches of *L. pealei* prerecruits increased with increasing bottom temperature, whereas catches of recruits peaked at intermediate levels (11–16°C).

Catches of *I. illecebrosus* prerecruits and recruits also varied (Fig. 5C) with bottom temperature, where zones I, II, and III were 5.1 to 10.2°C (n=122), 10.2 to 12.9°C (n=242), and 12.9 to 25.5°C (n=121), respectively. For *I. illecebrosus* prerecruits, mean catches were greatest in temperature zones I and II, and the mean catch of recruits peaked in zone II. Mean catches of *I. illecebrosus* prerecruits and recruits were lowest in temperature zones I and III, respectively. For prerecruits, mean catches were significantly different only between temperature zones I and II (Fig. 5C), whereas mean catches of recruits were significantly different only between zones II and III. The mean ratio of prerecruit to recruit catches was greatest in temperature zones II and III (Fig. 5D), however there was no significant difference between the three zones. Overall, catches of *I. illecebrosus* prerecruits and recruits were relatively similar over the range of observed bottom temperatures (5–25°C).

Mean catches of *L. pealei* prerecruits and recruits differed with surface temperature (Fig. 6A) where temperature zones I, II, and III were 7.1 to 14.8°C (n=615), 14.8 to 20.9°C (n=1,178), and 20.9 to 28.3°C (n=460), respectively. Mean catches of prerecruits and recruits peaked in temperature zone II, whereas the lowest mean catch of prerecruits and recruits occurred in temperature zone I. Mean catches of both prerecruits and recruits were significantly different across all surface temperature zones (Fig. 6A). The mean ratio of prerecruit to recruit catches peaked in temperature zone II and the mean ratios were significantly different across all surface temperature zones (Fig. 6B). Overall, catches of *L. pealei* prerecruits and recruits peaked at intermediate surface temperatures (15–21°C).

Mean catches of *I. illecebrosus* prerecruits and recruits (Fig. 6C) also varied with surface temperature, where temperature zones I, II, and III were 7.8 to 14.4°C (n=123), 14.4 to 20.6°C (n=242), and 20.6 to 26.5°C (n=131), respectively. For *I. illecebrosus* prerecruits, mean catch peaked in temperature zone II but exhibited no trend across zones. In contrast, mean catch of recruits peaked in temperature zone III and exhibited an increasing trend with surface temperature. There were no significant differences in mean catch of prerecruits, by surface temperature zone (Fig. 6C), but mean catches of recruits were significantly different between temperature zones I and III. The mean ratio of prerecruit to recruit catch peaked in temperature zone I (Fig. 6D) and declined with increasing surface temperature. These mean ratios were significantly different between zones I and III. Over-

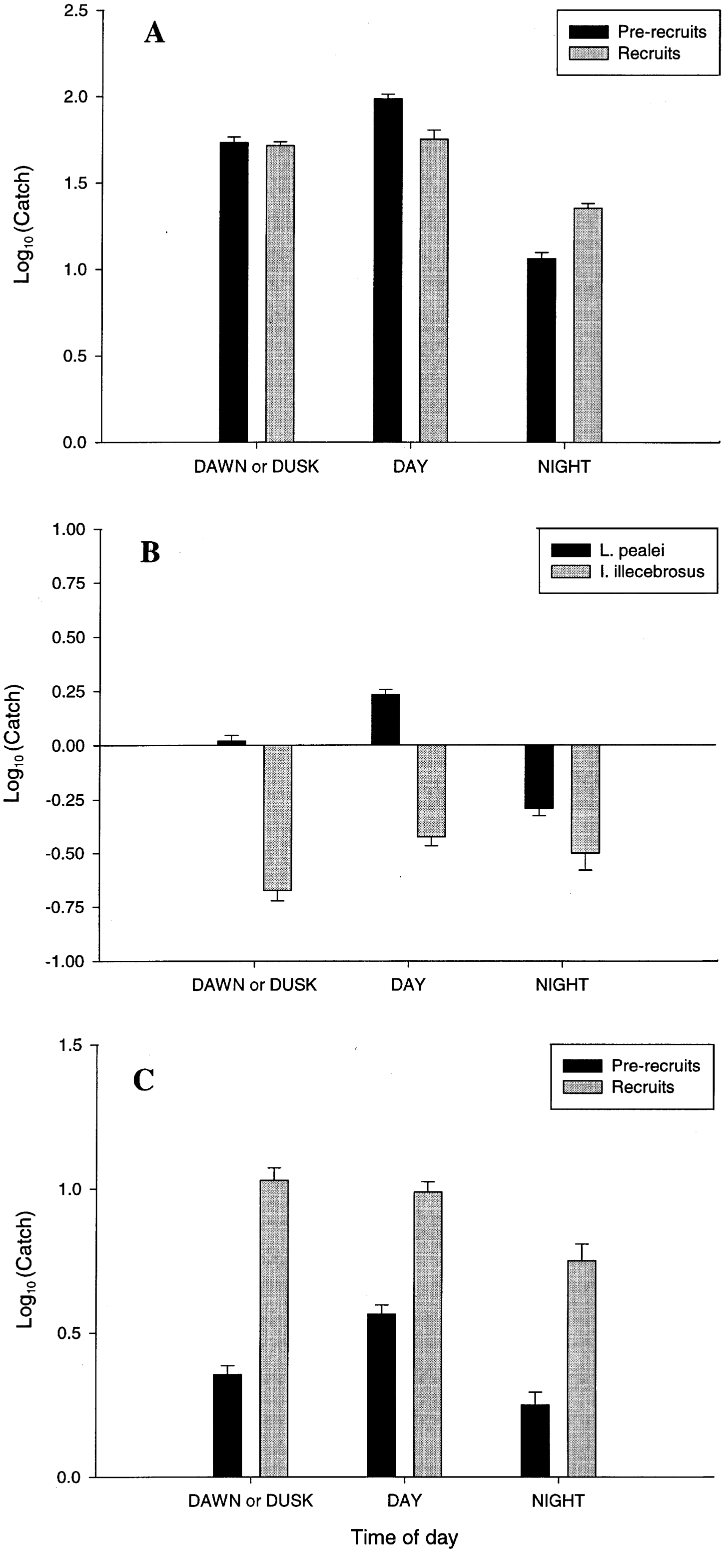

Figure 4

(**A**) Mean catch of *L. pealei*, (**B**) mean ratio of prerecruit to recruit catches, and (**C**) mean catch of *I. illecebrosus* by time of day for positive catches of *L. pealei* and *I. illecebrosus* prerecruits and recruits.

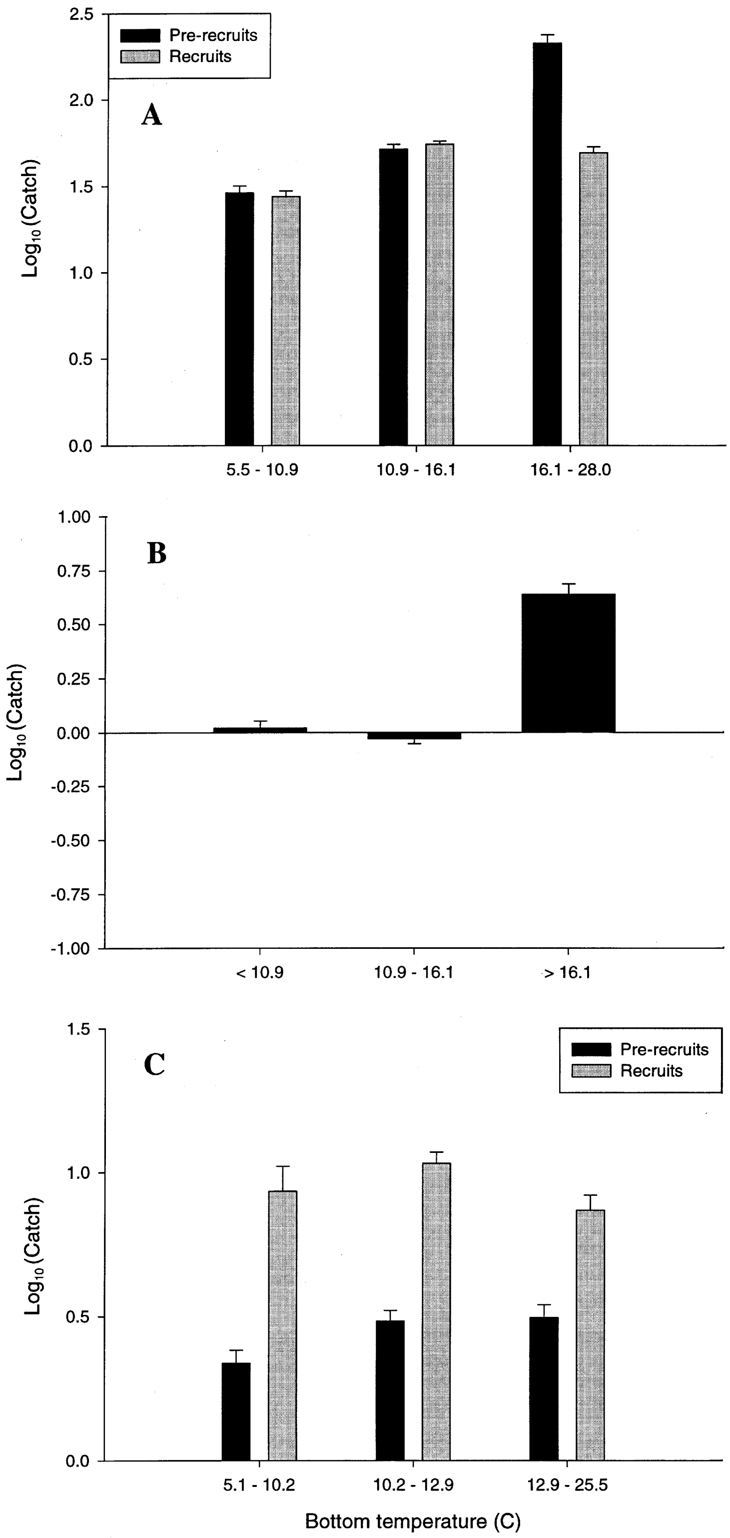

Figure 5

(**A**) Mean catch of *L. pealei*, (**B**) mean ratio of *L. pealei* prerecruit to recruit catches, (**C**) mean catch of *I. illecebrosus*, and (**D**) mean ratio of *I. illecebrosus* prerecruit to recruit catches by bottom temperature for positive catches of prerecruits and recruits.

all, catches of *I. illecebrosus* prerecruits were similar across the range of observed surface temperatures (8–26°C), whereas catches of recruits increased with surface temperature.

Diel correction factors

Diel effects from the GLM analyses were significant for *L. pealei* prerecruits and recruits and for *I. illecebrosus* prerecruits (Table 3). For *L. pealei* prerecruits, the time period effect was highly significant (F_S=280.79, P<0.001), and the year (F_S=6.05, P<0.001) and stratum effects (F_S=16.23, P<0.001) were also significant. Estimates of the diel effects coefficients for *L. pealei* prerecruits were T_I = 0.0873 with 95% CI of [0.0713, 0.1068] and T_{II} = 0.4654 with 95%CI of [0.3958, 0.5472]. For comparison, daytime catch rates of *L. pealei* prerecruits were roughly were about 11.5 times higher than time zone I values and 2.1 times higher than time zone II values. Similarly, for *L. pealei* recruits, the time period effect was highly significant (F_S=100.06, P<0.001), and the year (F_S=9.84, P<0.001) and stratum (F_S=12.45, P<0.001) effects were also significant. Estimates of the diel effects coefficients for *L. pealei* recruits were T_I = 0.3420 with 95% CI of [0.2939, 0.3979] and T_{II} = 0.8325 with 95%CI of [0.7372, 0.9402]. Time zone III catch rates of *L. pealei* recruits were roughly 2.9 times higher than time zone I values and about 1.2 times higher than zone II values. For *I. illecebrosus* prerecruits, the time period effect was significant (F_S=20.23, P<0.001). The stratum effect was also significant (F_S=1.98, P<0.001) but the year effect was not (F_S=1.48, P=0.057). Diel effects coefficients were estimated to be T_I = 0.4251 with 95% CI of [0.3158, 0.5724] and T_{II} = 0.6281 with 95%CI of [0.5093, 0.7746]. By comparison, time zone III catch rates of *I. illecebrosus* prerecruits were about 2.4 times higher than zone I values and roughly 1.6 times higher than time zone II values. For *I. illecebrosus* recruits, the time period effect was not significant (F_S=2.25, P=0.106), although the year (F_S=5.41, P<0.001) and stratum (F_S=3.05, P<0.001) effects were significant. For both species, diel effects were more pronounced for prerecruits than for recruits.

Discussion

We found that *L. pealei* was consistently associated with all the environmental factors examined. The habitat associations of *L. pealei* with depth, bottom temperature, and surface temperature indicated that these factors were important determinants of its autumn distribution. The consistent association of *L. pealei* with time of day appeared to be a consequence of the behavioral ecology of the species as it moves upward in the water column during the night to avoid predation or to acquire prey.

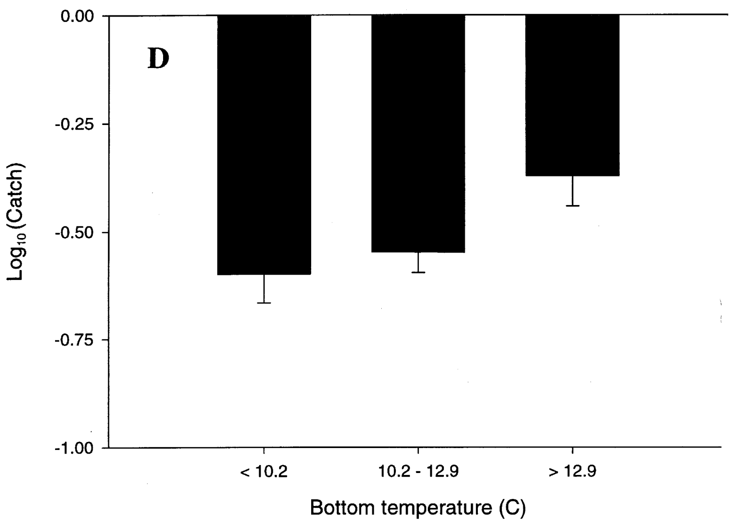

Figure 5 (continued)

In comparison with *L. pealei*, autumn survey catches of *I. illecebrosus* were much lower and associations with environmental factors were inconsistent. For many of the years examined**,** *I. illecebrosus* catches were not associated with depth, temperature, or time of day. *Illex illecebrosus* feeds opportunistically in continental shelf waters from Newfoundland to Cape Hatteras, during summer and autumn, prior to undertaking a lengthy offshore migration to spawning areas south of Cape Hatteras (O'Dor and Dawe, in press). Therefore, the lack of consistent habitat associations may be partly due to incomplete survey coverage of *I. illecebrosus* habitat during autumn and a lack of availability of this species to the bottom trawl survey gear. For example, the timing of the offshore and southward migration of *I. illecebrosus* may precede rather than follow the timing of the autumn survey in some years. In addition, few stations are sampled in the autumn habitat of this species, at the shoreward edge of the convergence zone, and these low sample sizes may make it difficult to detect habitat associations. Nevertheless, *I. illecebrosus* catches were significantly associated with depth, time of day, and surface temperature in approximately half of the years examined. Depth and surface temperature may be determinants of preferred habitat of *I. Illecebrosus;* however the importance of these factors varied between years**.** The significant association of *I. illecebrosus* catches with daylight indicated that the species undertakes vertical migrations similar to those of *L. pealei*, but with less regularity as might be expected of an ommastrephid (Roper and Young, 1975).

Table 3

Analysis of variance tables for general linear model results to estimate diel correction factors for *L. pealei* and *I. illecebrosus* prerecruits and recruits, where df is degrees of freedom, SS is type-III sums of squares, MS is mean square, F_S is the *F*-statistic, and *P* is the probability value.

Source of variation	df	SS	MS	F_S	*P*
L. pealei prerecruits					
Year	27	104.824	3.882	6.05	<0.001
Stratum	50	520.624	10.413	16.23	<0.001
Time of day	2	360.353	180.176	280.79	<0.001
L. pealei recruits					
Year	27	96.171	3.562	9.84	<0.001
Stratum	50	225.257	4.505	12.45	<0.001
Time of day	2	72.439	36.220	100.06	<0.001
I. illecebrosus prerecruits					
Year	27	9.761	0.362	1.48	0.057
Stratum	50	24.114	0.482	1.98	<0.001
Time of day	2	9.866	4.933	20.23	<0.001
I. illecebrosus recruits					
Year	27	41.351	1.532	5.41	<0.001
Stratum	50	43.274	0.865	3.05	<0.001
Time of day	2	1.275	0.637	2.25	0.106

Depth had an important effect on the magnitude of juvenile and adult *L. pealei* catches. This association with depth corroborated previous studies. Serchuk and Rathjen (1974) examined the distribution and relative abundance of *L. pealei* and found that the highest catches were at depths less than 100 m during autumn. Vovk (1978) reported that the primary depth range of *L. pealei* was 50–100 m during September–November, and Lange and Sissen-

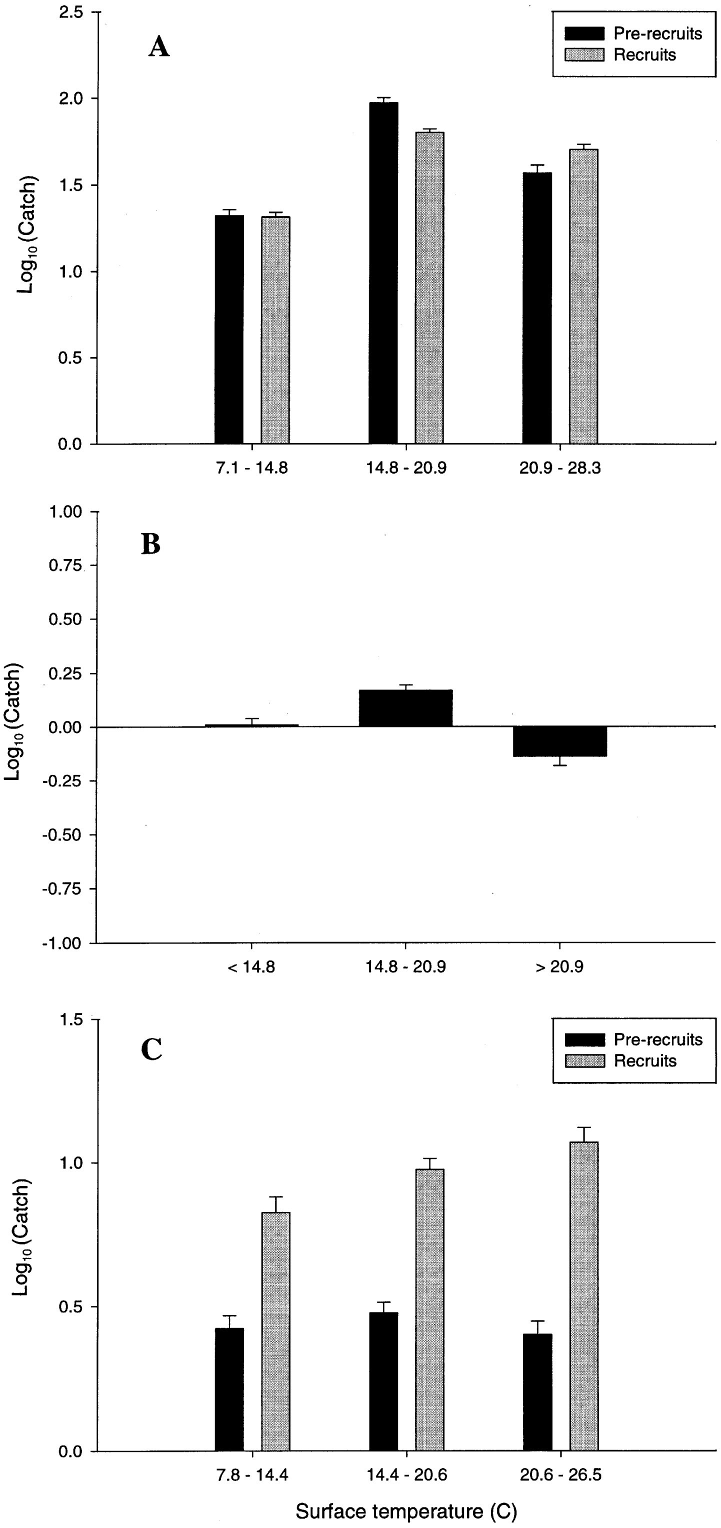

Figure 6

(**A**) Mean catch of *L. pealei*, (**B**) mean ratio of *L. pealei* prerecruit to recruit catches, (**C**) mean catch of *I. illecebrosus*, and (**D**) mean ratio of *I. illecebrosus* prerecruit to recruit catches by surface temperature for positive catches of prerecruits and recruits.

wine (1983) reported relatively high catches at shallow (27–55 m) and also intermediate depths (111–185 m). In this study, however, depth affected catches of juvenile and adult *L. pealei* differently. Most shallow-water catches comprised juveniles, and this finding indicated that nearshore waters of the continental shelf constitute a preferred habitat of *L. pealei* juveniles during autumn. Catches of juveniles also decreased at greater depths. In contrast, catches of *L. pealei* adults peaked at depths near the edge of the continental shelf. We detected a bathymetric pattern of larger *L. pealei* with increasing depth. This pattern was also reported by Vovk (1978) on the basis of distant water fleet catches of *L. pealei* and is similar to the ontogenetic descent reported for some other loliginids (*L. gahi*, Hatfield et al., 1990; *L. vulgaris reynaudii*, Augustyn et al., 1992).

In comparison with *L. pealei*, the effect of depth on *I. illecebrosus* was similar but less pronounced. This difference was probably due to the fact that *I. illecebrosus* utilize a wider range of depths than do *L. pealei* as they feed in shallow nearshore areas and undertake long distance migrations in continental slope waters (O' Dor and Dawe, in press). Nonetheless, the empirical patterns of *I. illecebrosus* catches in relation to depth in our study area were consistent with those from different areas. In particular, Whitaker (1980) reported that *I. illecebrosus* catches were relatively low at depths less than 56 m and peaked at depths between 186 and 366 m in waters south of Cape Hatteras, whereas Grinkov and Rikhter[3] reported that *I. illecebrosus* catches peaked at depths of 100–150 m along the edge of the continental shelf off Nova Scotia. In our study, much of the *I. illecebrosus* catch occurred at depths of roughly 80–150 m. As with *L. pealei*, we found that depth affected the catch of *I. illecebrosus* juveniles and adults differ-

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[3] Grinkov, Y. A., and V. A. Rikhter. 1981. Some data on distribution of groundfish and short-finned squid along the oceanic slopes of the Scotian Shelf in spring, 1979. Northwest Atlantic Fisheries Organization (NAFO) SCR Doc. 81/VI/63, ser. no. N347, 13 p.

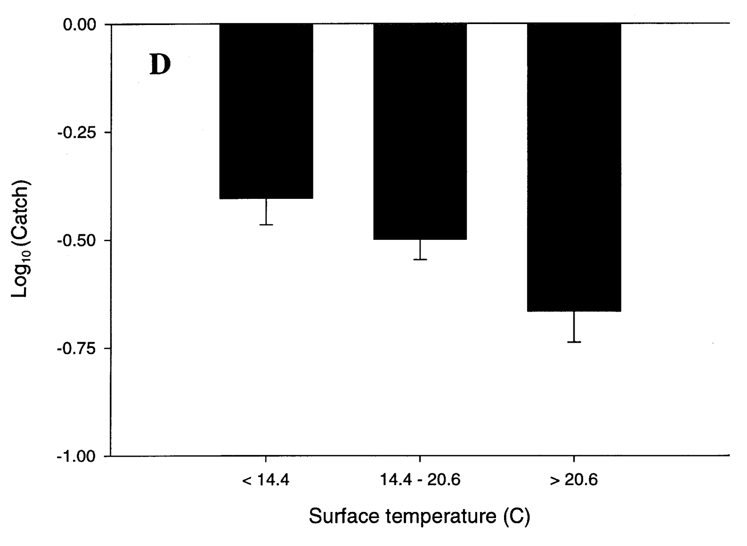

Figure 6 (continued)

ently. Catches of juveniles decreased at greater depths, and there was a bathymetric pattern of larger *I. illecebrosus* with increasing depth. Although catches of adults increased with depth, in contrast with *L. pealei*, catches of *I. illecebrosus* adults peaked at depths of 186–366 m. This depth range corresponds to the convergence zone between continental shelf and slope waters and intersects the shelf edge at roughly 150–200 m (Bowman, 1977). Commercial fishery catch data were consistent with this observation, as Lange, Ingham, and Price[4] reported, noting that the highest catch rates recorded by domestic observers in the distant-water *I. illecebrosus* fishery were generally located within several miles of the shelf-slope front, at the shoreward edge of the convergence zone, between continental shelf and slope water. Overall, these observations suggested that the shelf-slope convergence zone is an important habitat for adult *I. illecebrosus* during autumn.

Our analyses also demonstrated the importance of diel effects on *L. pealei* catches. This generally corroborated previous observations. Summers (1968) observed that *L. pealei* migrated vertically and that squid could be observed near the surface at night. Summers (1969) and Lange and Sissenwine (1983) observed that survey catches of *L. pealei* during the day were consistently higher than catches at night. Serchuk and Rathjen (1974) observed that 90% of *L. pealei* survey catches occurred during daylight, and Sissenwine and Bowman (1978) found that *L. pealei* catches were significantly higher during day. In our study, significant differences in diel effects were detected for both juveniles and adults. Catches of *L. pealei* juveniles and adults increased with increasing light availability although the diel effects were more pronounced for juveniles. In particular, time zone I and II catches of juveniles were 92% and 54% below mean catch during the day, whereas zone I and II catches of adults were 66% and 17% lower. The fact that the diel effect was more pronounced for juvenile *L. pealei* may be related to differences in feeding behavior between juveniles and adults. *L. pealei* hatchlings must feed near the surface until their tentacles develop and they can capture larger prey (Vecchione, 1981) whereas adults are primarily demersal and commonly rest on the bottom (Hanlon et al., 1983). Small juveniles feed primarily on crustaceans and gradually shift to a more diverse diet of crustaceans, fish, and squid as they grow and can capture larger and more energetically valuable prey (Vovk, 1972; Macy, 1982; Vovk, 1985; Anderson and Griswold, 1988). As a result, juveniles need to undertake vertical migrations at night more frequently to capture a sufficient amount of suitable prey.

The fact that *I. illecebrosus* catches were moderately associated with time of day was consistent with Sissenwine and Bowman (1978) and Shepherd and Forrester[2] who found that time of day had an important effect on catches of *I. illecebrosus*. Diel vertical migrations may be related to *I. illecebrosus* feeding activity. Vinogradov and Noskov (1979) found that the feeding intensity of this species is greatest at night and lowest during the day. Similar to catches of *L. pealei*, catches of *I. illecebrosus* were higher during day, and diel effects were more important for juveniles than adults. In particular, catches of juveniles at night and those at dawn and dusk were 37% and 57% below mean catch during the day. Guided by a review of the NEFSC domestic sea sampling program database, fishermen targeting *I. illecebrosus* take advantage of the behavior of this species by fishing only between dawn and dusk, when the squid are available to commercial bottom trawl gear. Schools of *I. illecebrosus* are not targeted at night because they are too dispersed near the surface of the water column. Instead schools of *I. illecebrosus* are targeted beginning at dawn, when they can be

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[4] Lange, A. M. T., M. C. Ingham, and C. A. Price. 1984. Distribution of maturing *Illex illecebrosus* relative to the shelf-slope water front of the northeastern United States. NAFO SCR Doc. 84/IX/109, Ser. No. N906, 18 p.

consistently seen on sonar returning to the seabed.[5] In contrast, the ratios of juvenile to adult catches of *I. illecebrosus* were considerably lower than those for *L. pealei*. In part, this difference in ratios between species may reflect the importance of cannibalism for larger *I. illecebrosus* adults during autumn (O'Dor and Dawe, in press). Although diel effects on *I. illecebrosus* juvenile catches were similar to *L. pealei*, they were less consistent.

We found that bottom temperature had a significant effect on catches of *L. pealei* juveniles and adults. This generally corroborated prior studies. In particular, Summers (1969) observed that large catches of *L. pealei* during winter were restricted to bottom temperatures of 8°C or higher. This lower temperature limitation was supported by Serchuk and Rathjen (1974) and Vovk (1978) who reported that the majority of *L. pealei* catches during autumn occurred at bottom temperatures of roughly 9–14°C. Similarly, in our study, much of the *L. pealei* catch occurred at 11–15°C. However, catches of *L. pealei* juveniles were highest when bottom temperatures exceeded 16°C, whereas catches of adults were highest when bottom temperatures were 11–16°C. Our results suggest that *L. pealei* juveniles generally prefer warmer bottom temperatures than do adults that appear to prefer intermediate bottom temperatures. This difference in temperature preference might be expected if minor differences in temperature have a substantial impact upon growth rates of young squid (Forsythe, 1993).

In contrast to bottom temperature, catches of *L. pealei* juveniles and adults had a similar pattern with respect to surface temperature. The highest catches of both *L. pealei* juveniles and adults occurred at temperatures of 15–21°C, whereas catches were lowest for temperatures below 15°C. Although *L. pealei* catches might be expected to increase with warmer water temperatures, adult catches peaked at intermediate bottom and surface temperatures and then declined at higher temperatures. This decline suggested that the higher temperature ranges observed in the survey were not optimal for *L. pealei* adults. Overall, the strong association of *L. pealei* with water temperature suggested that annual variation in patterns of ocean temperature affects the distribution and influences growth and survival of this neritic species.

In comparison to *L. pealei*, the less frequent associations of *I. illecebrosus* catches with bottom and surface temperatures suggested that temperature has a variable influence on the distribution of *I. illecebrosus* from Cape Hatteras to the Gulf of Maine. Other studies generally supported the notion that *I. illecebrosus* are distributed over a broad range of temperatures. In particular, Whitaker (1980) reported that *I. illecebrosus* catches occurred over a wide range of bottom temperatures of 7–27°C, but that roughly 80% of the catch was taken in 8–10°C waters. Murawksi (1993) examined the mean latitudinal occurrence of *I. illecebrosus* in relation to bottom and surface temperatures during autumn NEFSC bottom trawl surveys but found no statistically significant relationship. Rowell et al. (1985b) reported that *I. illecebrosus* appear to prefer bottom temperatures in excess of 6°C during summer on the Scotian Shelf, but that temperature did not appear to be a limiting factor. In the present study, much of the *I. illecebrosus* catch occurred at bottom temperatures of 9–13°C and surface temperatures of 13–20°C. In comparison to *L. pealei*, *I. illecebrosus* appeared to prefer cooler bottom temperatures and surface temperatures. However, in contrast with *L. pealei*, bottom temperature had a similar affect on catches of juvenile and adult *I. illecebrosus*. Surface temperature affected catches of juveniles and adults differently and, in particular, adult *I. illecebrosus* catches increased with surface temperature. Overall, *I. illecebrosus* catches occurred over a broader range of water temperatures in comparison with *L. pealei*, as might be expected of an oceanic species with a range that extends from temperate to boreal waters**.**

Because the bottom trawl gear used on the NEFSC autumn survey only fishes 3.2 m above the seabed, diel differences in squid catches are expected when squid migrate vertically to acquire prey or to avoid predators. Significant differences were detected between catches by time of day for both juvenile and adult *L. pealei*. As a consequence, it was inferred that diel correction factors were appropriate for survey catches of this neritic species. In contrast, diel effects on survey catches of adult *I. illecebrosus* were not significant and diel correction factors were not developed for this oceanic species. The diel catchability of *L. pealei* presents some challenges for the analysis and interpretation of bottom trawl survey data to estimate squid population totals. On one hand, diel correction factors developed in this study can be applied to time zone I and II catches to provide a stratified mean catch per tow adjusted to daylight units. Resampling techniques, such as mirror-match bootstrapping, could be applied to estimate its variance (Smith, 1997) under appropriate distributional assumptions. In this case, all survey data could be used at the expense of additional computational cost and potential bias induced by applying the diel correction factors to all survey strata. On

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[5] Goodwin, G. 1997. Captain of *F/V Relentless* and *F/V Persistence.* Davisville, Rhode Island, 02882. Personal commun.

the other hand, squid population size and its variance could be calculated on the basis of only daylight tows in the standard manner. In this case, roughly 1/3 of the available survey data would be used owing to the exclusion of time zone I and II tows. As a result, some survey strata would be undersampled and precision would be lower. In general, the trade-off between bias due to diel correction and loss of precision due to use of only daylight tows warrants further study.

Differences between *L. pealei* and *I. illecebrosus* catches by depth suggest that the stratification of the NEFSC bottom trawl survey, which was designed to sample groundfish populations, is appropriate for both species. Differences in *L. pealei* and *I. illecebrosus* catches by temperature imply that preferred temperature ranges likely exist for both species within the survey region. However, temperature would not be a useful stratification variable for analysis of squid catches because temperature strata are dynamic and would fluctuate each year and because such a variable would lead to overstratification given the current depth and geographic stratification of the NEFSC survey. Regardless of how temperature affects survey catches of squids, the growth, recruitment, and abundance of *L. pealei* and *I. illecebrosus* can be expected to vary with ocean temperature regime (e.g. Dawe and Warren, 1993; Brodziak and Macy, 1996) because both are ecological opportunists with high, intrinsic population growth rates. Understanding how environmental factors, such as temperature, influence the productivity and distribution of squid stocks remains an important topic for fisheries research and management.

Acknowledgments

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