

Catchability, Growth, and Mortality of Larval Fishes

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ABSTRACT: The catchability of fish larvae with a 61 cm bongo net was determined from analysis of day, night, and twilight samples from 8,312 stations made off the northeast United States during 1977–84. Night catches exceeded day catches by 62% and twilight exceeded day catches by 44%. Catchability by year and month revealed some variations; however, night catches still dominated. The daily cycle in catchability of all larvae showed that the maximum catch occurred at approximately 0200, and was about 2.5 times the minimum catches at 1700. Changes in catchability with water column depth reflected changes in species composition of the catches.

Analysis of 36 taxa revealed 11 significant differences in day:night, day:twilight, and night:twilight catch ratios. Length-dependent catchability and correction factors were determined for 26 species. Corrected length frequencies were used to calculate length-dependent mortalities which are shown to be positively correlated with water temperature. Larval growth rates were also found to be temperature dependent and, by incorporating a length-weight coefficient, larval length was converted to age. Age-frequencies were used to calculate daily larval mortality and, for most species, the ratio of mortality rate to growth rate was approximately 0.8. Those species with ratios at or over 1.0, i.e., bluefish, *Pomatomus saltatrix*; *Sebastes* spp.; Atlantic mackerel, *Scomber scombrus*; cunner, *Tautoglabrus adspersus*; and, to some extent, haddock, *Melanogrammus aeglefinus*, probably exhibit significant net avoidance.

Surveys of ichthyoplankton in the marine environment have been an integral part of fisheries science for nearly a century. Today large marine ecosystems are routinely monitored for both physical and biological parameters to study multispecies interactions during the early life history of fishes (Sherman 1986). One of the major goals of large marine ecosystem surveys is to monitor the inter- and intra-annual changes in larval fish abundance and mortality and their relationship to recruitment of fishable biomass.

Demonstrating the relationship between larval abundance and recruitment has remained elusive owing, in part, to the complexities of the interactions of the physical and biological factors that affect survival of fish during the first year of life. However, a number of theories have been proposed that attempt to link larval fish survival and, by inference, recruitment with their food supply. These include the “critical period” theory (Hjort 1914; May 1974), the “match-mismatch” theory (Cushing 1975), and the mixed layer stability hypothesis (Lasker 1981).

A requisite condition for the testing of these and other theories using broadscale ichthyoplankton surveys is what Zweifel and Smith (1981) call an “effective sampler size”. This involves accounting for the “effect of environmental and behavioral factors on the content of the samples or collections”. The objective of accounting for these factors is to standardize the sampling gear by applying correction factors in order to minimize sampling variability and to make samples comparable (Smith and Richardson 1977). A key consideration and a possible serious source of bias in larval fish collections is net avoidance (Clutter and Anraku 1968). Fish larvae can avoid capture by swimming out of the path of an approaching net or by migrating below the maximum depth sampled by the net. If detection of an approaching net by larvae is visual, changes in light intensity or net coloration will alter catchability. The magnitude of visually cued avoidance is indicated by the variation in day versus night catches.

Differences in day versus night catches for numerous species have been reported for the past 60 years (e.g., Johansen 1925; Russell 1926; Ahlstrom 1954; Bridger 1956; Miller et al. 1963; Lenarz 1973). In most cases night catches exceed day catches. But there is evidence that gear configuration and towing speed affect the ratio of day-to-night catches (Bridger 1956; Clutter and Anraku 1968). For example, Miller et al. (1963) attributed the lack of difference in day-to-night catches of haddock, *Melanogrammus aeglefinus*, to the high speed (4 m/s) gear they used.

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Accounting for the various sources of sampling bias and for standardizing larval catches facilitates the calculation of the critical population parameters of abundance and mortality. These parameters are the basis for testing the possible effects of biotic and abiotic variables upon larval fish survival and recruitment and are often used to support or reject a particular hypothesis. The general effect of net avoidance is an increase in estimates of mortality (Clutter and Anraku 1968), which in turn can lead to unrealistic conclusions.

The interrelationship of mortality and growth parameters has been firmly established for fishes in the marine ecosystem (Beverton and Holt 1957; Ursin 1967; Ware 1975; Shepherd and Cushing 1980; Peterson and Wroblewski 1984; Houde 1987; and others). The underlying assumptions for this relationship are that mortality is the result of predation and that predation rates decrease as prey size increases. This simplistic model was described as the "cube root rule" (Ursin 1967) where mortality is equal to the cube root of the weight. Peterson and Wroblewski (1984) expanded this relationship to include growth efficiency and metabolism and estimated the annual mortality rate (M) for larval and adult fishes weighing between 10^{-5} and 10^3 g as $M = (1.92 * \text{year}^{-1}) \text{weight}^{-25}$. Pauly (1980) noted the rather weak relationship between fish size and mortality ($r^2 = 0.38$) and found that the inclusion of environmental temperature significantly improved the fit ($r^2 = 0.71$) of mortality to maximum length and growth rate for 175 fish stocks. The objectives of this study are to determine the changes in larval fish catches during day, night, and twilight hours and provide correction factors to standardize catches for net avoidance. These corrections can significantly change the abundance and mortality estimates of those species that show a difference in day, night, or twilight catches. Length-dependent larval mortality is estimated from avoidance-corrected abundances for 26 fish taxa and is related to water temperatures. The relationships of larval growth, mortality, and water temperature are explored to determine if net avoidance is, in fact, a serious problem as it relates to estimates of larval mortality.

METHODS

Continental shelf and slope waters off the northeast United States have been sampled six to eight times each year since 1977 to provide infor-

mation on the distribution and abundance of fish eggs and larvae as well as to provide fisheries independent estimates of spawning biomass. A total of 8,312 stations were occupied from 1977 through 1984 between Cape Hatteras, NC, and Nova Scotia (Fig. 1). At each station a 61 cm bongo net frame, fitted with 505 μ and 333 μ mesh nets and flowmeters, was lowered at 50 m/min to within 5 m of the bottom or to 200 m maximum and retrieved at 20 m/min. Ship speed was adjusted to maintain a wire angle of 45 degrees; the 505 μ mesh net was used for ichthyoplankton analysis; and samples were preserved in 5% formalin. All fish larvae were identified to the lowest taxon possible, enumerated, and measured to the nearest 0.1 mm standard or notochord length. If more than 50 specimens of a particular taxon were captured in a tow, then 50 randomly selected larvae were measured. Water temperature profiles were taken at each station. A detailed account of all shipboard and laboratory methods, and sampling locations is provided in Sibunka and Silverman (1984).

Larval catches were standardized (S) to the number under 10 m² of sea surface by the equation:

$$S = 10 * N * D * A^{-1} * M^{-1} \quad (1)$$

where N is the number of larvae in the sample, D is the maximum depth of the tow in meters, A is the area of the mouth of the net, and M is the distance the net was towed in meters determined from the calibrated flowmeter (Smith and Richardson 1977). All analyses followed standardizing of catches to the number of larvae under 10 or 100 m² and rounding of lengths to the nearest mm.

Each station was assigned to day, night, or twilight hours according to the recorded time at the beginning of the tow. Twilight was designated as one hour before and after both sunrise and sunset while day or night was assigned between the two twilight intervals.

Catches of all larvae were analyzed by hour of the day to determine if a daily cycle in catchability could be detected. The assumption in this analysis is that the daily cycle of incident light is the controlling factor for visual detection of the net. The seasonal and latitudinal changes in the duration of daylight hours (e.g., 8.6 hours in winter to 15.4 hours in summer) made it necessary, in order to maintain equivalent light regimes across seasons and areas in the analysis, to partition the day into 24 intervals of 10 for

daylight, 10 for nighttime, and 2 for each of the twilight times. The number of hours (H) between sunrise and sunset for each station was calculated using latitude and Julian day (Iqbol 1983), as follows

$$H = -7.6393 * \arcs[\sin(L) * \sin(C)/(\cos(L) * \cos(C))]$$

where $L = 0.0172(\text{latitude})$.

$$C = 0.3964 - 22.9133 * \cos(Z) + 4.1580 * \sin(Z) - 0.3964 * \cos(2Z) + 0.5197 * \sin(2Z) - 0.1545 * \cos(3Z) + 0.0848 * \sin(3Z), \text{ and}$$

$$Z = 0.0172 (\text{Julian day} - 1).$$

Twilight hours remained one hour before and after sunrise and sunset and were partitioned into hour intervals 5–6 and 17–18, respectively, and accounted for 4 of the 24 h day. The remaining daylight hours ($H - 2$), where H is time from sunrise to sunset, were partitioned into 10 equal intervals (i.e., hours 7–16). Nighttime hours ($24 - (H + 2)$) were also partitioned into 10 intervals corresponding to hours 0–4 and 19–23. The time interval for a daylight “hour” ranged from about 52 minutes in winter to 92 minutes in summer. Each station was assigned an “hour” interval and analysis was performed during this interval.

The occurrence of tows that did not contain larvae or that did not contain the particular taxon of interest presented a special problem in day-versus night-catch analysis. The absence of larvae might have occurred because there were no larvae within the path of the net or because of net avoidance by the larvae. This being the case, all stations in cruises that contained at least one occurrence of the taxon being investigated, except where noted, were included in calculations of mean catch per 10 m². The result of including these zero tows was a reduction in the mean catch, but a stability in the catch ratios. In addition, the survey area was divided into four sub-areas: Middle Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GB), and Gulf of Maine (GOM) (Fig. 1). The subareas were used to stratify the entire survey area during analysis for those taxa that spawn in a limited area. For example, if no larvae of a particular species were caught in GOM subarea then all GOM stations were ignored for the analysis of that species. The calculation of the mean catch and its variance using zero tows followed the methods of Pennington (1983) for the Delta distribution of catch frequencies. Ratios of all larvae for day, night, and twilight were based on mean catch per 10 m², and ratios for millimeter length increments were based on mean catch per

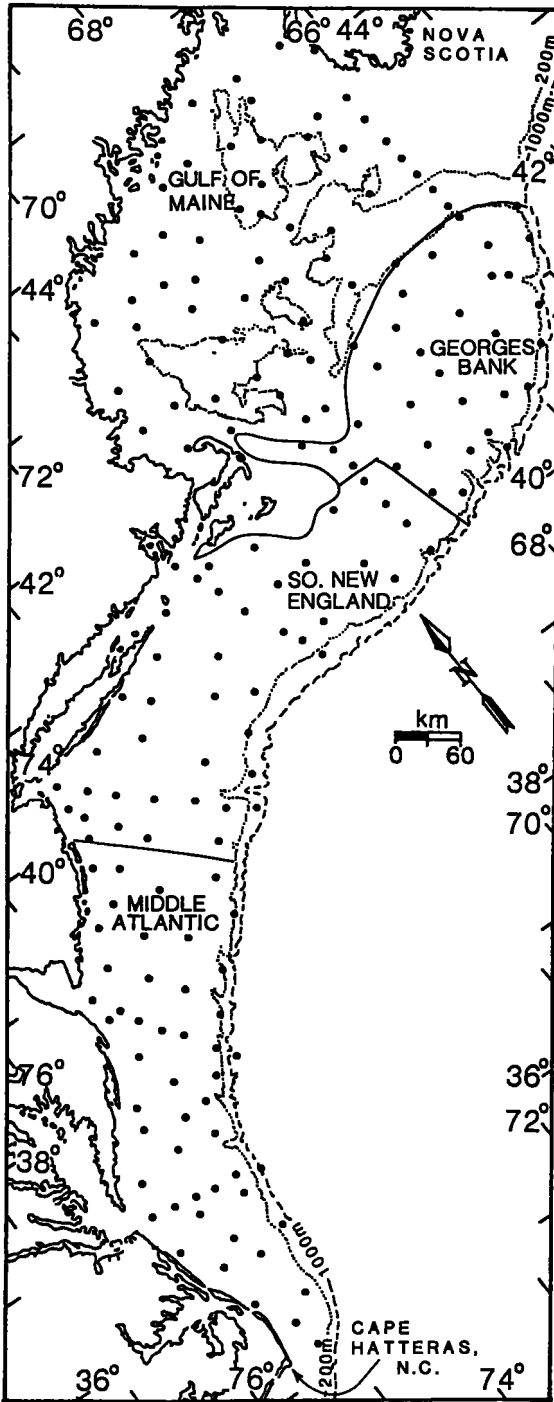


FIGURE 1.—Map of area surveyed, station locations and subareas off the northeast United States.

100 m². Other statistics were calculated according to Zar (1984).

The analysis to derive correction factors for day, night, and twilight catchability and to derive estimates of larval mortality for 26 species involved three steps. The larval length-interval used was calculated from the modal length, which was always greater than the minimum length captured, to the maximum length that was captured in all three light regimes. I assumed that the modal length was the minimum length fully retained by the 505 μ mesh net. If extrusion of larvae at modal lengths or greater is significant, length-dependent mortalities will be underestimated and will have no effect on catch ratios. The exponential decay regression model was fitted to the larval length (X_i) and catch per 100 m² (Y_i) as

$$Y_i = \alpha \exp(-\beta X_i) + \epsilon_i \quad (2)$$

for each species by day, night, and twilight catches. The expected catches from these regressions were then used to estimate the ratios of catch by length for night:day and twilight:day. The predictive nonlinear second-order polynomial regression model:

$$R_i = \alpha + \beta_1 X_i + \beta_2 X_i^2 + \epsilon_i \quad (3)$$

was fitted to the ratios by length. (The predicted ratio (R_i) of night:twilight catches for any length (X_i) is, of course, the ratio of night:day at X_i divided by the twilight:day ratio at X_i .) The catches at each length per 100 m² were then corrected using the predicted ratios that maxi-

mized the catches. The exponential decay model was again fitted to the corrected catches and the slope of the line was used as an estimate of length-dependent mortality.

RESULTS

All Larvae

The initial analysis examined the catches for all taxa combined for all 8,312 stations, of which 6,530 contained fish larvae. The mean catch per 100 m² was calculated for 3,578 day stations, 3,332 night stations, and 1,402 twilight stations (Table 1). A significant difference ($P < 0.05$) was found between night-versus-day and night-versus-twilight catches with the ratios of the mean catches of 1.62:1 and 1.44:1, respectively. The combining of all data raises the question of whether one or more year's data might have been anomalous and produced the significant difference in catches. Each year was analyzed separately and is shown in Table 1. For each year the highest mean catches always occurred at night and in six of the eight years twilight catches exceeded day catches. In four of the eight years a significant difference ($P < 0.05$) was found between night and day catches (1977, 1982-84). The consistent interannual relationships in catches indicate that the combined years' ratios are good indicators of average catchability of all larvae during the 8 yr study.

The analysis of the combined data-set integrates the areal and temporal heterogeneity in the distribution and abundance inherent within the larval fish community. To determine if the

TABLE 1.—The mean catch per tow (#/100 m²) by day, night, and twilight of fish larvae collected off the northeast United States for years 1977-84 and combined. Numbers in parenthesis are standard error of the mean and sample size. Values of Student *t* test for differences in mean catches.

Year	Day (D)	Night (N)	Twilight (T)	t-value		
				D vs. N	D vs. T	N vs. T
1977	162.868(20.774,591)	260.308(34.274,555)	206.796(46.380,209)	2.4649*	0.9871	0.8536
1978	143.513(22.610,434)	197.502(34.681,401)	121.823(27.723,178)	1.3233	0.5488	1.3698
1979	159.847(19.779,410)	228.784(34.595,178)	170.466(32.641,153)	1.7871	0.2793	1.0248
1980	154.223(20.147,455)	241.296(35.886,397)	187.856(40.815,164)	2.1845	0.8096	0.8661
1981	195.026(27.800,426)	264.761(36.220,412)	178.697(33.435,180)	1.5336	0.3403	1.4562
1982	127.302(18.571,372)	237.059(37.154,366)	126.952(28.913,154)	2.6552*	0.0102	1.8262
1983	134.868(20.838,401)	265.698(47.486,396)	215.808(57.246,172)	2.5379*	1.6468	0.6142
1984	145.628(18.225,489)	287.115(41.634,452)	169.497(32.560,192)	3.1947**	0.6719	1.7468
All	155.379(7.948,3578)	251.673(14.582,3332)	174.533(13.931,1402)	5.9058**	1.2435	3.1837**

* = $P < 0.05$.

** = $P < 0.01$.

ratios of day, night, and twilight catches show seasonal or areal differences, separate ratios of the mean catch per 10 m² were calculated for each month for all subareas and by subarea (Table 2). In all months the ratios of night-versus-day catches for all subareas combined were greater than one. Night-to-day ratios ranged from 1.01 in September to 3.23 in January and the mean for all months was 1.82 (SD = 0.56). The extreme values in January and September may be related to the relatively low sample sizes for these two months; however, the higher catches at night relative to both day and

twilight catches remained quite consistent regardless of month.

Considerably more variability in the ratios between months is evident when each subarea is analyzed separately, but the general trend of dominance in night catches is still evident within each subarea. The extraordinarily low ratio for twilight-versus-day catches for January in the Gulf of Maine results from a few extremely high twilight catches and relatively low sampling intensity (*N* = 17).

Catches of all larvae grouped by water column depth are shown in Figure 2. They peak at

TABLE 2.—Ratios of night (N):day (D) and twilight (T):day (D) mean catches of larval fish caught off the northeast United States, 1977–84, by subarea and combined by month. *n* = number of samples; MAB = Middle Atlantic Bight; SNE = Southern New England; GB = Georges Bank; GOM = Gulf of Maine.

Month	<i>n</i>	All		MAB		SNE		GB		GOM	
		N/D	T/D	N/D	T/D	N/D	T/D	N/D	T/D	N/D	T/D
Jan.	166	3.23	0.37	—	—	—	—	1.47	0.58	1.85	0.07
Feb.	536	1.92	1.15	2.38	1.00	0.81	0.68	1.19	1.25	2.70	4.35
Mar.	906	1.51	1.02	1.33	0.86	1.47	1.39	0.90	0.41	0.47	1.92
Apr.	897	1.45	0.96	2.13	1.75	1.56	1.12	1.15	0.56	0.59	0.45
May	1,112	1.49	1.11	1.10	0.56	1.88	1.64	1.52	1.23	1.28	1.69
June	727	2.43	1.16	2.63	0.79	1.89	1.27	1.01	1.30	3.23	0.99
July	690	2.00	1.06	2.86	1.47	1.20	0.84	7.69	1.75	1.09	0.46
Aug.	850	1.69	1.32	1.25	1.89	2.50	1.19	1.47	1.33	1.35	0.84
Sept.	277	1.01	0.83	1.24	0.79	0.99	—	—	—	—	—
Oct.	1,015	1.75	1.04	0.94	0.42	1.75	1.61	1.85	1.45	2.00	0.56
Nov.	654	1.69	1.85	0.68	0.66	2.01	2.13	1.85	0.43	4.54	7.14
Dec.	482	1.68	1.64	—	—	0.76	1.79	3.23	6.25	4.76	0.91

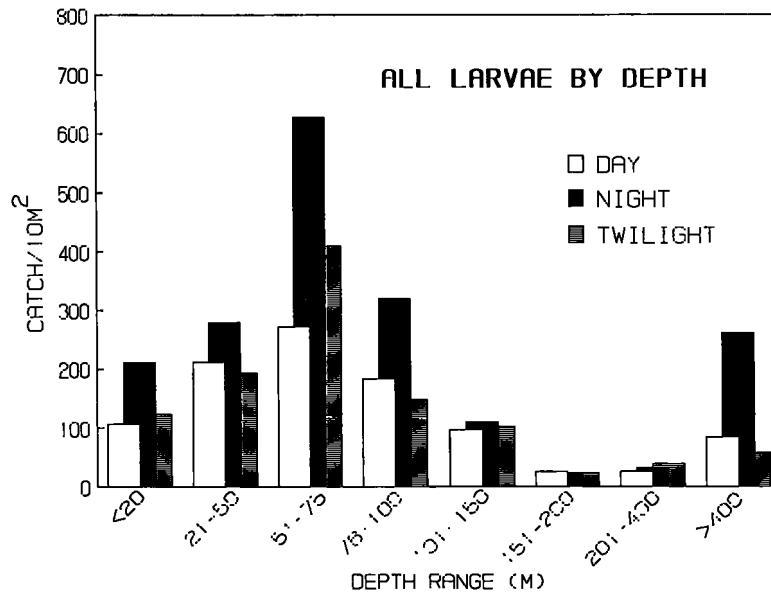


FIGURE 2.—Mean catch of all larvae by bottom depth interval for day, night, and twilight.

depths between 51 and 75 m, decrease to a low at 151–200 m, and then increase again at depths >400 m. The increase in catch per tow at the deep water stations is due to the dominance of two mesopelagic lantern fishes, *Ceratospopelus maderensis* and *Benthoosema glaciale*, which account for 47% of all larvae at these depths. Night catches exceeded day and twilight catches except between 101 and 400 m. At these water column depths the dominant taxa are *Sebastes* spp.; silver hake, *Merluccius bilinearis*; offshore hake, *Merluccius albidus*; Gulf Stream flounder, *Citharichthys arctifrons*; *Urophycis* spp.; Atlantic herring, *Clupea harengus*; and

Ammodytes spp., all of which comprise 71% of the total catch. The twilight catch at column depths between 101 and 150 m exceeds both the night and day catches and reflects the high twilight catches for Gulf Stream flounder, offshore hake, and to some extent butterfish, *Peprilus triacanthus*.

The daily cycle in mean catch per 10 m² for all larvae is shown in Figure 3a. Catches were highest between hour intervals 1 and 6, with maximum catches at hour 2. Minimum catches occurred between intervals 10 and 17 and averaged only 39% of the catch at interval 2. The ratios of the catch at each hour interval, divided by the

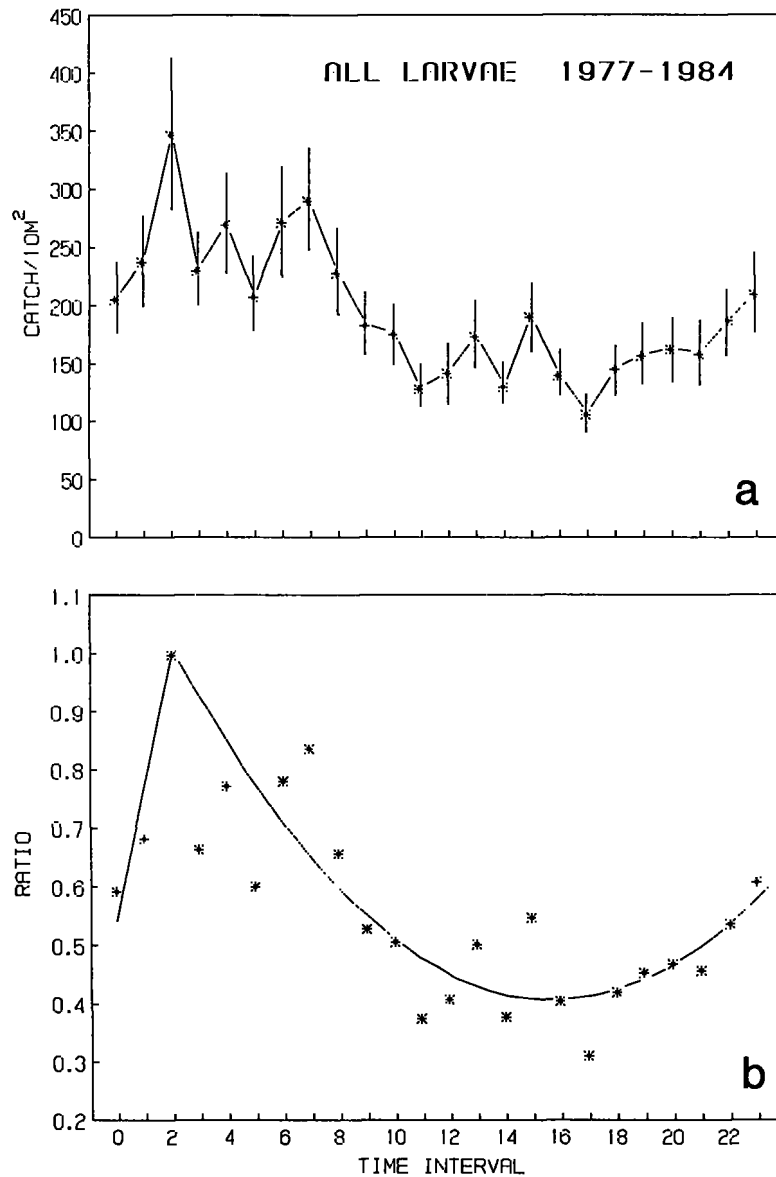


FIGURE 3.—Mean catch per 10 m² by time intervals and standard error bars and plot of ratios of catch at time interval 2 with the fitted curves.

catch at hour 2, yield a correction factor to standardize the catch of all larvae for net avoidance. Two linear functions were fit to the ratios for hour intervals 0–2 and intervals 2–23 for the purpose of calculating the correction factor to account for the daily cycle in catches (Fig. 3b).

The equations are

$$C = 0.5575 + 0.2025 * H$$

$$r^2 = 0.91 \quad n = 3 \quad \text{for } H < 3$$

$$C = 1.1992 - 0.1012 * H + 0.00323 * H^2$$

$$r^2 = 0.81 \quad n = 21 \quad \text{for } H > 2$$

where C = the correction factor and H = the hour interval.

Individual Taxa

A total of 36 taxa, representing 17 families, were analyzed for day, night, and twilight catches based upon their abundance within the data set. These taxa represented fewer than 11% of all taxa caught during the 8 yr study but account for over 90% of all larvae captured. They were selected because their abundance is adequate for statistical comparisons of catches. Of the 36 taxa, four were identified to the generic level due to the uncertainty of species identifications, the rest to the specific level. Table 3, a phylogenetic listing (Robins et al. 1980) of the catch data, analyzes the variance (ANOVA) of the delta mean catch per 10 m² for each of the 36 taxa by day, night, and twilight and presents Tukey tests of paired means when the ANOVA showed significant differences. The ANOVA showed that the catches of 11 of the 36 taxa have significant differences: day versus night for 9 taxa, day versus twilight for 1 species, and night versus twilight for 7 species. It is interesting to note that the first three taxa listed in Table 3, i.e., the top of the phylogenetic list, contain 25% of all the significant differences found.

In a review of larval swimming needs, Theilacker and Dorsey (1980) showed that jack mackerel, *Trachurus symmetricus*; Pacific mackerel, *Scomber japonicus*; and herring, *Clupea harengus* (two short-bodied and a long-bodied morph) are fast swimmers while sardine, *Sardina pilchardus*; and northern anchovy, *Engraulis mordax* (two long-bodied larvae) are slow swimmers. The implication is, of course, that fast swimming larvae will avoid the approaching net and are most likely to show differ-

ences between day and night catches. The larvae of Atlantic menhaden, *Brevoortia tyrannus*; Atlantic herring, *C. maderensis*; and *Ammodytes* spp. are long-bodied, while *B. glaciale*; Atlantic mackerel, *Scomber scombrus*; and *Auxis* spp. are short-bodied. At this point no clear relationship seems evident between general morphology and net avoidance; in fact, the results of this study appear counterintuitive.

The occurrences of the 11 significant differences shown in Table 3 are surprising, given the length frequencies of most species considered. The dual effects of larval mortality and net avoidance produce an exponential decline in the abundance of larvae with increasing length. This results in a concentration of larval abundance in the smallest length intervals (usually 3–7 mm), which should be the lengths that are least able to avoid the net. Because of the preponderance of small larvae in the catches, the mean catch per 10 m² most reflects the abundance of these small larvae, and thus the statistical significance or insignificance of the differences in catches may not reveal the changes in catchability with increasing larval length. It is interesting to note that 29 of the 36 taxa (81%) show higher night catches than day catches, though statistical significance is met in only 9 taxa.

The changes in catchability with length were investigated by calculating the mean catch per 100 m² for each mm length-increment by day, night, and twilight for 26 taxa (Fig. 4). The range of lengths for each species does not show the entire length range captured; rather, they show sequential lengths where positive day, night, and twilight catches were made. For example, *Ammodytes* spp. were captured during day, night, and twilight between lengths 3 and 32 mm but the total length range represented in the 8 yr data set is 1–141 mm. Obviously a mean catch-per-tow of zero cannot be corrected for net avoidance and is therefore not considered in this analysis.

The most common ratios of catches, and the most easily explained in terms of visual net avoidance, are night equals or exceeds day catches, with increasing ratios as larval length increases. The ratios for each length of night:day for expected catches from the regression analysis follow this pattern for 17 of the 26 species analyzed. The magnitude of the difference between night and day varies greatly between species, but the general trend is clearly evident in all 17 species. The only species that shows day catches exceeding night catches at all lengths is

TABLE 3.—Mean larval fish catches per 10 m² for day, night, and twilight made off the significant differences. Numbers in parenthesis

Taxa	Day (D)	Night (N)
<i>Brevoortia tyrannus</i> ¹	0.656(0.180,847)	3.434(1.036,861)
Atlantic menhaden		
<i>Clupea harengus</i> ²	3.943(0.941,1314)	10.048(1.846,1589)
Atlantic herring		
<i>Ceratoscopelus maderensis</i> ³	0.982(0.181,1759)	5.652(0.925,1532)
<i>Benthoosema glaciale</i>	1.725(0.305,2201)	2.066(0.329,1928)
<i>Lophius americanus</i>	0.621(0.052,2543)	0.488(0.053,1994)
Goosefish		
<i>Urophycis</i> spp.	21.505(2.221,2668)	25.563(2.967,2294)
hakes		
<i>Enchelyopus cimbrius</i>	0.694(0.073,2675)	0.838(0.103,2327)
Fourbeard rockling		
<i>Gadus morhua</i>	2.441(0.285,2813)	2.218(0.248,2685)
Atlantic cod		
<i>Melanogrammus aeglefinus</i> ³	6.250(1.031,1456)	4.838(1.058,1211)
Haddock		
<i>Pollachius virens</i> ²	0.683(0.095,1961)	1.083(0.141,2044)
Pollock		
<i>Merluccius albidus</i>	1.289(0.216,1838)	1.662(0.315,1597)
Offshore hake		
<i>Merluccius bilinearis</i>	13.442(1.408,2514)	15.814(1.794,2239)
Silver hake		
<i>Centropristis striata</i> ¹	1.151(0.186,1274)	1.841(0.334,955)
Black seabass		
<i>Pomatomus saltatrix</i> ¹	16.212(2.814,931)	25.967(6.050,585)
Bluefish		
<i>Cynoscion regalis</i> ¹	0.894(0.230,908)	1.515(0.487,695)
Weakfish		
<i>Micropogonias undulatus</i> ¹	5.083(2.144,893)	4.806(1.733,812)
Atlantic croaker		
<i>Tautoglabrus adspersus</i>	3.778(0.518,1363)	8.557(1.528,966)
Cunner		
<i>Tautoga onitis</i> ¹	0.337(0.079,761)	0.688(0.251,498)
Tautog		
<i>Lumpenus lumpreataeformis</i> ³	0.500(0.145,700)	0.250(0.070,581)
Snakeblenny		
<i>Ulvaria subbifurcata</i> ³	0.462(0.152,633)	0.656(0.185,401)
Radiated shanny		
<i>Pholis gunnelus</i>	0.405(0.085,1245)	0.564(0.090,1164)
Rock gunnel		
<i>Ammodytes</i> spp.	48.001(5.311,2267)	125.737(15.608,2125)
Sand lances		
<i>Auxis</i> spp.	2.326(0.500,590)	7.549(1.838,397)
Mackerels		
<i>Scomber scombrus</i>	18.195(4.133,1284)	35.886(10.866,772)
Atlantic mackerel		
<i>Peprilus triacanthus</i>	5.299(0.507,2566)	6.025(0.716,2019)
Butterfish		
<i>Sebastes</i> spp. ³	2.276(0.295,1541)	3.006(0.467,1169)
Redfishes		
<i>Myoxocephalus octodecemspinosus</i>	0.249(0.056,707)	0.699(0.132,731)
Longhorn sculpin		
<i>Citharichthys arctifrons</i> ²	16.288(1.882,1970)	19.577(2.511,1620)
Gulf Stream flounder		
<i>Etropus microstomus</i> ¹	5.977(0.755,1658)	7.873(1.125,1339)
Smallmouth flounder		
<i>Paralichthys dentatus</i> ²	1.795(0.262,1458)	2.135(0.260,1554)
Summer flounder		
<i>Paralichthys oblongus</i> ²	8.089(0.689,1691)	7.578(0.785,1324)
Fourspot flounder		
<i>Scophthalmus aquosus</i> ²	2.694(0.246,2174)	3.348(0.319,1864)
Windowpane flounder		
<i>Hippoglossoides platessoides</i> ³	1.580(0.427,989)	1.268(0.276,700)
American plaice		

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northeast United States during 1977–85 and analysis of variance (F) and Tukey (q) tests for are standard error of the mean catch and sample size.

Taxa	Twilight (T)	F value	q		
			D:N	D:T	N:T
<i>Brevoortia tyrannus</i> ¹ Atlantic menhaden	2.072(1.079,340)	3.542*	**	—	—
<i>Clupea harengus</i> ² Atlantic herring	7.137(2.276,620)	3.898**	**	—	—
<i>Ceratoscopelus maderensis</i> ³ <i>Benthoosema glaciale</i>	2.125(0.636,642) 1.781(0.392,838)	15.928** 0.328	**	—	*
<i>Lophius americanus</i> Goosefish	0.508(0.073,920)	1.814			
<i>Urophycis</i> spp. hakes	28.091(5.008,991)	1.085			
<i>Enchelyopus cimbrius</i> Fourbeard rockling	0.707(0.126,1008)	0.760			
<i>Gadus morhua</i> Atlantic cod	1.552(0.260,1106)	1.776			
<i>Melanogrammus aeglefinus</i> ³ Haddock	3.967(0.961,550)	0.982			
<i>Pollachius virens</i> ² Pollock	0.705(0.141,813)	3.361*	*	—	—
<i>Merluccius albidus</i> Offshore hake	3.284(0.842,682)	5.584**		**	*
<i>Merluccius bilinearis</i> Silver hake	12.235(1.940,964)	0.977			
<i>Centropristis striata</i> ¹ Black seabass	0.857(0.256,433)	3.020*	—	—	*
<i>Pomatomus saltatrix</i> ¹ Bluefish	10.948(3.418,313)	2.467			
<i>Cynoscion regalis</i> ¹ Weakfish	0.981(0.313,331)	0.922			
<i>Micropogonias undulatus</i> ¹ Atlantic croaker	0.842(0.348,327)	0.838			
<i>Tautoglabrus adspersus</i> Cunner	4.217(1.052,467)	6.633**	**	—	*
<i>Tautoga onitis</i> ¹ Tautog	0.527(0.223,244)	1.275			
<i>Lumpenus lumpretaeformis</i> ³ Snakeblenny	0.272(0.147,273)	1.307			
<i>Ulvaria subbifurcata</i> ² Radiated shanny	0.436(0.224,192)	0.403			
<i>Pholis gunnelus</i> Rock gunnel	0.482(0.119,494)	0.862			
<i>Ammodytes</i> spp. Sand lances	71.144(10.956,896)	13.376**	**	—	**
<i>Auxis</i> spp. Mackerels	2.091(0.891,194)	6.901**	**	—	*
<i>Scomber scombrus</i> Atlantic mackerel	15.607(5.899,410)	2.128			
<i>Pepilus triacanthus</i> Butterfish	5.741(0.918,915)	0.372			
<i>Sebastes</i> spp. ³ Redfishes	1.985(0.350,560)	1.580			
<i>Myoxocephalus octodecemspinosus</i> Longhorn sculpin	0.324(0.122,329)	4.853**	**	—	—
<i>Citharichthys arctifrons</i> ² Gulf Stream flounder	21.337(4.178,703)	0.943			
<i>Etropus microstomus</i> ¹ Smallmouth flounder	3.921(0.947,589)	2.946			
<i>Paralichthys dentatus</i> ² Summer flounder	1.872(0.402,600)	0.452			
<i>Paralichthys oblongus</i> ² Fourspot flounder	7.705(1.235,597)	0.125			
<i>Scophthalmus aquosus</i> ² Windowpane flounder	3.647(0.626,787)	1.928			
<i>Hippoglossoides platessoides</i> ³ American plaice	2.614(1.237,329)	1.093			

TABLE 3.—Continued.

Taxa	Day (D)	Night (N)
<i>Glyptocephalus cynoglossus</i> Witch flounder	0.908(0.080,2716)	0.987(0.120,2122)
<i>Limanda ferruginea</i> Yellowtail flounder	5.488(0.510,2110)	8.241(0.963,1492)
<i>Pseudopleuronectes americanus</i> Winter flounder	0.358(0.063,1317)	0.561(0.116,907)

* = $P < 0.05$.

** = $P < 0.01$.

¹samples from Middle Atlantic Bight and Southern New England subareas.

²samples from Middle Atlantic, Southern New England, and Georges Bank subareas.

³samples from Southern New England, Georges Bank, and Gulf of Maine subareas.

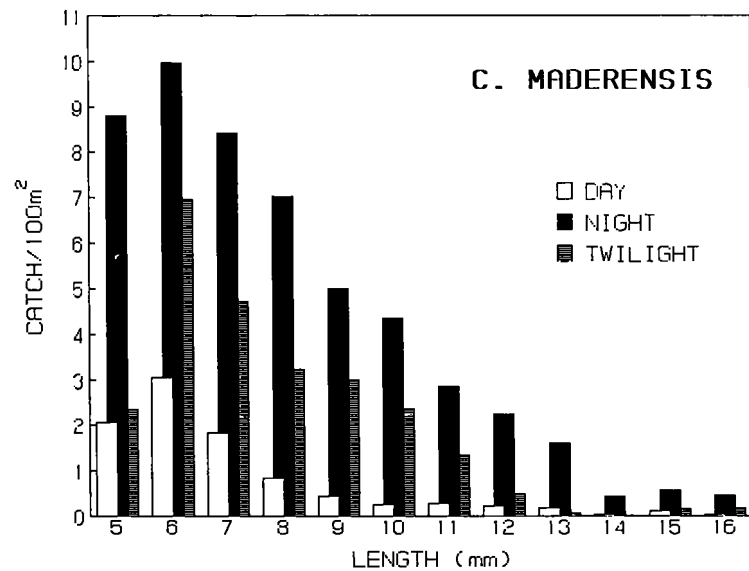
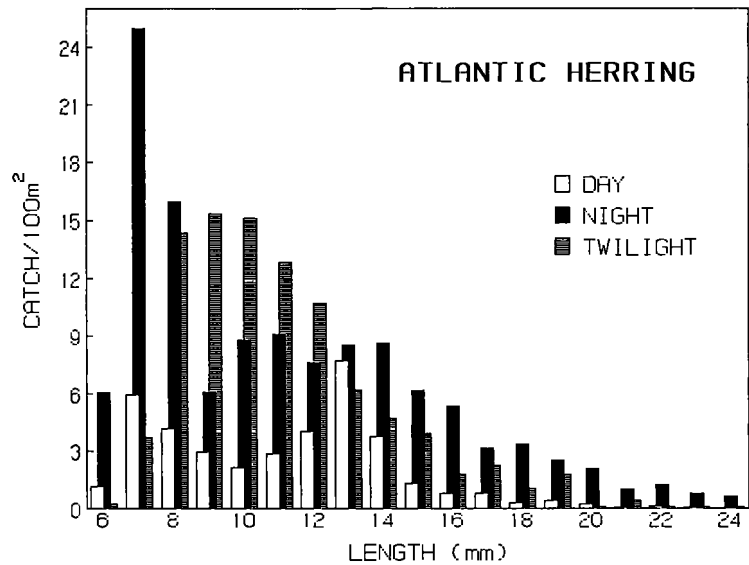
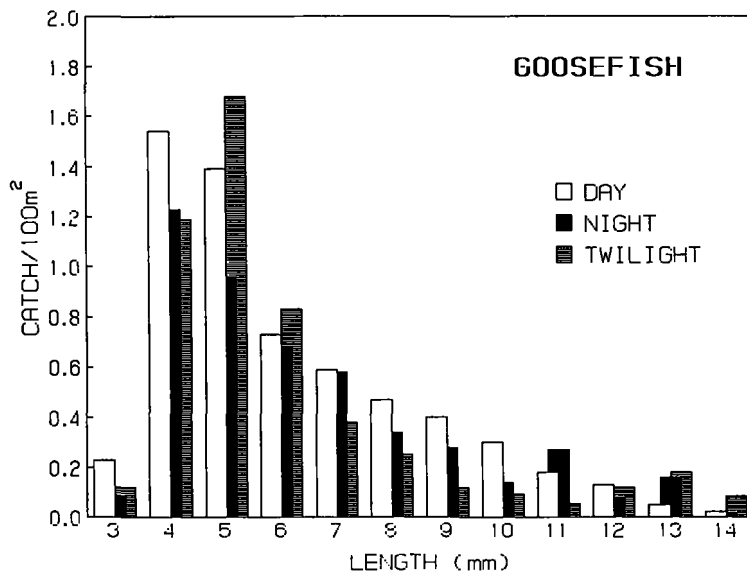
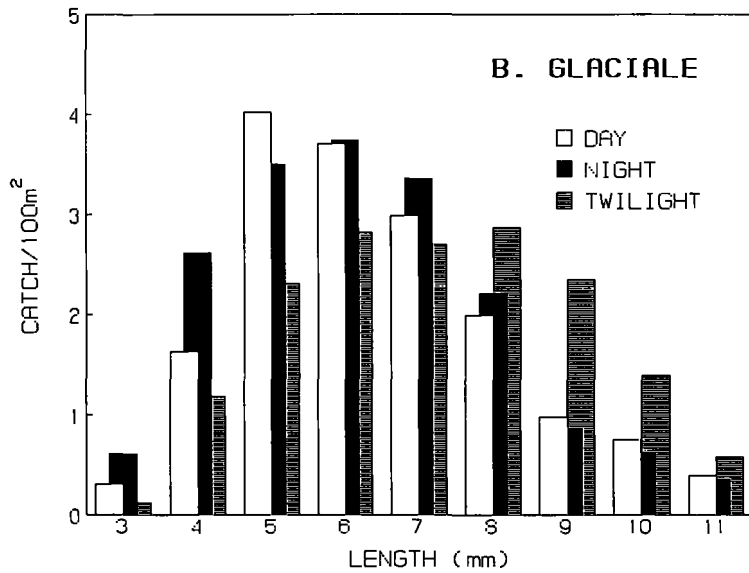


FIGURE 4 a-g.—Plots of mean catch per 100 m² by length for day, night, United States,

Taxa	Twilight (T)	F value	q		
			D:N	D:T	N:T
<i>Glyptocephalus cynoglossus</i> Witch flounder	0.702(0.102,974)	1.297			
<i>Limanda ferruginea</i> Yellowtail flounder	5.589(0.972,706)	4.237*	**	—	*
<i>Pseudopleuronectes americanus</i> Winter flounder	0.388(0.127,453)	1.460			



and twilight for 26 taxa of fish larvae collected off the northeast 1977-84.

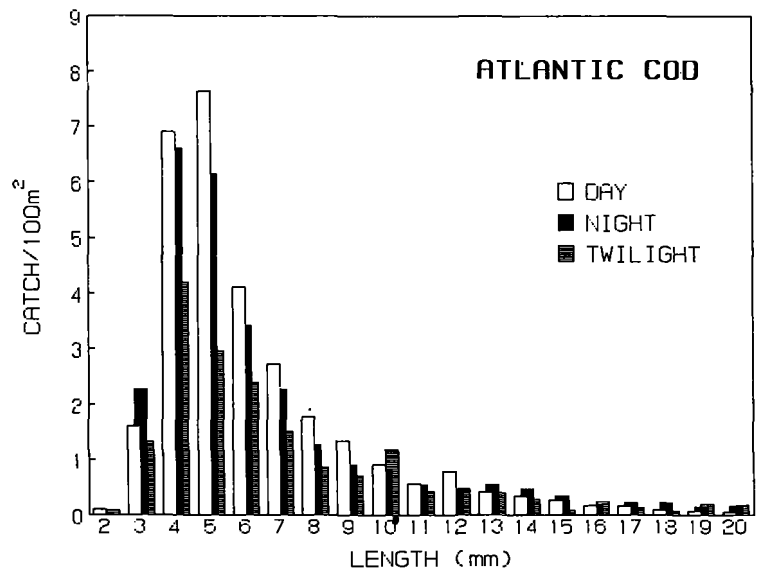
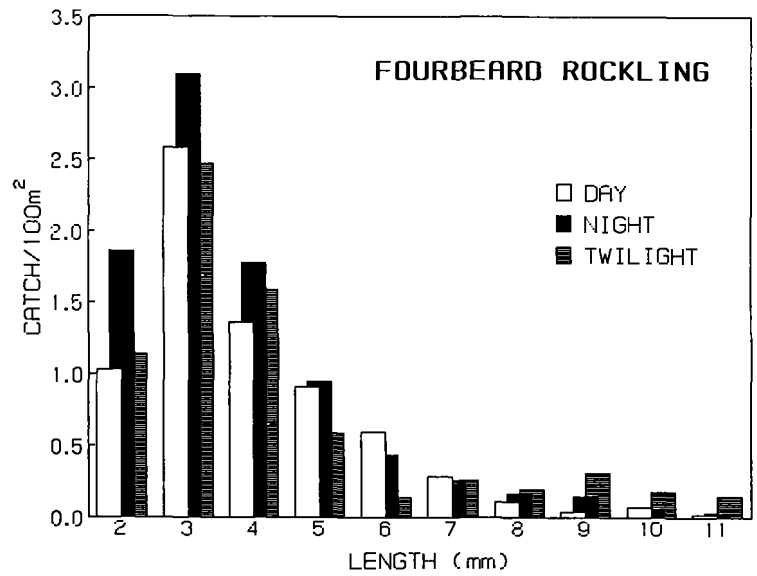
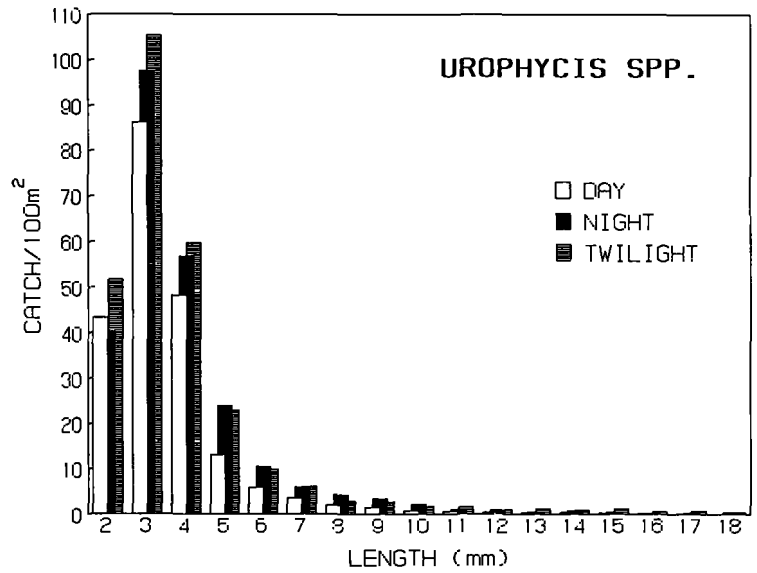
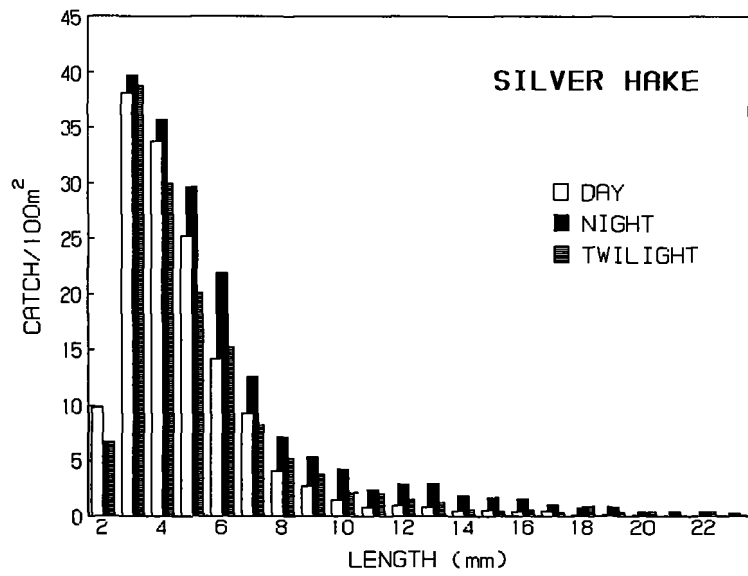
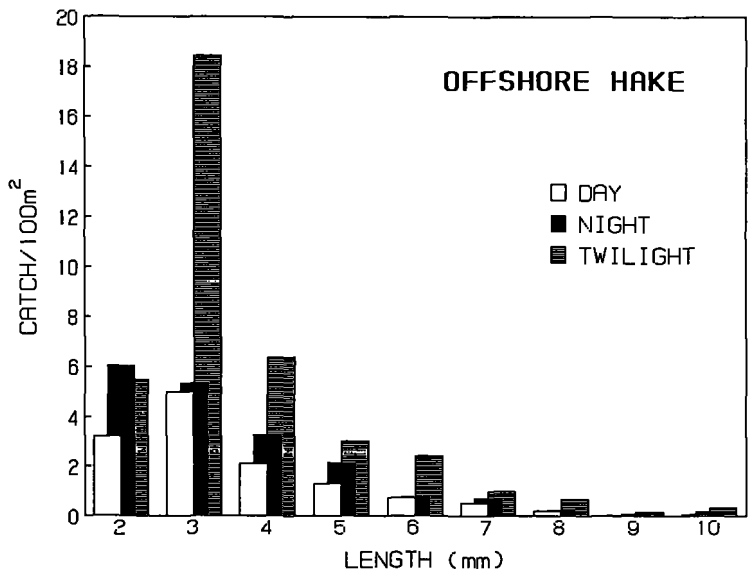
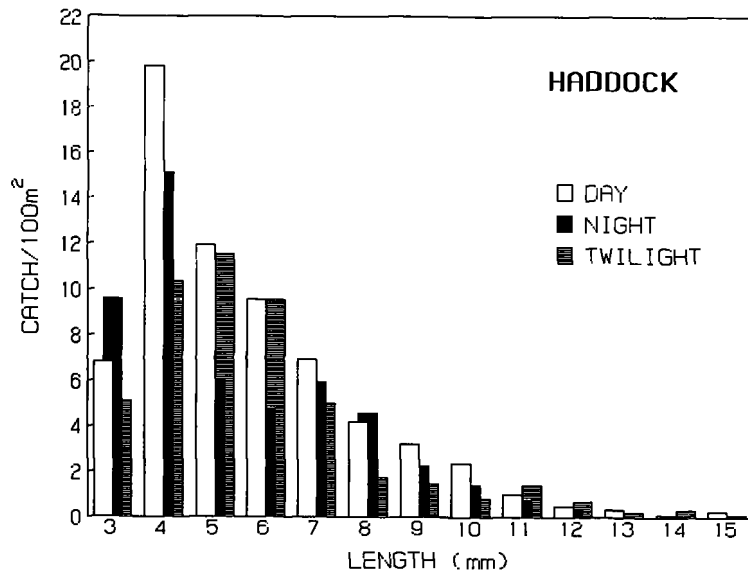


FIGURE 4.—Continued.

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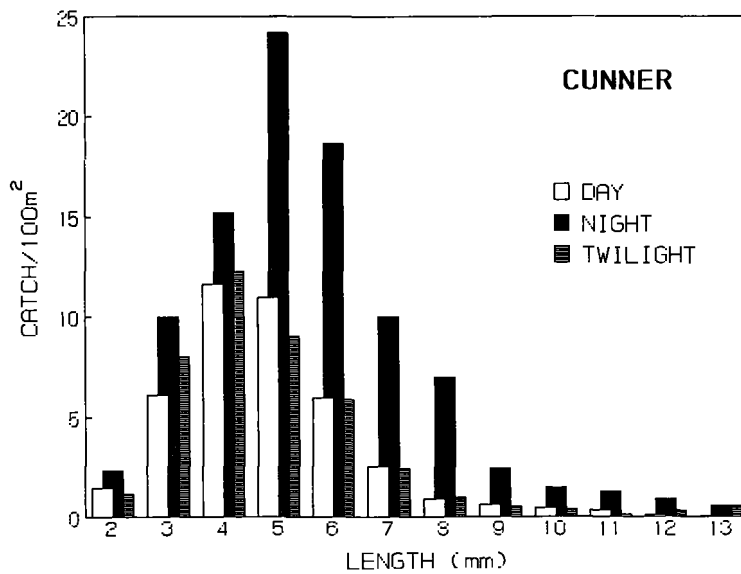
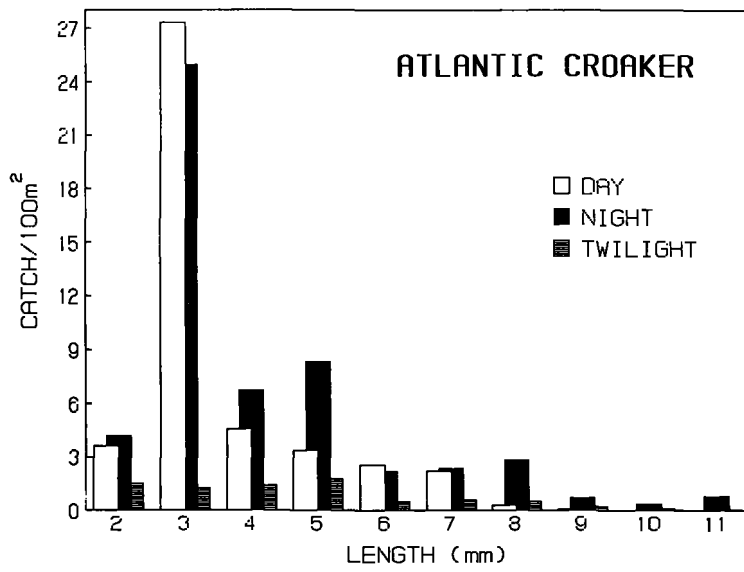
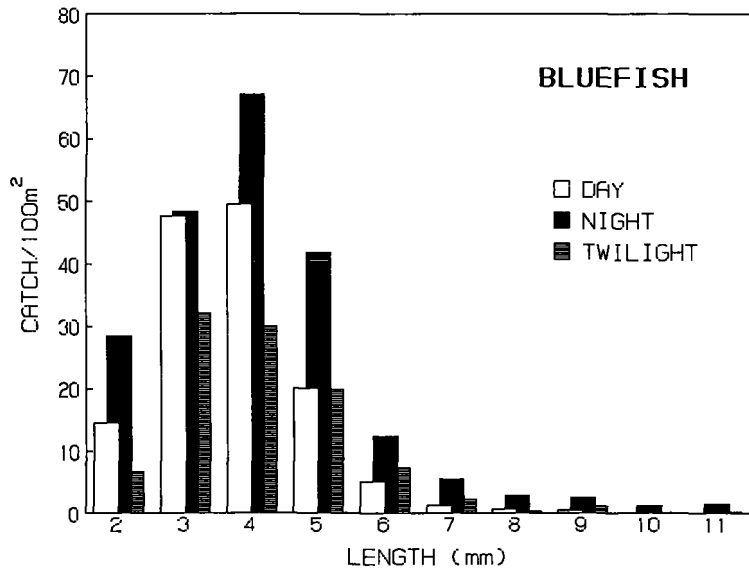
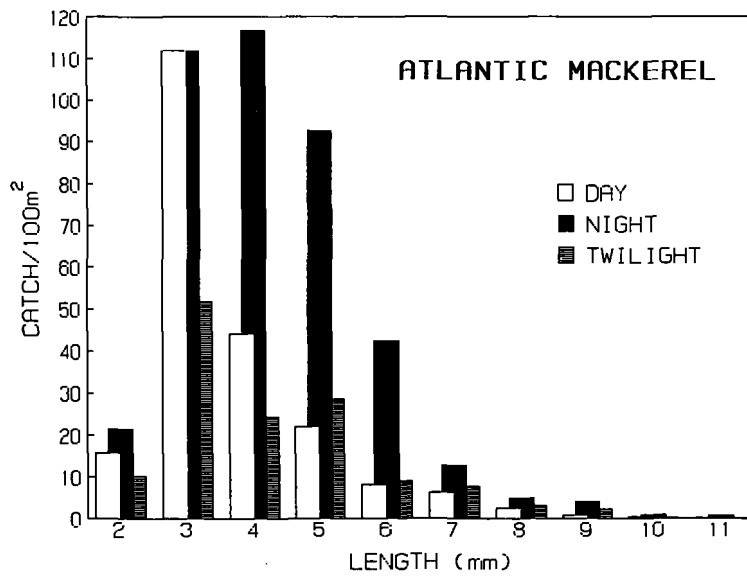
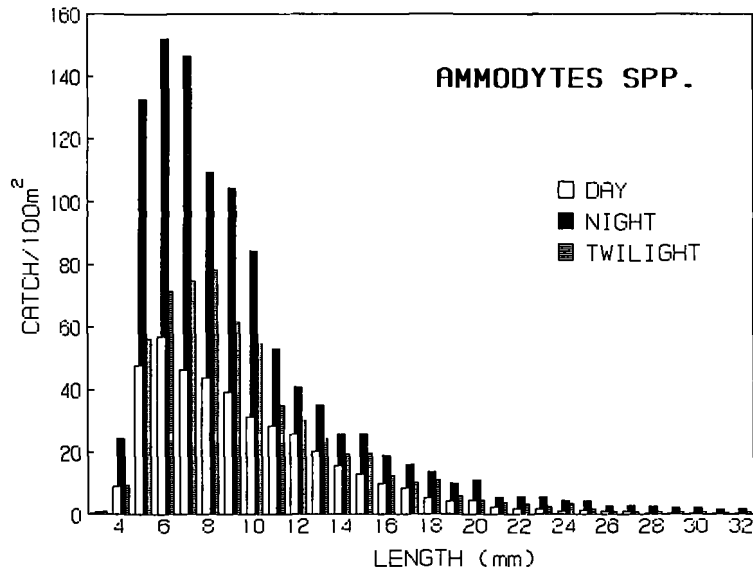
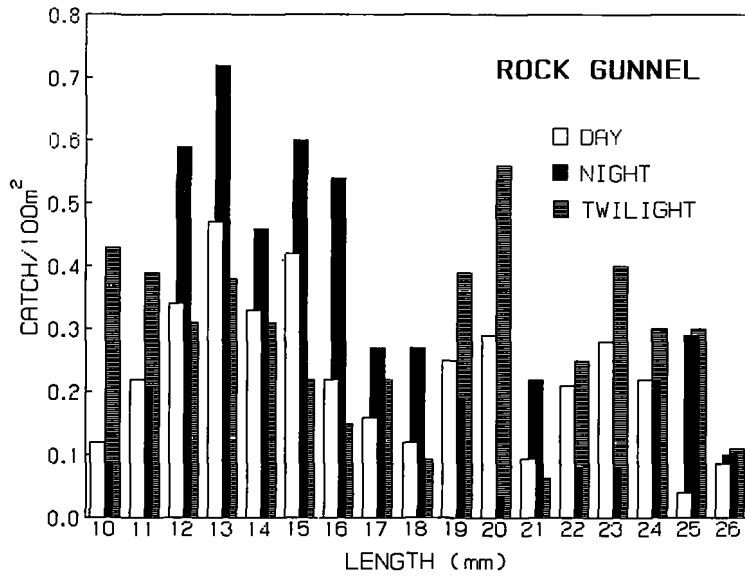


FIGURE 4.—Continued.

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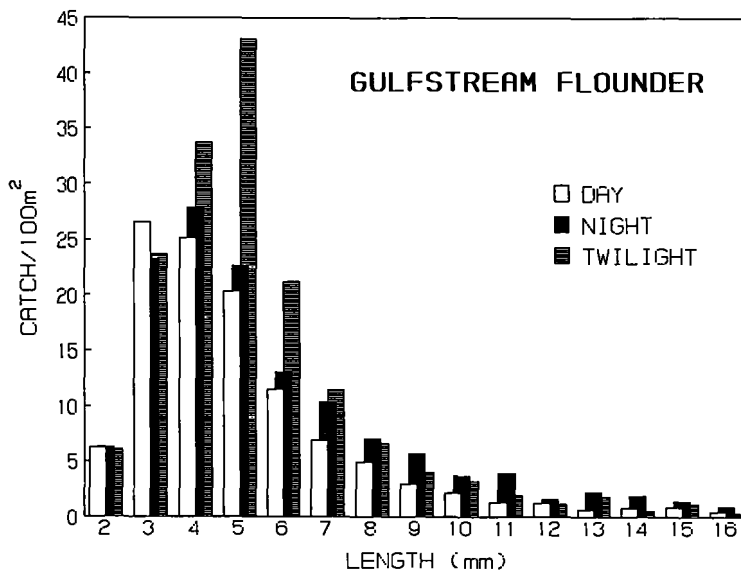
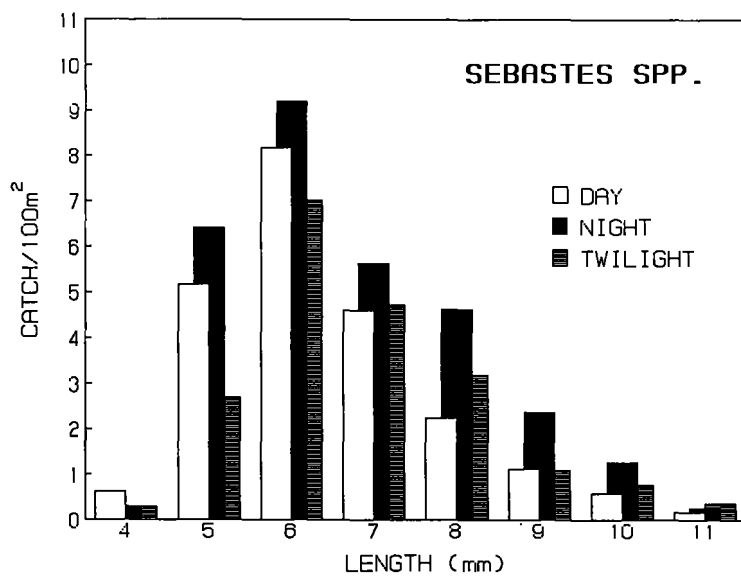
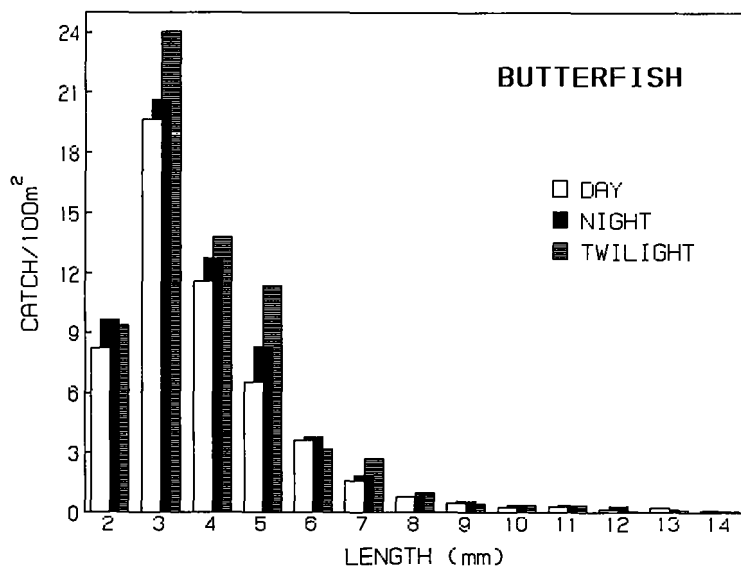
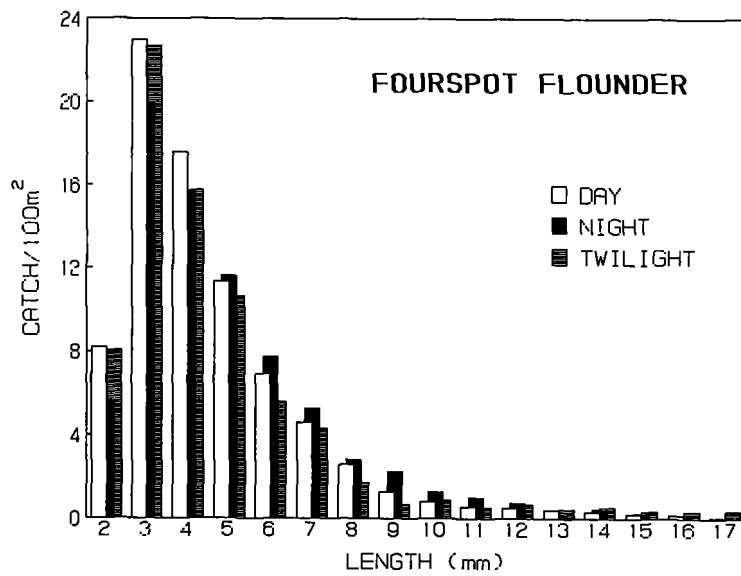
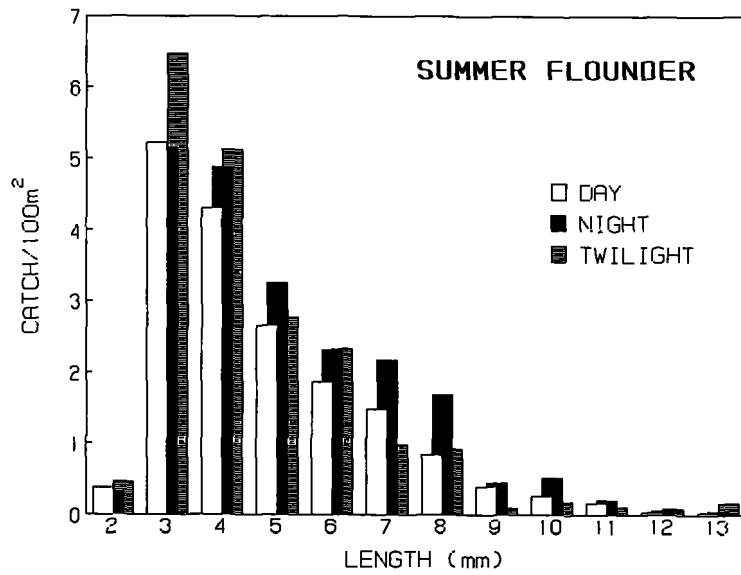
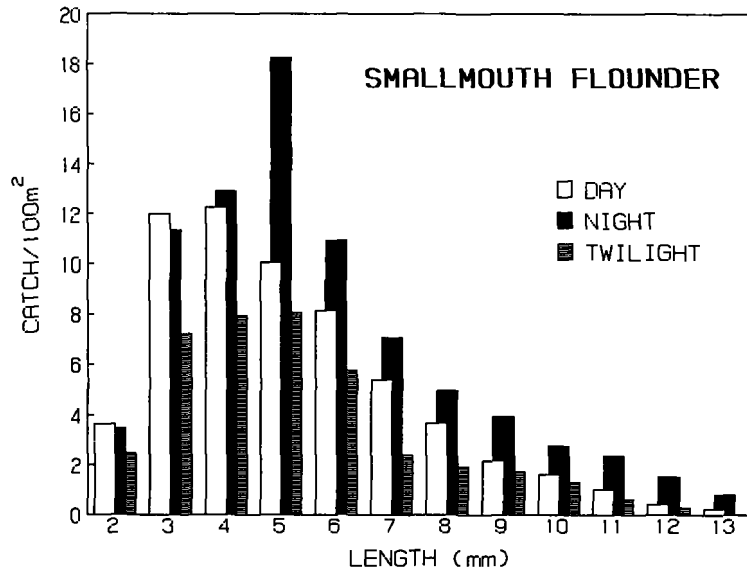


FIGURE 4.—Continued.

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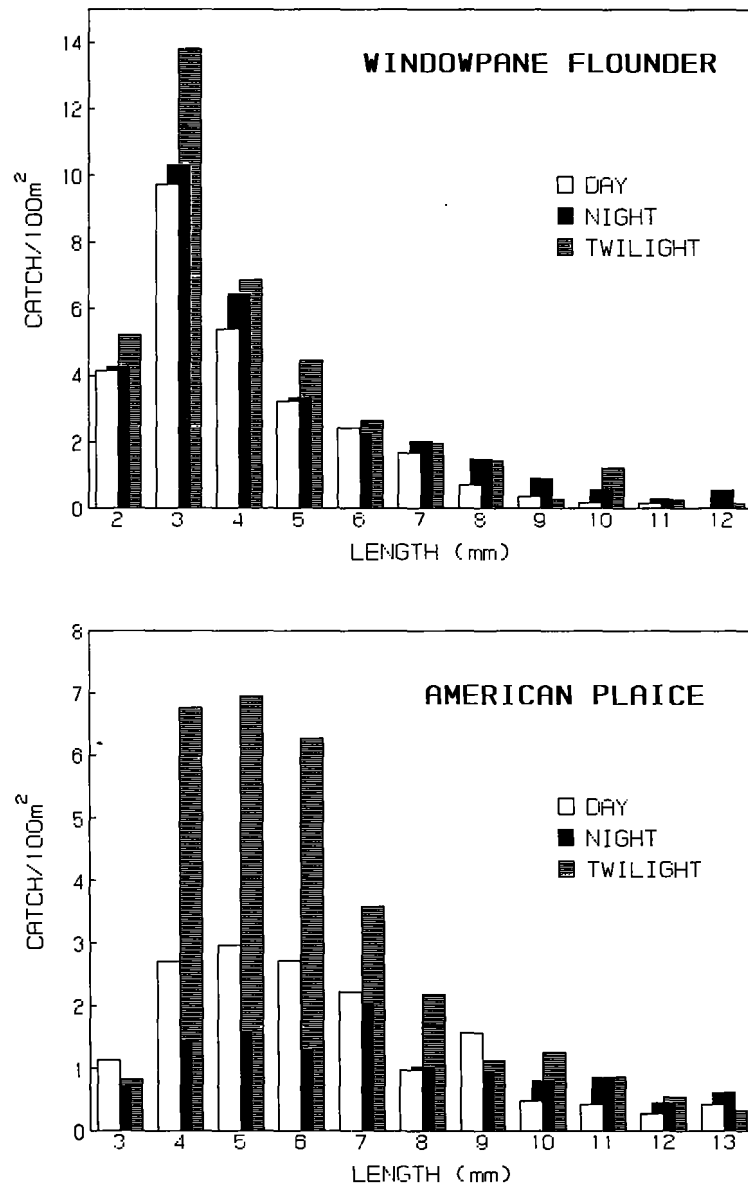
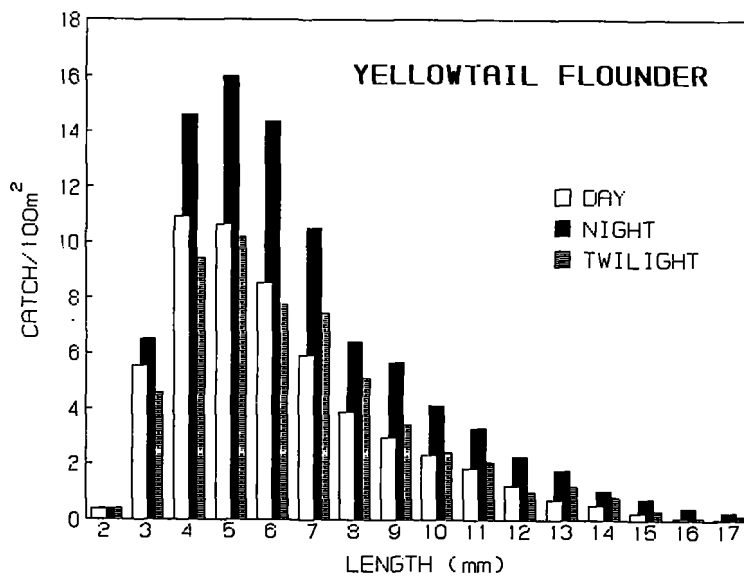
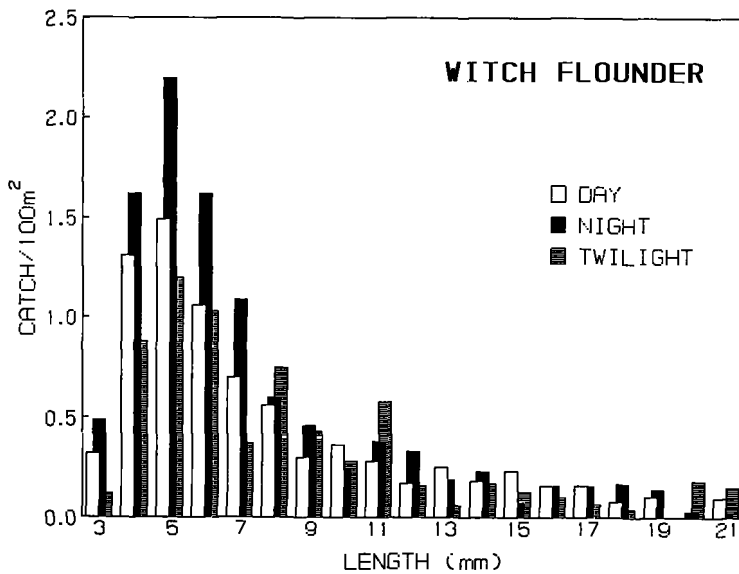


FIGURE 4.—Continued.

the haddock. Both butterfish and *B. glaciale* catches are about the same for night and day, regardless of length. Three species show a trend of decreasing ratios of night:day with increasing length with night catches exceeding day catches at the smaller lengths: witch flounder, *Glyptocephalus cynoglossus*; fourspot flounder, *Paralichthys oblongus*; and fourbeard rockling, *Enchelyopus cimbrius*. The last three species, Atlantic cod, *Gadus morhua*; goosetfish; and American plaice, *Hippoglossoides platessoides*, have day catches exceeding night catches at the small lengths and as they grow the ratios of night:day equal or exceed one.

If net avoidance by fish larvae is visually cued, the expected ratios of twilight-to-day catches

would exceed one and increase with increasing fish length. Another expectation would be that night catches would exceed, on average, twilight catches. As shown in Table 3, 16 of 36 taxa conform to the ranking of night > twilight > day catches. A total of 16 of the 26 taxa analyzed by length (Fig. 4) shows increasing twilight:day catch ratios, determined from expected values from the regression analysis, with increasing length. However, Figure 4 also shows twilight catches often exceeding night catches at some lengths for many taxa. Outstanding examples of dominant twilight catches are offshore hake, American plaice, butterfish, and windowpane flounder, *Scophthalmus aquosus*. The catches of offshore hake show that twilight catches domi-



nate at all lengths ($\approx 50\%$ of the total catch) and day catches amount approximately to only 20% of the total. This relationship of catches is unique among the 26 taxa analyzed and is statistically significant ($P < 0.01$, Table 3). Offshore hake larvae occur mostly at the shelf break in depths > 200 m (Morse et al. 1987). Since the maximum water column depth sampled by the net was 200 m, collections of this species may reflect a vertical migration pattern into the net sampling area during twilight as well as visually cued net avoidance.

The catches of *B. glaciale*, *C. maderensis*, Atlantic herring, and rock gunnel, *Pholis gunnelus*, reveal some unique characteristics as analyzed by day, night, and twilight. The length

range for *B. glaciale* in Figure 4 is 3–11 mm, but the entire range sampled during this study is from 3 to 52 mm. At 12 mm, the length at which metamorphosis occurs (Halliday 1970), this species is virtually absent from all daylight catches (i.e., 3 individuals > 11 mm in 2,201 tows) though they are abundant, measuring up to about 25 mm long, in both night and twilight tows. Larvae are most abundant at the offshore extreme of the survey area (Morse et al. 1987), and the average bottom depth where they occur is about 400 m while the maximum tow depth is 200 m. Assuming fish begin at metamorphosis, the characteristic vertical migrations of juveniles and adults, this extreme case of net avoidance represents the effect of vertical migration

during the day below the path of the net. Halliday (1970) found the center of distribution during the day is below 450 m (250 fathoms) and at night between 45 and 90 m (25 and 50 fathoms). In contrast to *B. glaciale*, the lanternfish, *C. maderensis*, was captured in all light regimes up to 16 mm. With this species, night catches dominated both day and twilight catches by up to 10 times, but the total length range captured changed little, regardless of light conditions. The length frequencies of Atlantic herring show a distinct polymodality for both day and night catches with peaks occurring at various lengths, depending upon the light regime considered (Fig. 4).

The catches of rock gunnel larvae are the most erratic of the 26 species presented. There appears to be little decrease in abundance with increasing length and they have the lowest ratios of day, night, and twilight catches of any taxa. Figure 4 shows a slight dominance of night catches at the smaller sizes and of twilight catches at the larger sizes. The minimum length (10 mm) corresponds to the large hatching size of rock gunnel and is the largest of any taxa treated here.

Correction Factors

The estimates of the coefficients of the expon-

TABLE 4.—Regression coefficients and mean square error (MSE) for the relationship of mean catch per 100 m² United States, 1977–84. Regression constants for the quadratic equation relating the ratios (*R*) of night:day and the estimate.

Taxon	Day			Night			Twilight		
	<i>a</i>	<i>b</i>	MSE	<i>a</i>	<i>b</i>	MSE	<i>a</i>	<i>b</i>	MSE
Atlantic herring	4.318 (0.478)	-0.290 (0.0293)	0.415	4.306 (0.241)	-0.186 (0.0147)	0.106	5.606 (0.623)	-0.323 (0.0381)	0.703
<i>Ceratoscopelus maderensis</i>	3.150 (0.484)	-0.400 (0.0423)	0.197	4.595 (0.321)	-0.338 (0.0280)	0.086	5.215 (1.043)	-0.504 (0.0912)	0.914
<i>Benthoosema glaciale</i>	3.691 (0.334)	-0.404 (0.0405)	0.046	3.790 (0.507)	-0.422 (0.0615)	0.106	2.281 (0.654)	-0.204 (0.0794)	0.176
Goosefish	2.225 (0.308)	-0.383 (0.0323)	0.115	1.769 (0.514)	-0.348 (0.0539)	0.320	1.268 (0.573)	-0.299 (0.0600)	0.396
<i>Urophycis</i> spp.	4.602 (0.383)	-0.410 (0.0334)	0.379	4.828 (0.355)	-0.371 (0.0310)	0.326	4.488 (0.394)	-0.321 (0.0344)	0.402
Fourbeard rockling	2.809 (0.332)	-0.600 (0.0445)	0.119	2.688 (0.181)	-0.550 (0.0243)	0.035	1.193 (0.622)	-0.310 (0.0834)	0.417
Atlantic cod	3.185 (0.118)	-0.307 (0.0091)	0.034	2.423 (0.212)	-0.233 (0.0163)	0.109	1.972 (0.291)	-0.223 (0.0225)	0.206
Haddock	4.887 (0.339)	-0.442 (0.0336)	0.161	5.237 (0.458)	-0.546 (0.0453)	0.293	4.354 (0.333)	-0.418 (0.0329)	0.155
Offshore hake	3.521 (0.531)	-0.653 (0.0770)	0.249	3.384 (0.435)	-0.568 (0.0631)	0.167	4.432 (0.484)	-0.616 (0.0702)	0.207
Silver hake	4.560 (0.217)	-0.357 (0.0151)	0.176	4.195 (0.148)	-0.242 (0.0103)	0.082	4.043 (0.280)	-0.276 (0.0196)	0.294
Bluefish	7.453 (0.412)	-0.947 (0.0526)	0.116	6.260 (0.536)	-0.588 (0.0683)	0.196	6.406 (0.890)	-0.770 (0.113)	0.540
Atlantic croaker	5.974 (0.622)	-0.913 (0.0834)	0.417	4.065 (0.505)	-0.445 (0.0677)	0.275	1.891 (0.379)	-0.379 (0.0508)	0.155
Cunner	5.586 (0.385)	-0.655 (0.0411)	0.101	5.721 (0.279)	-0.497 (0.0298)	0.053	3.978 (0.923)	-0.449 (0.0990)	0.584
Rock gunnel	0.414 (0.707)	-0.106 (0.0355)	0.286	1.072 (0.912)	-0.133 (0.0458)	0.477	-0.253 (1.051)	-0.0712 (0.0527)	0.633
<i>Ammodytes</i> spp.	5.710 (0.104)	-0.223 (0.0050)	0.045	5.926 (0.117)	-0.177 (0.0056)	0.056	5.775 (0.141)	-0.203 (0.0067)	0.081
Atlantic mackerel	7.019 (0.181)	-0.782 (0.0243)	0.035	7.484 (0.432)	-0.701 (0.0579)	0.201	6.583 (0.651)	-0.732 (0.0873)	0.457

ential regression equations fitted to the mean catch per 100 m² and to the length for each taxa are shown in Table 4. The regression fitted to twilight catches is often not as accurate as for day or night. This is not surprising because twilight catches represent the transitional time between light and dark regimes when visual avoidance responses to the net are expected to be most variable. This variability is evident in the often high twilight catches at the larger sizes.

The ratios of expected catches calculated from the exponential regressions for night:day and twilight:day catches were fit to polynomial equations and yield corrections for catchability for day, night, and twilight catches (Table 4).

Mortality

Catches of each taxa were corrected for day, night, and twilight catchability, and the mean catch per tow (number/100 m²) was again calculated for each mm length and the exponential decay model fit to the length frequencies. The slope of the fitted line was used as an estimate of length-dependent mortality (Ebert 1973). Mortalities ranged from 0.114 for rock gunnel to 0.701 for Atlantic mackerel (Table 5). A review of the spawning times of the 26 taxa (Colton et al. 1979; Morse et al. 1987) reveals that 4 of the 6 taxa with the lowest mortalities are winter spawners, and 5 of the 6 taxa with the highest

(C) versus larval length (mm) as $C = a \cdot \exp(\text{length} \cdot b)$ for day, night, and twilight by taxon for larvae caught off the northeast twilight:day mean catches versus larval length (L) where $R = a + b_1 L + b_2 L^2$. Numbers in parenthesis are standard error of

Taxon	N/D ratios			T/D ratios		
	a	b ₁	b ₂	a	b ₁	b ₂
Atlantic herring	3.101 (0.260)	-0.325 (0.0360)	0.0287 (0.00115)	3.580 (0.00341)	-0.109 (4.72 × 10 ⁻⁴)	0.00118 (1.51 × 10 ⁻⁵)
<i>Caratoscopelus maderensis</i>	4.572 (0.0372)	0.168 (0.00714)	0.0164 (3.22 × 10 ⁻⁴)	7.146 (0.0530)	-0.576 (0.0102)	0.0140 (4.49 × 10 ⁻⁴)
<i>Bentosema glaciale</i>	1.104 (4.77 × 10 ⁻⁵)	-0.0200 (1.25 × 10 ⁻⁵)	1.59 × 10 ⁻⁴ (7.70 × 10 ⁻⁷)	0.777 (0.0815)	-0.145 (0.0213)	0.0249 (0.00132)
Goosefish	0.637 (0.0815)	0.0209 (0.0213)	5.31 × 10 ⁻⁴ (0.00132)	0.424 (4.45 × 10 ⁻⁴)	0.0173 (1.07 × 10 ⁻⁴)	0.00297 (5.86 × 10 ⁻⁶)
<i>Urophycis</i> spp.	1.266 (0.00204)	0.0437 (4.32 × 10 ⁻⁴)	0.00142 (2.02 × 10 ⁻⁵)	1.061 (0.0296)	0.0181 (0.00630)	0.00909 (2.94 × 10 ⁻⁴)
Fourbeard rockling	0.892 (0.00101)	0.0407 (3.15 × 10 ⁻⁴)	0.00153 (2.22 × 10 ⁻⁵)	1.369 (0.268)	-0.477 (0.0834)	0.0707 (0.00588)
Atlantic cod	0.546 (0.0118)	0.0106 (0.00217)	0.00320 (8.90 × 10 ⁻⁵)	0.380 (0.0126)	3.7 × 10 ⁻⁴ (0.00231)	0.00299 (9.47 × 10 ⁻⁵)
Haddock	1.336 (0.00839)	-0.113 (0.00192)	0.00293 (9.97 × 10 ⁻⁵)	0.588 (1.37 × 10 ⁻⁴)	0.0136 (3.13 × 10 ⁻⁵)	2.09 × 10 ⁻⁴ (1.63 × 10 ⁻⁶)
Offshore hake	0.901 (0.00521)	0.0585 (0.00174)	0.00554 (1.32 × 10 ⁻⁴)	2.491 (8.63 × 10 ⁻⁴)	0.0883 (2.87 × 10 ⁻⁴)	0.00213 (2.18 × 10 ⁻⁵)
Silver hake	1.571 (0.164)	-0.180 (0.0284)	0.0227 (0.00107)	0.765 (0.0292)	-0.00350 (0.00505)	0.00575 (1.90 × 10 ⁻⁴)
Bluefish	8.415 (1.744)	-3.021 (0.495)	0.332 (0.0327)	0.688 (0.0570)	-0.0769 (0.0162)	0.0216 (0.00107)
Atlantic croaker	12.443 (3.420)	-5.265 (1.064)	0.572 (0.0750)	3.331 (0.981)	-1.408 (0.305)	0.146 (0.0215)
Cunner	2.614 (0.217)	-0.314 (0.0509)	0.0610 (0.00280)	1.032 (0.133)	-0.232 (0.0313)	0.0288 (0.00172)
Rock gunnel	1.902 (0.00146)	-0.0472 (1.53 × 10 ⁻⁴)	4.17 × 10 ⁻⁴ (3.93 × 10 ⁻⁶)	0.557 (0.00289)	0.0114 (3.5 × 10 ⁻⁴)	6.35 × 10 ⁻⁴ (7.78 × 10 ⁻⁶)
<i>Ammodytes</i> spp.	1.474 (0.0270)	0.0146 (0.00306)	0.00351 (7.72 × 10 ⁻⁵)	1.080 (0.00130)	0.0204 (1.48 × 10 ⁻⁴)	3.71 × 10 ⁻⁴ (3.73 × 10 ⁻⁶)
Atlantic mackerel	1.648 (0.00987)	0.100 (0.00309)	0.00918 (2.16 × 10 ⁻⁴)	0.651 (7.47 × 10 ⁻⁴)	0.0298 (2.32 × 10 ⁻⁴)	0.00113 (1.64 × 10 ⁻⁴)

TABLE 4.—Continued

Taxon	Day			Night			Twilight		
	a	b	MSE	a	b	MSE	a	b	MSE
Butterfish	4.061 (0.332)	-0.479 (0.0362)	0.188	4.226 (0.276)	-0.482 (0.0300)	0.129	4.694 (0.323)	-0.548 (0.0353)	0.178
<i>Sebastes</i> spp.	6.661 (0.363)	-0.738 (0.0418)	0.030	6.415 (0.886)	-0.651 (0.102)	0.183	5.733 (0.395)	-0.606 (0.0455)	0.036
Gulf Stream flounder	4.637 (0.232)	-0.332 (0.0217)	0.086	4.624 (0.168)	-0.274 (0.0157)	0.045	5.524 (0.311)	-0.387 (0.0291)	0.154
Smallmouth flounder	6.088 (0.923)	-0.620 (0.0930)	0.714	4.802 (0.246)	-0.386 (0.0248)	0.051	5.145 (0.610)	-0.555 (0.0615)	0.312
Summer flounder	3.624 (0.271)	-0.516 (0.0315)	0.109	3.655 (0.378)	-0.481 (0.0439)	0.212	3.279 (0.517)	-0.468 (0.0601)	0.398
Fourspot flounder	4.218 (0.175)	-0.396 (0.0161)	0.072	4.635 (0.266)	-0.440 (0.0244)	0.166	3.514 (0.347)	-0.311 (0.0320)	0.287
Windowpane flounder	4.361 (0.361)	-0.612 (0.0450)	0.167	3.212 (0.261)	-0.365 (0.0325)	0.087	3.864 (0.449)	-0.466 (0.0560)	0.258
American plaice	2.460 (0.355)	-0.282 (0.0395)	0.129	1.117 (0.238)	-0.129 (0.0266)	0.058	3.650 (0.216)	-0.356 (0.0240)	0.048
Witch flounder	0.636 (0.220)	-0.153 (0.0158)	0.102	1.497 (0.329)	-0.222 (0.0237)	0.229	0.423 (0.446)	-0.148 (0.0321)	0.421
Yellowtail flounder	4.841 (0.323)	-0.421 (0.0278)	0.141	4.656 (0.140)	-0.331 (0.0120)	0.026	4.557 (0.337)	-0.376 (0.0290)	0.153

TABLE 5.—A list by taxa of the mean surface water temperature (T) of larval fish samples, the instantaneous growth rate (G_w), the minimum length (L_n) and maximum length (L_m) used in the analysis, the days (t) between L_n and L_m , and the instantaneous length (Z_i) and daily (Z_t) mortality rates.

Taxon	T (°C)	G_w	L_n (mm)	L_m (mm)	t (d)	Z_i	Z_t
Atlantic herring	10.5	0.134	7	24	38.16	0.196	0.0873
<i>C. maderensis</i>	19.9	0.269	6	16	15.13	0.338	0.223
<i>B. glaciale</i>	12.4	0.161	5	11	20.32	0.161	0.0780
Goosefish	19.3	0.261	4	14	19.92	0.366	0.261
<i>Urophycis</i> spp.	20.0	0.271	3	18	27.44	0.330	0.180
Fourbeard rockling	15.6	0.207	4	11	26.05	0.399	0.123
Atlantic cod	5.8	0.0661	4	20	101.20	0.259	0.0409
Haddock	6.5	0.0762	4	15	72.17	0.442	0.0674
Offshore hake	16.4	0.219	3	10	22.83	0.616	0.189
Silver hake	17.0	0.227	3	23	37.24	0.242	0.130
Bluefish	23.3	0.318	4	11	13.20	0.588	0.312
Atlantic croaker	20.5	0.278	3	11	19.40	0.481	0.198
Cunner	20.7	0.281	3	13	14.11	0.497	0.282
Rock gunnel	4.4	0.0459	13	26	62.67	0.114	0.0236
<i>Ammodytes</i> spp.	4.6	0.0488	5	32	157.86	0.177	0.0303
Atlantic mackerel	14.4	0.190	3	11	28.38	0.701	0.198
Butterfish	21.6	0.294	3	14	21.74	0.503	0.255
<i>Sebastes</i> spp.	13.3	0.174	6	11	14.46	0.606	0.225
Gulf Stream flounder	23.2	0.317	5	16	15.23	0.298	0.215
Smallmouth flounder	24.5	0.335	4	13	14.60	0.393	0.242
Summer flounder	15.1	0.200	3	13	30.43	0.481	0.158
Fourspot flounder	21.6	0.294	3	17	24.49	0.359	0.205
Windowpane flounder	16.2	0.216	3	12	26.63	0.403	0.136
American plaice	8.6	0.132	4	13	37.06	0.326	0.0791
Witch flounder	10.0	0.127	5	20	45.30	0.185	0.0612
Yellowtail flounder	13.8	0.181	5	17	28.06	0.331	0.142

Taxon	N/D ratios			T/D ratios		
	<i>a</i>	<i>b</i> ₁	<i>b</i> ₂	<i>a</i>	<i>b</i> ₁	<i>b</i> ₂
Butterfish	1.174 (*.)	-0.00383 (*.)	6.10×10 ⁻⁶ (*.)	1.847 (0.00378)	-0.116 (9.81×10 ⁻⁴)	0.00251 (5.68×10 ⁻⁵)
<i>Sebastes</i> spp.	0.868 (0.00959)	0.0376 (0.00232)	0.00619 (1.36×10 ⁻⁴)	0.603 (0.0251)	-0.0189 (0.00608)	0.0107 (3.56×10 ⁻⁴)
Gulf Stream flounder	1.025 (0.00547)	0.0438 (0.00119)	0.00300 (5.88×10 ⁻⁵)	2.394 (0.00367)	-0.120 (7.99×10 ⁻⁴)	0.00213 (3.94×10 ⁻⁵)
Smallmouth flounder	2.969 (0.460)	-0.771 (0.103)	0.0763 (0.00536)	0.410 (0.00265)	0.0182 (5.73×10 ⁻⁴)	0.00152 (2.99×10 ⁻⁵)
Summer flounder	1.035 (5.52×10 ⁻⁴)	0.0346 (1.52×10 ⁻⁴)	8.42×10 ⁻⁴ (9.34×10 ⁻⁶)	0.715 (0.00106)	0.0309 (2.93×10 ⁻⁴)	0.00119 (1.80×10 ⁻⁵)
Fourspot flounder	1.508 (0.00136)	-0.0623 (3.03×10 ⁻⁴)	9.47×10 ⁻⁴ (1.49×10 ⁻⁵)	0.562 (0.0119)	0.0164 (0.00264)	0.00429 (1.30×10 ⁻⁴)
Windowpane flounder	1.527 (0.266)	-0.452 (0.0778)	0.0688 (0.00511)	0.854 (0.471)	-0.0232 (0.0137)	0.0203 (9.03×10 ⁻⁴)
American plaice	0.479 (0.0363)	-0.0424 (0.00920)	0.0116 (5.35×10 ⁻⁴)	3.222 (0.00740)	-0.214 (0.00187)	0.00484 (1.09×10 ⁻⁴)
Witch flounder	2.256 (0.00962)	-0.130 (0.00161)	0.00235 (6.12×10 ⁻⁵)	0.808 (*.)	0.00429 (*.)	1.23×10 ⁻⁵ (*.)
Yellowtail flounder	1.061 (0.0310)	0.00562 (0.00606)	0.00905 (2.72×10 ⁻⁴)	0.770 (0.00207)	0.0282 (4.04×10 ⁻⁴)	0.00121 (1.82×10 ⁻⁵)

mortalities are summer spawners. The relationship of spawning time and mortality was investigated by calculating the weighted mean surface temperature for each taxa and plotting it against

mortality (Fig. 5). Two linear regression lines are fitted to the data points: one for all the data (*n* = 26); and another without haddock, *Sebastes* spp., offshore hake, and Atlantic mackerel,

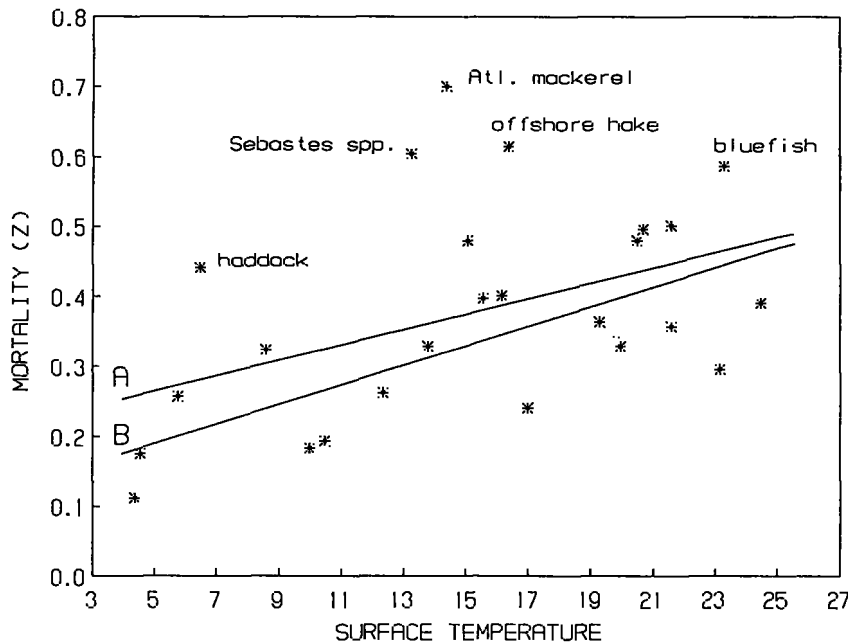


FIGURE 5.—Estimated length-dependent mortality versus mean surface water temperature for 26 larval fish taxa, 1977–84 (curve A, *n* = 26). Labeled points, except bluefish, were excluded from curve B, *n* = 22.

(those with the highest mortality ($n = 22$)). The correlations are significant for both data sets ($P = 0.023$ for $n = 26$ and $P = 0.001$ for $n = 22$) where $r^2 = 0.20$ and 0.51 , respectively.

DISCUSSION

Net Avoidance

The correction of combined catches of all larvae presents a complex problem because of the interaction of the changes in catchability with the light regime, differential catchability with larval length, and the species composition of catches. The light regime and larval length appear to interact with the catches nonlinearly, as evidenced by the curvilinearity of the relationships of the ratios of night:day catches and larval length. The species composition of the catches represent an amalgam of the differing catchabilities of each taxa. This is illustrated in the catches by depth. Here the changing species composition with depth can be seen to change the ratios of day, night, and twilight catches. The correction for catchability on a station-by-station basis would require individual correction factors for each species in order to correct the entire survey catch. The correction factors presented here allow approximately 90% of all larvae, by numbers, to be corrected for light regime and larval-length catchability interactions.

Much has been written about net avoidance by fish larvae and the need to model length- and gear-dependent net avoidance (e.g., Clutter and Anraku 1968; Murphy and Clutter 1972; Barkley 1972; Ware and Lambert 1985). The models relate reaction distance, i.e., the distance between the net and larva when the net is first detected by the larva, larval swimming speeds, and net characteristics. The theories assume that, if a larva can detect the approaching net and produce sufficient swimming speed relative to net speed, it will avoid capture. This assumption seems unrealistic when compared with catchability using other types of gear. For example, if detection factors and swimming speed of fishes were applied to bottom trawls instead of plankton gear, it is clear that very few species of adult fishes would be captured. Catchability obviously involves numerous factors, and Barkley (1972) concluded that the application of net avoidance theory requires detailed knowledge of larval behavior, and net design and its fishing characteristics.

Corrections for day, night, and twilight catchability are not intended to account for all net avoidance by larvae. These corrections are intended to standardize the abundance of larvae from net catches, regardless of the light conditions. Obviously, net avoidance may and probably does occur (see Murphy and Clutter 1972), regardless of the light conditions, but before the application of theoretical corrections for net avoidance are attempted, it is appropriate to standardize the catches. Changes in catchability with varying light conditions and larval length are clearly demonstrated from this study. Many of the taxa show the expected relationship, if visual detection of the net is the primary cue for net avoidance, of night > twilight > day catches. Night:day catch ratios exceeding one are reported for a variety of gears and taxa (Alhstrom 1954; Bridger 1956; Richards and Kendall 1973; Lenarz 1973; Lough et al. 1982; Potter and Lough 1987; etc.). However, the dominance of twilight catches for Gulf Stream flounder, butterfish, American plaice, and offshore hake reveals a more complex nature for net avoidance and the need for species-specific studies as they relate to gear avoidance. It is difficult to speculate what behavioral mechanism is producing the increased twilight catches for these taxa, but perhaps light intensity within the water column and feeding behavior may be interacting to increase catchability of these larvae. A study of gut fullness and catchability, i.e., decreased mobility of larvae with full guts, could reveal a relationship between feeding, light intensity, and catchability.

Bimodal or polymodal length frequencies of Atlantic herring larvae appear common in field samples (e.g., Salla Lambert 1984 and Lough 1981), and are attributed to successive hatchings of larvae into the plankton community. It is unlikely that the combined-years' length frequencies in Figure 4 could reveal cohorts as described by Lambert (1984). A close look at the catches of larvae show day catches have just two or perhaps three modes and night catches have at least five modes while twilight catches have at most two modes. The combined length frequency of all larvae captured, regardless of hour of capture, is unimodal at 7 mm. At this point it is difficult to speculate on the causes of different polymodal length frequencies for day and night catches, but future studies of Atlantic herring larval abundance should be done cautiously when examining length-frequency curves.

Mortality and Growth

Survey timing has a profound effect on the mortality estimates from either length- or age-frequency curves. This is most evident if samples are not taken systematically during the spawning season and surveys are not timed and spaced evenly along the spawning curve (Hewitt and Methot 1982; Morse and Hauser 1985; Hauser et al. 1988). Mortality is overestimated from samples taken when spawning or larval production is increasing and underestimated when spawning is decreasing. The magnitude of the bias in mortality estimation shows a twofold to threefold decrease with samples from the beginning to the end of spawning. However, if survey samples are summed over the larval production cycle and at least four surveys are spaced evenly throughout the spawning cycle, the over- and underestimates cancel out and the combined data give a good estimate of mortality (Hewitt and Methot 1982). The process of combining surveys across years increases the number of samples taken during the spawning cycle from approximately 2 to 5 for each year to an observation every 4 to 10 days during the combined production cycle for each taxa. The result of this process is the calculation of an average length-dependent larval mortality for the eight years covered by this study.

The relationship of larval mortality and water temperature has some interesting implications about larval growth rates. Mortality, as an expression of the decrease in numbers over time by substituting time (t_i) for length (X_i) in Equation 2, is directly related to larval growth rate by the term t_i . The assumption is that, as fish larvae grow, mortality rate decreases (Ware 1975). With constant predation rates, the amount of time spent at a given size, commonly referred to as "stage duration", will determine the number of surviving larvae. The implication of this relationship of growth rate and mortality is that, owing as water temperature increases, stage duration will decrease to increased growth rate and the shorter stage duration will decrease mortality. This assumes that adequate food supplies are available for the increased metabolic demands of increased growth rates. The link between "stage duration" and particle-size dependent mortality rates would appear to be valid for most pelagic fish larvae given the rather small size range of newly hatched fishes. However, if larval mortality rates were, in fact, dependent upon growth rates as outlined above, fishes

spawning in warm waters would derive a significant survival advantage over cold water spawners and mortality would be inversely correlated with growth rates.

According to population dynamics theory, mortality and growth rates must be positively correlated with the ratio of the instantaneous growth rate to instantaneous mortality rate, averaging > 1 for the biomass of a cohort of fish to increase (Beverton and Holt 1957; Ricker 1975; Ware 1975). If this were not the case, the maximum biomass of a cohort would occur at the egg stage. The results presented here (Fig. 5) show that length-dependent larval mortality is positively correlated with mean surface water temperature, and it seems clear that estimated mortalities are higher in the warm-water months than during winter. The association of temperature and larval growth rate was determined from a review of laboratory studies of larval growth rates (Table 6). The relationship of increasing growth rate with increasing temperature is not surprising, but the high coefficient of determination (93%) is surprising, given the variety of experimental procedures, prey species, densities, and fish species utilized by the experimenters. The data in Table 6 and the relationship of temperature to mortality confirm the positive correlation of growth and mortality.

Because expected ratios of instantaneous growth and mortality rates have been shown to be temperature-dependent, either rate is easily determined if the other is known. This ability to calculate either rate would have direct applications in modeling larval fish populations as it relates to survivorship, predator-prey dynamics, and the expected effect of environmental temperatures. For this study, if growth rate is known, then the mortality rates from field samples could be investigated to determine if net avoidance is a serious bias as often speculated. Growth rates in weight in Table 6 are rates per day, but mortalities in Figure 5 are rates per mm length interval. To convert lengths to ages ($t =$ days), the length (mm) to weight (μg), relationship and instantaneous growth rate are dimensioned in days and μg where

$$\text{Weight} = c * \text{Length}^b$$

and the instantaneous growth rate (G_n)

$$G_w = (\ln W_{i+1} - \ln W_i) / (t_{i+1} - t_i).$$

Thus

TABLE 6.—Listing of instantaneous larval growth rates per day and water temperatures (°C) from laboratory growth studies and linear regression analysis.

Species	Temp.	Growth	Source
Atlantic cod, <i>Gadus morhua</i>	4	0.0424	Laurence 1978
	7	0.0762	Laurence 1978
	10	0.0916	Laurence 1978
Haddock, <i>Melanogrammus aeglefinus</i>	4	0.0375	Laurence 1978
	7	0.0569	Laurence 1978
	9	0.1434	Laurence 1978
	6	0.0408	Buckley et al. 1987
	6	0.0367	Buckley et al. 1987
Sand lance, <i>Ammodytes</i> spp.	6	0.0877	Buckley et al. 1987
	6	0.0845	Buckley et al. 1987
	8	0.1065	Buckley et al. 1987
Atlantic mackerel, <i>Scomber scombrus</i>	15	0.1755	Buckley et al. 1987
	15	0.1948	Buckley et al. 1987
Pacific mackerel, <i>Scomber japonicus</i>	19	0.3383	Hunter and Kimbrell 1980
Atlantic herring, <i>Clupea harengus</i>	8	0.1165	Checkley 1984
Winter flounder, <i>Pseudopleuronectes americanus</i>	2	0.0263	Laurence 1975
	5	0.0598	Laurence 1975
	8	0.1065	Laurence 1975
Walleye pollock, <i>Theragra chalcogramma</i>	9.3	0.1031	Bailey and Stehr 1986
Bay anchovy, <i>Anchoa mitchilli</i>	26	0.3439	Houde and Schekter 1981
Sea bream, <i>Archosargus rhomboidalis</i>	26	0.4050	Houde and Schekter 1981
Lined sole, <i>Achirus lineatus</i>	28	0.3257	Houde and Schekter 1981

Linear Regression Analysis of growth rate (Y) on temperature (X):
 $Y = a + bX$ $a = -0.0174$ $b = 0.0144$ $S_{Y.X} = 0.0314$ $r^2 = 0.928$.

$$t_{i+1} - t_i = b(\ln L_{i+1} - \ln L_i)/G_w.$$

Then Z_t , the instantaneous mortality rate per day, where $t_{i+1} - t_i$ equals one day, is calculated as

$$-Z_t = (\ln N_0 - \ln N_t)/t$$

based on

$$N_t = N_0 e^{-Zt}$$

where N_0 is number at L_0 and N_t , adjusted for stage duration, is number at L_t . G_w for each species was estimated from the growth rate – temperature relationship in Table 6. The length-weight exponent (b) was estimated as the mean regression coefficient for seven species in Laurence (1979) at 4.15 (SE = 0.14). G_w and Z_t were calculated for 26 taxa and are shown in

Table 5. The equation relating mortality (Z_t) to temperature (T) is

$$Z_t = -0.2722 + 0.01015 T$$

$$r^2 = 0.80 \quad S_{Y.X} = 0.0380.$$

As mentioned above, the ratio of growth rate to mortality rate must exceed one and as Ware (1975) estimated from three data points, the ratio of mortality to growth is near 0.7. The slope of the linear regression for the species in Table 5 is 0.820. Five taxa are near or greater than a ratio of one (i.e., mortality \geq growth): Atlantic mackerel, *Sebastes* spp., haddock, cunner, and bluefish (Fig. 6). The mortality rates calculated for these taxa are suspect and may represent excessive net avoidance by the larger larvae. When these taxa are eliminated from the data the slope is 0.760 (SE = 0.051, $n = 22$). The

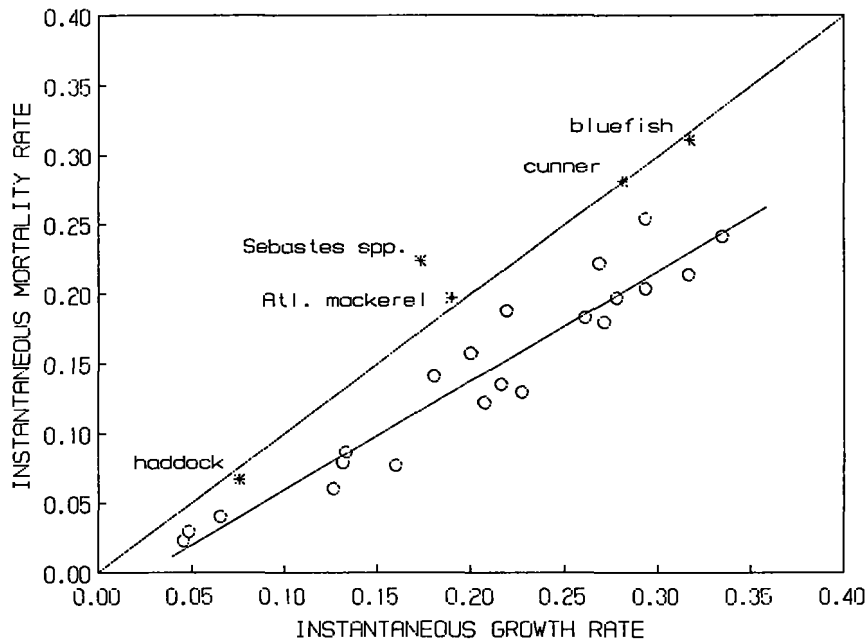


FIGURE 6—Plot of instantaneous larval mortality rates versus instantaneous growth rates for 26 larval fish taxa, 1977–84. Labeled points ($n = 5$) were excluded from the fitted curve.

ratios of mortality to growth coefficients for the rest of the taxa appear to be reasonable, i.e., approximately 0.7–0.8, and indicate that net avoidance is not a serious problem. It is interesting to note that the relationships of temperature- and length-dependent mortality (Fig. 5) showed that Atlantic mackerel, haddock, bluefish, and *Sebastes* spp. exhibit high mortality rates relative to the temperature, which lends support to the conclusion that net avoidance is the primary factor producing high mortality estimates. Offshore hake also shows a high mortality versus temperature, but does not exceed a ratio of one in the mortality versus growth rate plot. It is unclear which factor, temperature, net avoidance, mortality estimation, or a combination, is the dominant factor affecting the offshore hake data.

Contrary to this analysis, Houde (1989) found from a literature review of larval growth and mortality rates that mortality exceeded growth by about 40–100% over a temperature range of 5°–30°C. The relationship of growth to mortality during the larval stage has important implications about the life history dynamics during the first year of life. For example, when the expected growth and mortality rates at 10°C from Houde's study and this study are applied to 10^6 newly hatched larvae (weighing 0.05 mg each) until metamorphosis (38.2 mg), quite different

results are found.

	Z_t	G_w	Larval stage (d)	Metamorphosis	
				No.	Weight (g)
This study	0.094	0.1266	59.09	3,799	145.12
Houde (1989)	0.1486	0.0904	80.11	7	0.26

The 3–4 orders of magnitude difference in numbers and weight at metamorphosis between the two studies indicate that the growth and mortality rates during the juvenile stage must be very different for recruitment to be successful. If the biomass of a year-class declines during the larval stage, as indicated by Houde (1989), then the ratio of growth to mortality must be high during the juvenile stage. Since growth rate tends to decline during the juvenile stage (Cushing 1975), compared to the larval stage, then mortality of the juvenile stage must be very low.

The close interdependence of larval growth and mortality rates on temperature is clearly demonstrated in this study. It is important to realize that these results represent average conditions for larvae during the eight years from 1977 to 1984. The average values for mortality, growth, and temperature form a baseline against which areal, seasonal, or annual variations in these important early life history parameters can be compared. Thus hypotheses about larval

growth or mortality can be quantitatively tested for significant deviations from the average expected values presented here. In addition, catchability of fish larvae by various plankton samplers can be compared with the expected mortality to determine serious biases.

The three major hypotheses suggested as mechanisms that control survival of larval fishes are starvation, predation, and advection into unfavorable environments. Clearly, advection is a special case which differs little from predation in its effects on the larval population and may be viewed as simply an abiotic "predator". The predator-prey interactions in the pelagic ecosystem may then be partitioned, in terms of mortality, into starvation and predation. It is often not clear whether larvae actually die from lack of adequate food supplies or become more vulnerable to predation as a result of starvation. In any case, larval mortality increases with increasing temperature, thus a major and consistent agent of mortality must be associated with water temperature. If the assumptions of size-dependent mortality, as explained by the "cube root rule", are valid, and there is no reason to reject them, predation rates on larvae must be the primary agent of mortality. Since metabolic rates increase with temperature ($Q_{10} \approx 2-3$; Hoar 1966), predator consumption rate would also increase. Thus increased growth due to increases in temperature would appear to impart no advantage to reduce larval mortality because of the concomitant increase in consumption rates of the predator field. Pauly's (1980) conclusions for juvenile and adult fishes support this hypothesis. An interesting consequence of this hypothesis is that, within the pelagic ecosystem, mortality rates will change with temperature without altering the predator field. Thus investigations of predator-prey interactions must account for the confounding effects of temperature on growth, consumption, and mortality.

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