# Daily variability in abundance of larval fishes inside Beaufort Inlet

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**Abstract.**—We measured the daily abundance of larvae of eight species of ocean-spawned, estuarine-dependent fishes to determine the effect of sampling frequency on the mean and variance estimates during larval immigration past a permanent sampling station inside Beaufort Inlet, North Carolina, mid-November 1991 to mid-April 1992. Species of interest were *Brevoortia tyrannus, Lagodon rhomboides, Leiostomus xanthurus, Micropogonias undulatus, Mugil cephalus, Paralichthys albigutta, P. dentatus,* and *P. lethostigma.* Our data suggest that sampling at intervals >7 days can lead to excessive variance in abundance estimates. For all species, abundance varied as much as an order of magnitude from night to night. Proportional residuals from polynomial models of the seasonal recruitment pattern for a given species were used to assess the potential influence of nine environmental variables on daily densities. Twenty-seven of 72 correlations of proportional residuals with environmental variables were significant ($P<0.05$). Proportional residuals were positively correlated with time after dusk for six of eight species and were negatively correlated with turbidity for five of eight species. However, interpretation of correlations must be done cautiously because a species' recruitment pattern may coincide with normal seasonal change in one or more environmental variables. Variability in transport of larvae, from offshore to near the inlet and then through the inlet to the station, probably influences species abundance at the sampling station more than locally acting environmental variables. Daily collections of *B. tyrannus* larvae provided otoliths ($n$=1,341) showing that a large number of younger larvae, averaging 55 days posthatch, arrived at the station in mid-March on the date of maximum observed daily density (160 larvae per 100 $m^3$).

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From 1985 to the present, weekly sampling has been conducted near Beaufort Inlet to collect fish larvae entering the estuary during fall, winter, and spring (Warlen, 1994). Such inlets provide locations for sampling larvae in order to assess potential year-class strength of ocean-spawned but estuarine-dependent species. Abundance, size, and age data on early larvae in the sea, on advanced larvae in the inlets, and on juveniles in the estuaries can be used to understand when significant events such as mortality or rapid growth occur during a species' early life history. To obtain accurate abundance, size, and age estimates from the population of recruiting larvae, appropriate sampling protocol must be employed (Morse, 1989; Davis et al., 1990). Errors resulting from sampling bias can arise when larvae selectively avoid the sampling device or when there is nonrandom spatial (patchy) distribution of the larvae (Wiebe and Holland, 1968). Decreasing the time interval between sampling and decreasing the distance between stations in ichthyoplankton surveys increases the resolution of temporal or spatial patterns of species with patchy pelagic egg and larval distributions at both microscale (Houde and Lovdal, 1985) and mesoscale levels (Rowe and Epifanio, 1994).

Studies within NOAA's Southeast Atlantic Bight Recruitment Experiment (SABRE) are attempting to measure fluxes of larval fishes across the continental shelf and through inlets into estuaries amid myriad cyclical phenomena that bear directly on the larvae's abundance (Govoni and Pietrafesa, 1994; Stegmann and Yoder, 1996). The purpose of our SABRE study was to estimate the daily variation in abundance data collected on eight species of larval fish that seasonally ingress past the permanent sampling station at Pivers Island inside of Beaufort Inlet in order to determine an optimum sampling frequency for future sampling protocols. For one of these species, *Brevoortia tyrannus* (Atlantic menhaden), which has been the focus species in SABRE studies, additional analysis was conducted on age and growth with specimens collected daily. For all species, we used daily abundance data to calculate the decrease in precision of our relative abundance estimates as the interval between sampling events increased. Daily collections of larvae also allowed us to measure changes in size (length) of all eight species. Finally, environmental variables were tested for their correlation with abundance.

## Materials and methods

### Sampling location and period

The sampling station for larval fish abundance, located 2 km inside of Beaufort Inlet, North Carolina (34°43'N, 76°40'W), was a platform attached to a bridge over a 6-m-deep tidal channel adjacent to the Beaufort Laboratory at Pivers Island and has been the site of weekly larval fish sampling since the 1985–86 larvae ingress season (Warlen, 1994). We sampled every night, 20 November 1991 through 15 April 1992, a period that more or less encompasses the annual periods of recruitment of ocean-spawned estuarine-dependent larvae that pass through North Carolina inlets from autumn to spring.

### Fish and environment sampling

Oblique tows (bottom to surface) of a 1-m diameter, 800-μ mesh net were used to sample the water column for larvae. Three consecutive 4-min tows were made at 15-min intervals during the time of predicted maximum flood-tide current. Sampling was conducted only between dusk and dawn and about 50 minutes later each successive night because of the advancing tide stage. Oblique tows through the entire water column were chosen over surface, bottom, or other single-depth tows to eliminate depth bias. Species of concern, including *B. tyrannus*, are reported to be distributed by depth even in shallow, well-mixed North Carolina inlets (Lewis and Wilkens, 1971; Hettler and Barker, 1993 ).

The net was deployed by paying out the winch cable as the net, pulled downstream by the tidal current, sank to the bottom. It was then retrieved obliquely through the water column. A depth sounder with a deck readout (Standard Communications DS20) was attached to the net frame to indicate that the net had reached the bottom of the channel. Tow volume was measured with a General Oceanics model 2030R flow meter. Average tow time was 4.0 minutes. The target tow volume was 100 $m^3$, and target net retrieval speed was 1 m/sec.

Data on several environmental variables were collected concurrently with biological sampling. Salinity and temperature measurements were taken with a Hydrolab H20 water quality multiprobe. Water clarity was measured with a Sea Tech 25-cm transmissometer with a 660-nm filter. Tidal current speed was measured with a Marsh-McBirney model 201 flow meter. Wind speed and direction data were obtained from the NOAA C-MAN station at Cape Lookout, 15 km SE of the larval sampling platform. Tidal amplitude data were obtained from a NOAA tide gauge located on Pivers Island.

### Processing of larvae

After preservation in 70% ethanol, fish larvae were identified, counted, and up to 20 individuals of each species were indiscriminately selected for measurement of standard length. Ages and birth dates of all menhaden larvae retained for length measurements (1,341 individual fish) were determined by otolith daily increment counts (estimated age in days = increment count + 5) following the methods of Warlen (1992).

### Data analysis

Abundance was calculated from the number of larvae caught per tow and water volume sampled (density=number × 100 $m^{-3}$). Densities per unit volume were calculated rather than densities per unit area because all published relevant abundance data on these species is per unit volume. Mean densities by species for each date sampled were determined by averaging the densities from the three tows taken on that date. Although we sampled every night, no data were available for 10 dates during the sampling period (Fig. 1, A–D). This problem is explained by the following example. On 14 December, sampling started at 2359 h and ended around 0100 h, 15 December. The next night sampling began at 0033 h, 16 December. Thus, sampling never began on 15 December. Sampling on 15 December at the time of maximum flood tide current would have occurred before sampling on 14 December had ended. The same situation occurred on nine other dates.

Seasonal mean densities were determined by averaging the daily densities during the interval when each species was caught, including dates when no individuals of the species were caught. Variations in mean daily densities and associated variance estimates were derived by "sampling" individual density data sets for each species at intervals of 2, 3, 4, 5, 7, 14, and 30 days and by then comparing these with the actual data set (1-day intervals between sampling). From this exercise, a mean and standard deviation was generated for each sampling scheme. A 2-day cycle, for example, beginning on 20 November and continuing every other day at day 1, 3, 5 etc., produced one daily mean and standard deviation, whereas a 2-day cycle beginning a day later on 21 November and continuing every other day at day

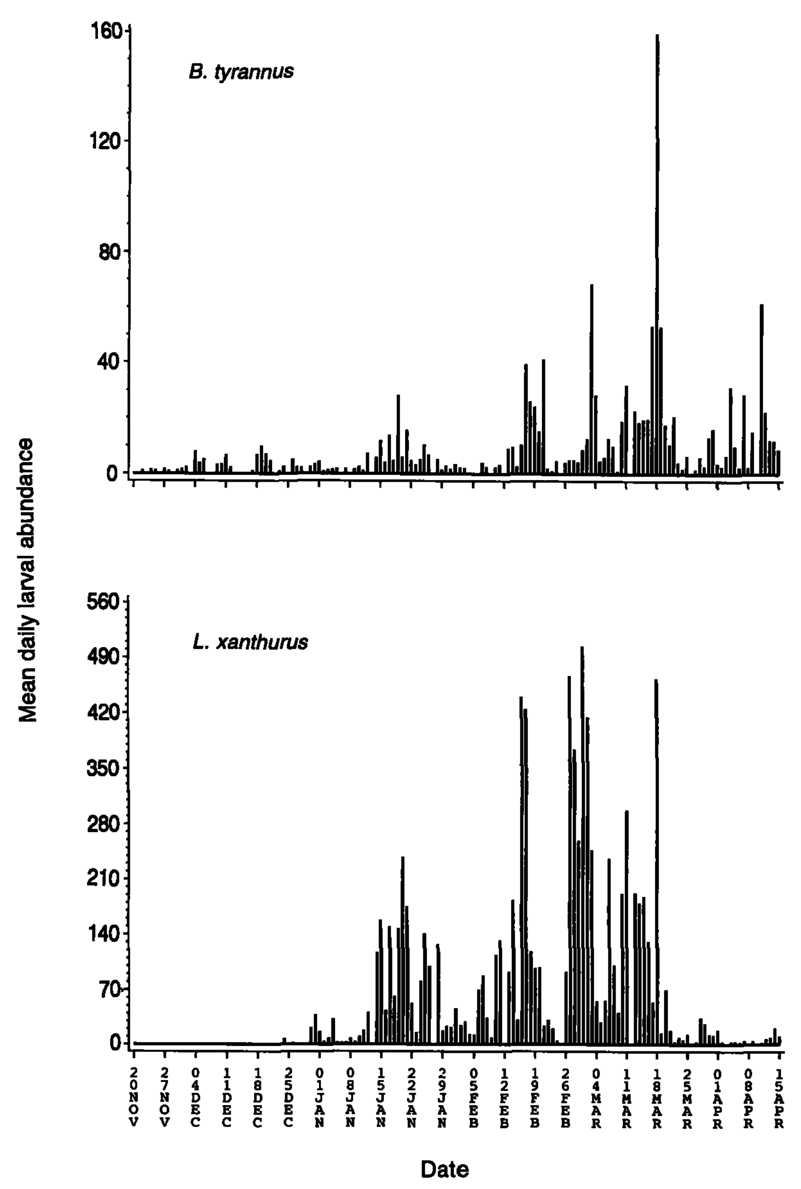

**Figure 1A**

Nightly mean densities (three tows each night) of larval Atlantic menhaden, *Brevoortia tyrannus*, and spot, *Leiostomus xanthurus*, caught near Beaufort Inlet, North Carolina.

2, 4, 6 etc. produced a different daily mean and standard deviation.

Spectral analysis (ARIMA procedure) was used to examine the time series of densities for each species for evidence of periodicities. Weekly density data based on two methods were compared by using a paired-mean Wilcoxon Signed Rank test. The Laird version (Laird et al., 1965) of the log-transformed Gompertz growth equation (Zweifel and Lasker, 1976) was used to describe the average growth of *B. tyrannus* larvae. The model was fitted to data for size and estimated age at time of capture. Log-transformed standard length (mm) and estimated age (in days) were used in the model (Warlen, 1992).

In order to examine the possible effects of environmental variables on observed larval densities, we first fitted polynomial regression models to the daily densities for each of the species' densities over time. Although a second-order polynomial was sufficient to describe the recruitment patterns of *Paralichthys*

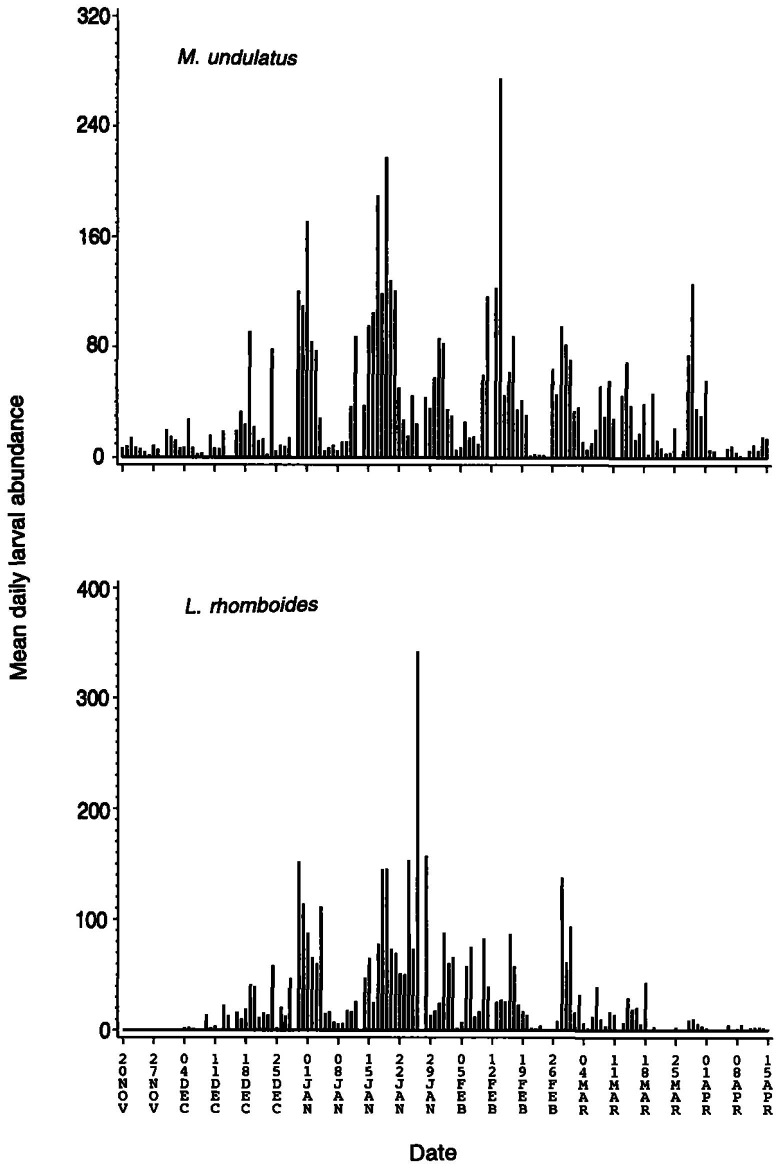

**Figure 1B**

Nightly mean densities (three tows each night) of larval Atlantic croaker, *Micropogonias undulatus*, and pinfish, *Lagodon rhomboides*, caught near Beaufort Inlet, North Carolina.

*dentatus* and *Micropogonias undulatus*, most species required a fourth-order polynomial, and *Brevoortia tyrannus* required a fifth-order polynomial. The polynomial models provided a means of estimating each species' density for each day as well as the difference between the observed density and the estimated density (residual). One would expect that if an environmental factor influenced observed density, it would do so in a proportional sense, i.e. its effects would be exhibited in relation to the expected density of the species at that date during the season of recruitment for that species. We therefore divided each residual by the expected density for that date to obtain a measure that took the species' recruitment pattern into account in looking at correlations with environmental variables. Durban-Watson statistics and first order autocorrelation coefficients were also computed to test the presence of autocorrelation and to measure its magnitude.

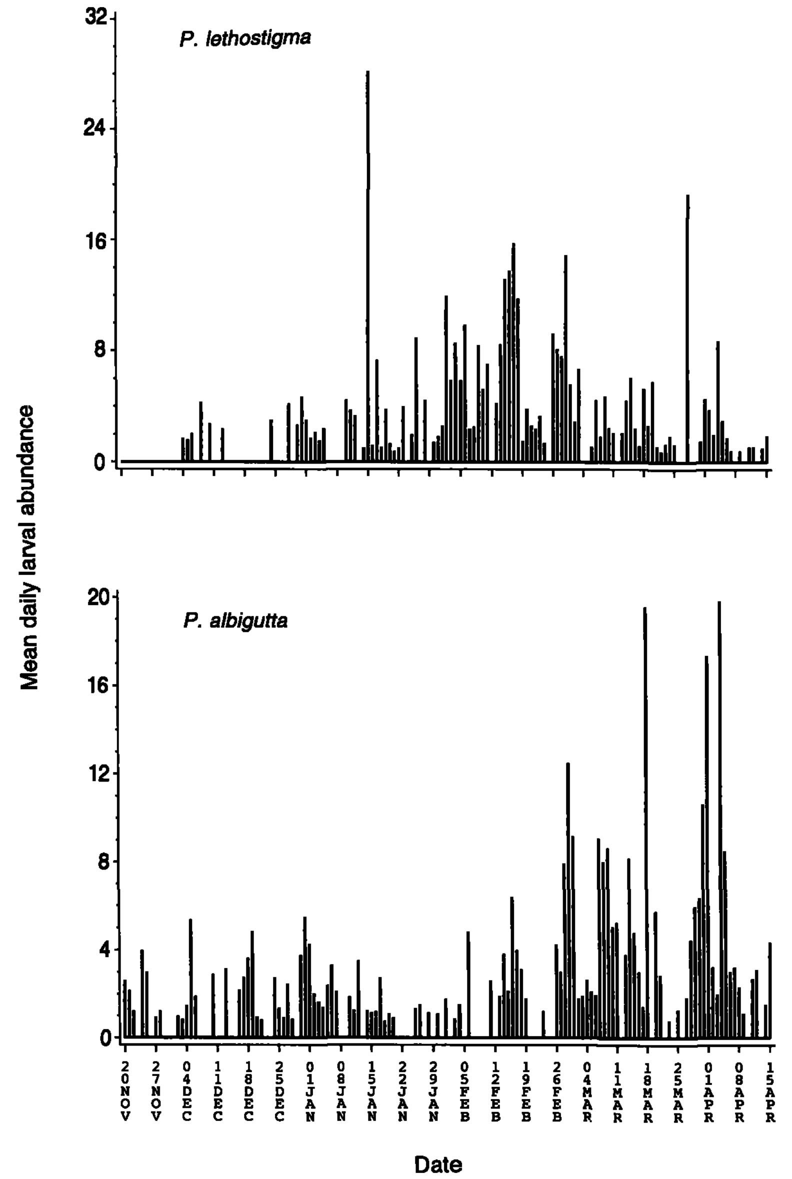

**Figure 1C**

Nightly mean densities (three tows each night) of larval southern flounder, *Paralichthys lethostigma*, and gulf flounder, *Paralichthys albigutta*, caught near Beaufort Inlet, North Carolina.

## Results

### Species abundance

The eight species selected for analysis accounted for 92% of the larvae caught during the period and are listed in Table 1 in order of decreasing abundance. Although abundance was not predictable from one night to the next for any species (Fig. 1, A–D), the Durban-Watson statistics for the polynomial regression models detected significant autocorrelation in the residuals for six of the eight species. However, one could not reject the null hypothesis that, for *Mugil cephalus* and for *Paralichthys albiguitta,* the test was inconclusive. The first-order autocorrelations for the other six species ranged from 0.30 for *Paralichthys dentatus* to 0.52 for *M. undulatus.* These reflect the serial dependency between densities on successive nights. On many dates, densities were two or more times less or more than the night

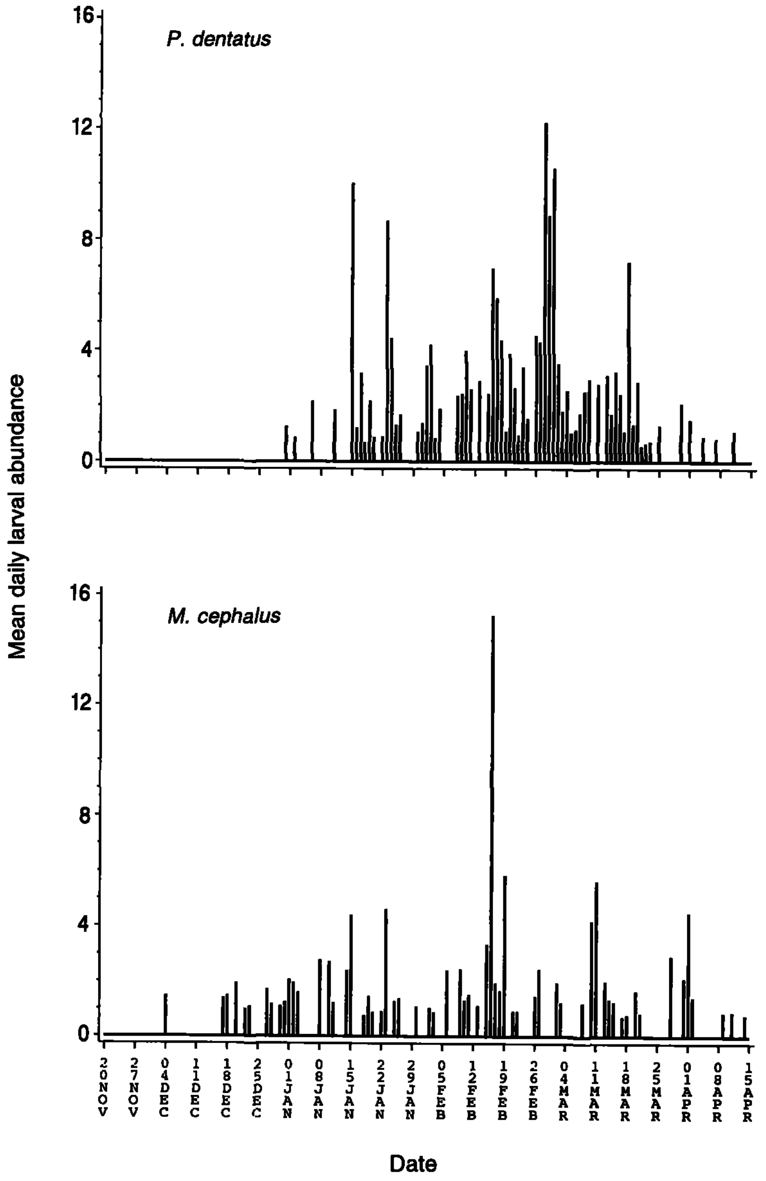

**Figure 1D**

Nightly mean densities (three tows each night) of larval summer flounder, *Paralichthys dentatus*, and striped mullet, *Mugil cephalus*, caught near Beaufort Inlet, North Carolina.

before; in some cases the difference between two consecutive nights was an order of magnitude (e.g, *Leiostomus xanthurus* on 18–19 March).

Although periods of low and high abundance can be seen along the time axis for each species, oscillations in abundance by each species did not occur at the same time in all cases. However, most of the species share periods of high abundance (mid January, mid February, early March, and mid March). We presumed that our data set would be a good candidate for time-series analysis. Spectral analyses of the estimated densities for each species was employed to reveal evidence of periodicities of varying length. All eight species exhibited a strong 14-day signal, most likely dominated by the lunar cycle. However, this 14-day signal turned out to be an artifact in the sampling method which was unavoidable. This artifact was due to sampling 50 min later each night in the sampling scheme (sampling at the same stage in the flood tide) until dawn, at which time the next sampling opportunity would be either 12 h 25 min later or 37 h 15 min later. We chose the later option (to

**Table 1**

Average seasonal density (=AveDen) and maximum daily density (=MaxDen) of target species listed in order of decreasing average density (larvae per 100 m$^3$). Sampling was conducted between 20 November 1991 and 15 April 1992.

| Scientific name | Common name | AveDen | MaxDen | Capture date |
|---|---|---|---|---|
| *Leiostomus xanthurus* | spot | 82.8 | 504.0 | 21 Dec–15 Apr |
| *Micropogonias undulatus* | Atlantic croaker | 37.9 | 274.2 | 20 Nov–15 Apr |
| *Lagodon rhomboides* | pinfish | 30.0 | 342.0 | 22 Nov–15 Apr |
| *Brevoortia tyrannus* | Atlantic menhaden | 10.0 | 159.8 | 22 Nov–15 Apr |
| *Paralichthys lethostigma* | southern flounder | 3.6 | 28.2 | 04 Dec–11 Apr |
| *P. albigutta* | gulf flounder | 2.7 | 19.7 | 20 Nov–15 Apr |
| *P. dentatus* | summer flounder | 2.0 | 12.2 | 31 Dec–15 Apr |
| *Mugil cephalus* | striped mullet | 1.0 | 15.2 | 04 Dec–14 Apr |

**Table 2**

Standard error of the mean abundance of larval species obtained at 2- to 30-day subsampling intervals of the actual daily sampling data set.

| | If the number of days between sampling had been | | | | | | |
|---|---|---|---|---|---|---|---|
| Scientific name | 2 | 3 | 4 | 5 | 7 | 14 | 30 |
| *B. tyrannus* | 0.78 | 0.89 | 0.93 | 1.32 | 1.98 | 1.93 | 1.54 |
| *L. rhomboides* | 2.60 | 2.36 | 1.62 | 3.05 | 4.14 | 4.14 | 3.89 |
| *L. xanthurus* | 0.73 | 5.22 | 2.52 | 7.99 | 5.68 | 12.86 | 9.50 |
| *M. undulatus* | 1.96 | 2.28 | 1.17 | 1.37 | 1.90 | 5.90 | 3.65 |
| *M. cephalus* | 0.31 | 0.26 | 0.22 | 0.21 | 0.38 | 0.24 | 0.33 |
| *P. albigutta* | 0.37 | 0.14 | 0.44 | 0.19 | 0.27 | 0.26 | 0.31 |
| *P. dentatus* | 0.07 | 0.26 | 0.14 | 0.09 | 0.19 | 0.32 | 0.38 |
| *P. lethostigma* | 0.15 | 0.24 | 0.43 | 0.22 | 0.42 | 0.48 | 0.46 |

avoid sampling twice on the same date), but either option would have resulted in an irregular pulse interval in the time line every 14 days and would have precluded further time-series analysis.

## Within-night variability

Variability between tows of the three tows each night was estimated by calculating the coefficient of variation (CV) for each night and for each species. The CV averaged about 50% for each species throughout the sampling period. Late in the immigration period, the CV in densities within a night increased for *Paralichthys lethostigma*; for all other species daily tow-to-tow variability was relatively constant throughout the time series.

## Sampling interval

The range in density estimates derived from subsampling the actual data set increased as the subsampling interval increased (Fig. 2), as did the standard error of the mean for most species (except *Mugil cephalus* and *Paralichthys albigutta*) (Table 2). For example, sampling every night yielded a seasonal mean of 10 *B. tyrannus* larvae per 100 m$^3$, but if we had sampled only every 30 days our estimate for the 1991–92 immigration season, seasonal mean abundance could have ranged from 3 to 43 larvae per 100 m$^3$, depending on which date we began sampling. Similarly, had we sampled for *L. xanthurus* every 30 days, our estimated seasonal mean could have ranged from 11 to 249 larvae per 100 m$^3$.

## Daily versus weekly sampling

Sampling methods were compared to see if the increased effort required for daily sampling provided better abundance estimates than did weekly sampling. Weekly estimates were calculated by using *B. tyrannus* abundance data from our daily 1-m-net oblique-tows and are plotted (Fig. 3) along with

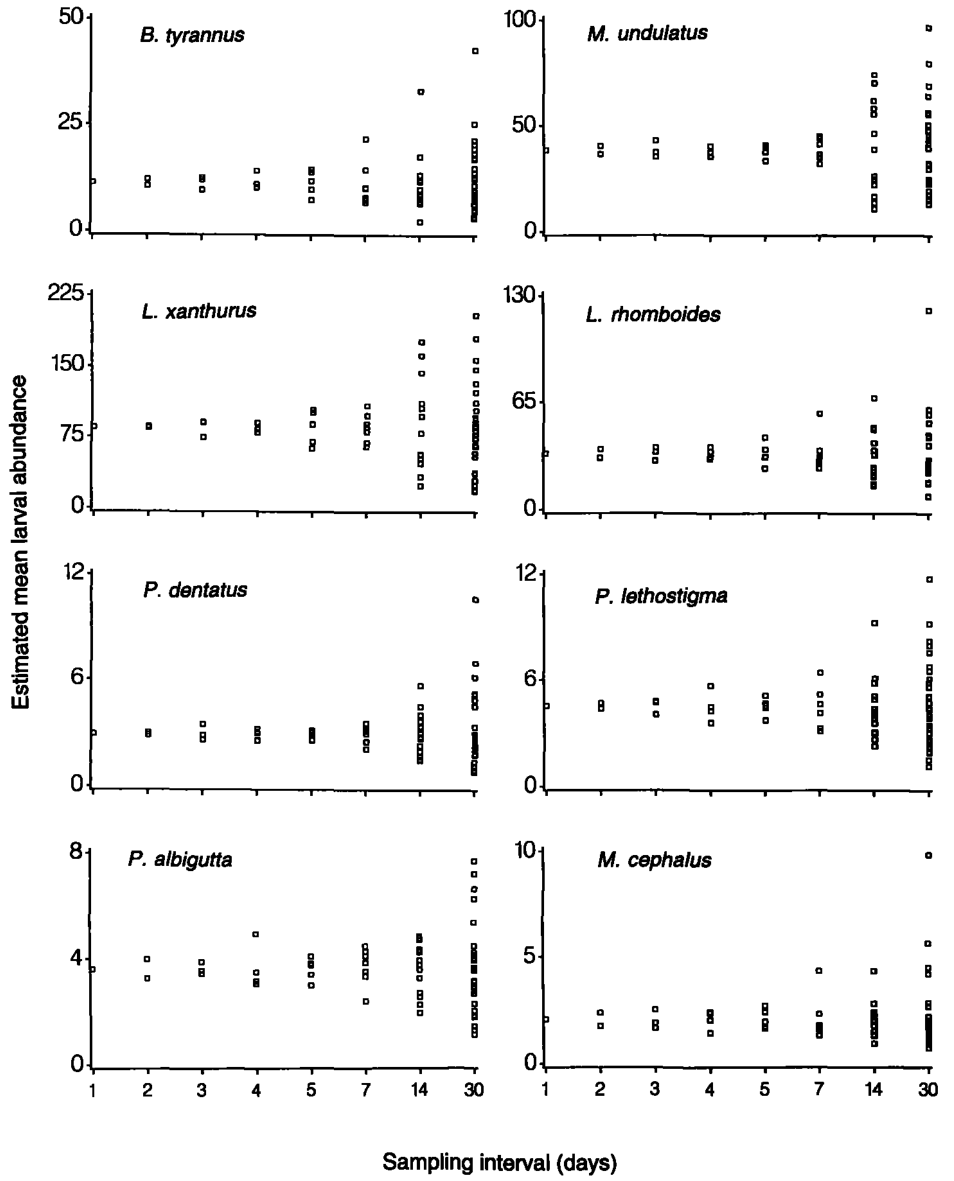

**Figure 2**

Estimated effect, based on daily sampling data, of sampling interval on estimated larval fish abundance.

*B. tyrannus* data obtained with a 1 × 2 m net fished near the surface (Warlen, 1994). Sampling with a 1 × 2 m surface net occurred at night, at approximately the same hour, from the same sampling platform, and during the same immigration season (1991–92) as our basic study. The seasonal weekly mean of the weekly means calculated from daily means obtained with the 1-m net was significantly different ($P<0.05$) from the seasonal weekly mean density obtained with the 1 × 2 m surface net. Sampling daily with the 1-m oblique net resulted in an average of 10.0 *B. tyrannus* larvae per 100 $m^3$ compared with 7.2 larvae in weekly sampling during the same season with the 1 × 2 m surface net (Warlen, 1994). The abundance of *B. tyrannus* in catches of the 1-m oblique net tows made only on the nights that the 1 × 2 m surface net was fished appeared similar to the weekly average of the daily catches with the 1-m oblique net tows (10.2 vs. 10.0 larvae per 100 $m^3$), but this similarity could not be statistically tested because the samples were not independent.

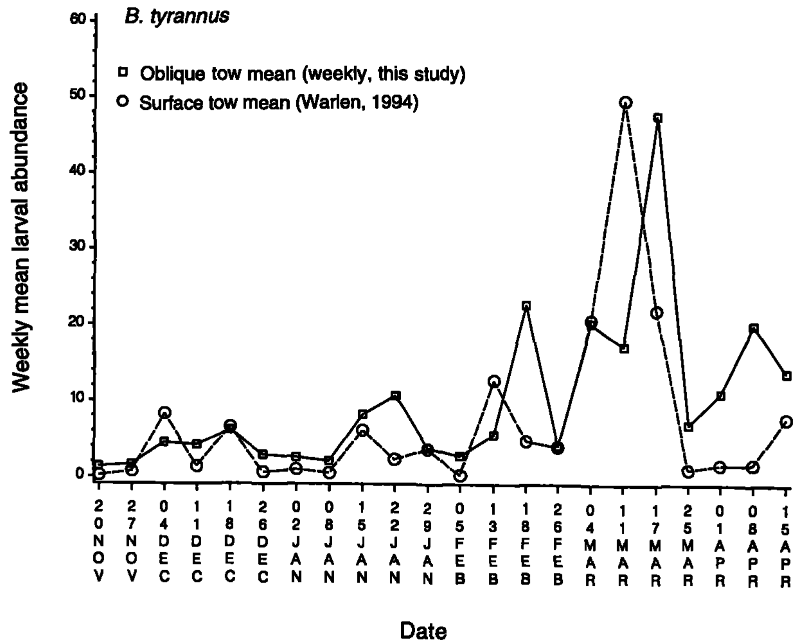

**Figure 3**

Comparison of mean densities from nightly sampling (oblique tows, 1-m-diameter net) averaged by week with mean densities estimated from Warlen's (1994) weekly sampling (surface tows, 1 × 2 m net).

## Size of larvae

Plots of mean length for the larval species produced a variety of seasonal patterns (Fig. 4). Although *B. tyrannus* increased in average size until mid-March and then decreased, the mean length of *M. undulatus, L. xanthurus,* and *Lagodon rhomboides* peaked in mid-February, then decreased. *M. undulatus* seemed to share peaks in abundance with peaks in increasing mean lengths (e.g. 30 December, 17 and 26 January, and 28 February). Larvae of *Paralichthys* or *Mugil* did not change substantially in length over the season.

## Age and growth of menhaden larvae

Because SABRE studies have centered around *B. tyrannus*, daily collections of this species provided a unique opportunity to test correlations of observed larval age structure with waves of immigrating larvae and environmental conditions. Otoliths of *B. tyrannus* (10–32 mm SL) showed a range in estimated age of 16 to 106 days (Fig. 5). The Gompertz growth equation predicted a size at hatching of 4.96 mm SL, which is above the reported size at hatching of 3.2–3.4 mm SL for laboratory-reared specimens (Powell, 1993). Average daily growth rate declined from 0.32 mm/day between days 30 and 40 to 0.03 mm/day between days 80 and 90.

According to back calculations from capture date, *B. tyrannus* ingressing Beaufort Inlet spawned from 12 October 1991 to 16 February 1992. Expressed as a percentage of the total Atlantic menhaden caught, two age cohorts, one in mid-December and another in late January, made up about 50% of the year's recruitment (Fig. 6). Almost 5% of the Atlantic menhaden larvae captured at the sampling station during the season were hatched on 13 December 1991.

The distribution of estimated ages of larvae by collection date is shown with an overlay plot of mean daily density (Fig. 7). The largest daily mean density of 159 larvae per 100 $m^3$ (18 March 1992) occurred during a decrease in age distribution of about 25 days and would suggest a significant import of a younger cohort of *B. tyrannus*.

## Environmental variables

The environmental conditions (except barometric pressure) recorded at the time of sampling are shown in Figure 8. Spearman correlation coefficients were computed for each of the eight species with each of the nine environmental variables (Table 3). Twenty-seven of the 72 coefficients were significant ($P<0.05$).

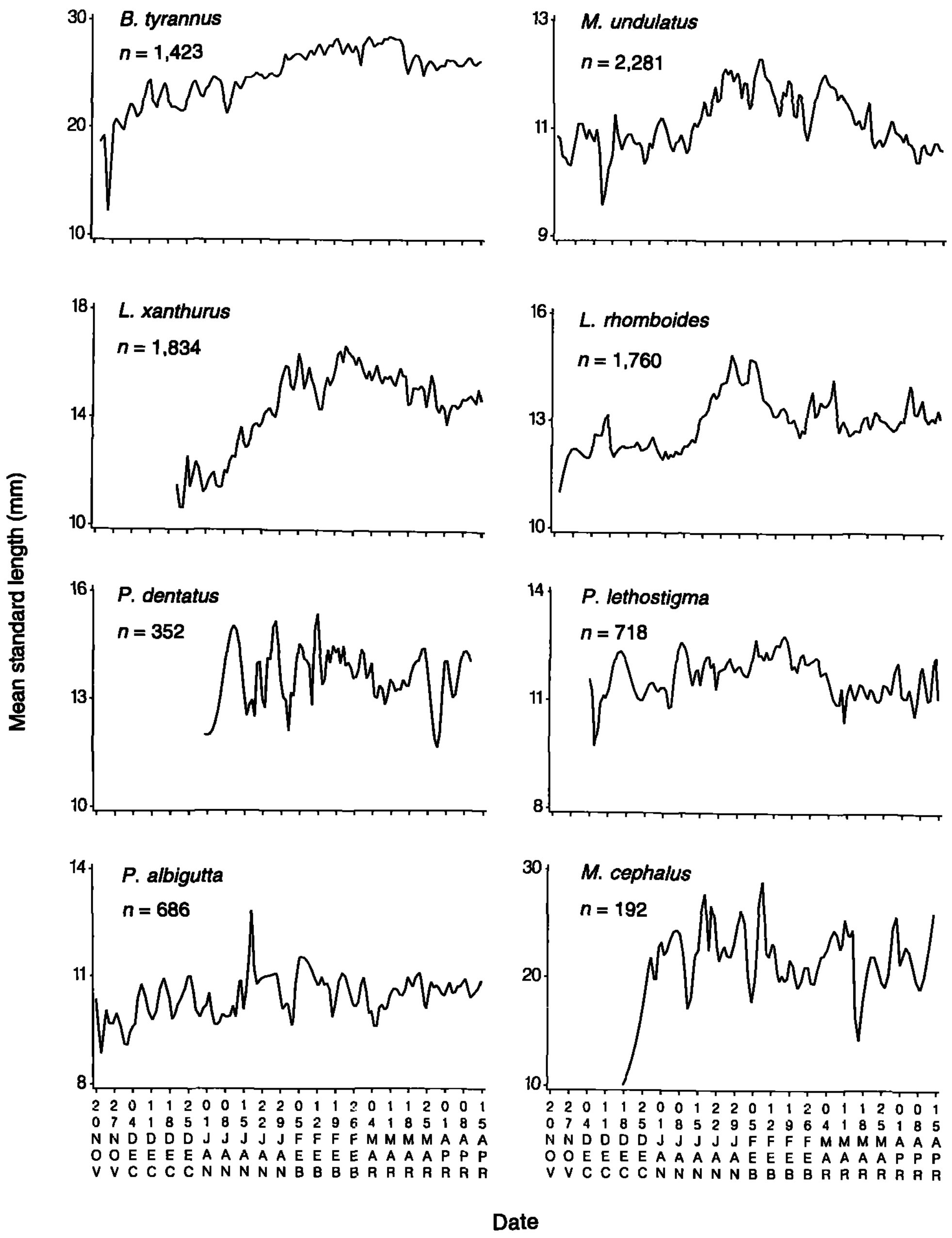

**Figure 4**

Standard lengths of each species; *n* = number of specimens measured.

The proportional residuals were positively correlated with hour of capture after dusk for six species and negatively correlated with turbidity for five species. As an example, the regressions of abundance of *B. tyrannus* on each environmental condition are shown in Figure 9. Significant correlations for this species were found with tidal amplitude, current speed, moon phase (=spring vs. neap tide), water clarity, and hours after dark when sampling occurred. *Paralichthys dentatus*, however, exhibited no correlations.

As would be expected, there were significant correlations between the nine environmental variables. The highest was between tidal amplitude and surface current (0.60), and the next highest was between atmospheric pressure and wind velocity (–0.44). However a principal components analysis yielded four

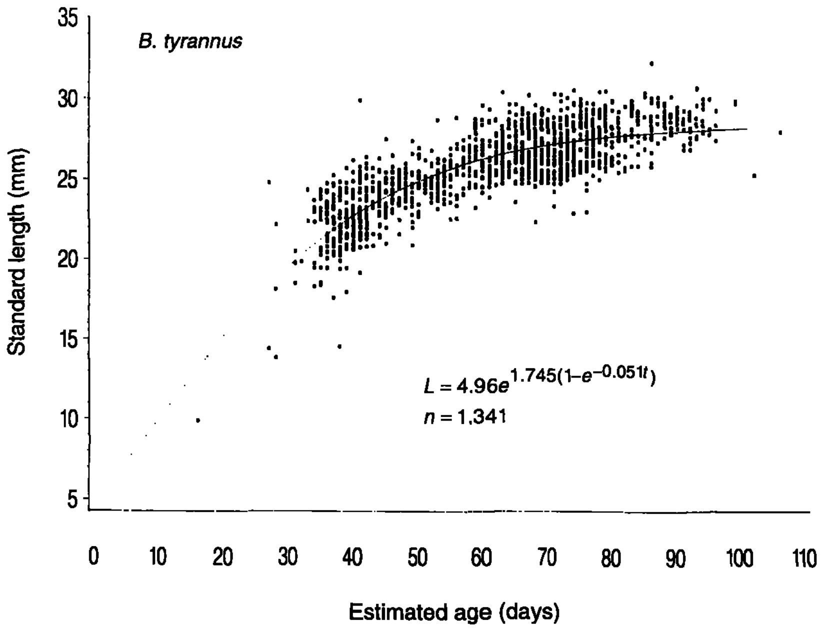

**Figure 5**

Growth of *B. tyrannus* larvae as described by the Gompertz model where $L$ = standard length in mm and $t$ = estimated age in days. Dots represent length-at-age measurement on each larva.

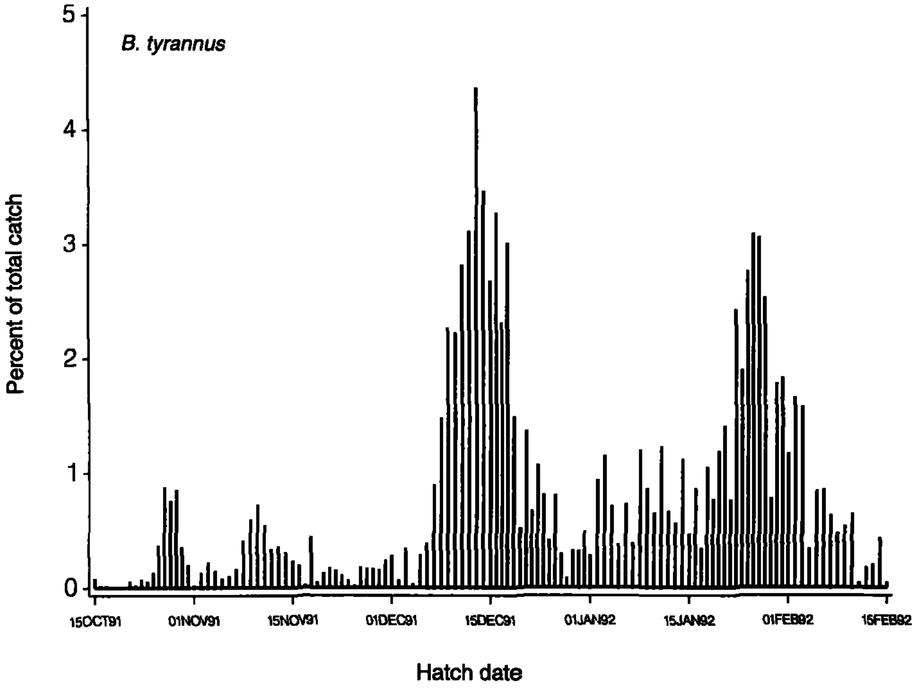

**Figure 6**

Density-weighted percentage of *B. tyrannus* larvae ingressing through Beaufort Inlet by back-calculated hatch date.

eigenvalues greater than 1.0, cumulatively accounting for only 66% of the variation, leading us to conclude that the structure of the environmental data was not simple.

## Discussion

The periodic nature of seasonal changes in some environmental variables and in reproduction of the dif-

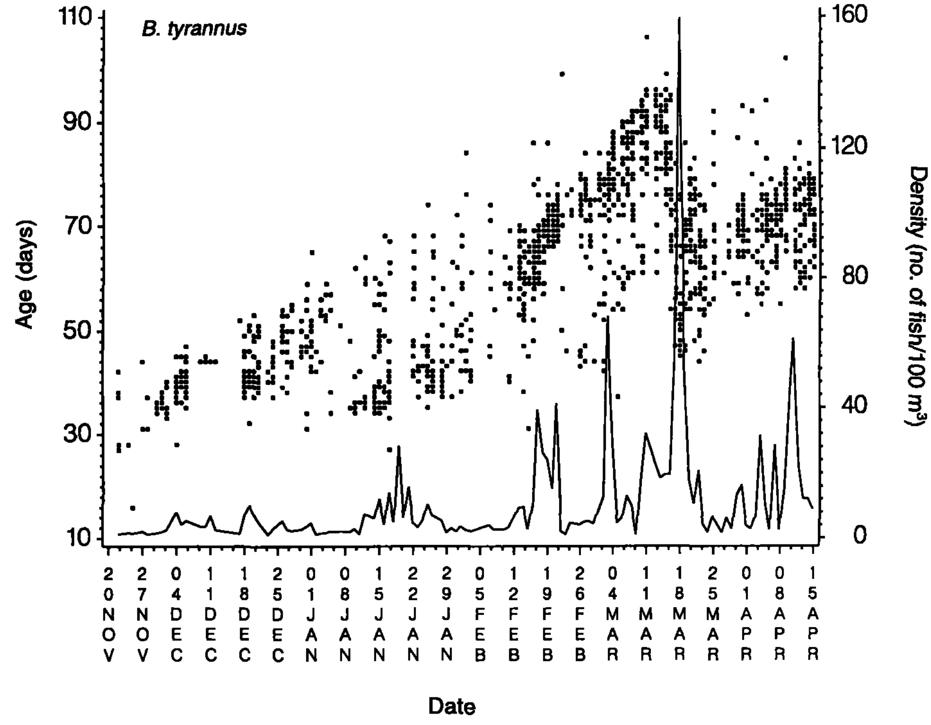

**Figure 7**

Distribution of estimated ages (points, left axis) and mean daily abundance (line, right axis) of *B. tyrannus* larvae collected throughout the sampling period.

**Table 3**

Spearman correlation coefficients between proportional residuals for species' densities and various environmental variables: amplitude = tidal amplitude; pressure = barometric pressure; current = flood tide current; hours = hours after sunset; spring tide = spring tide (versus neap tide); temperature = water temperature; wind velocity = average daily wind speed. Bt=*B. tyrannus*, Lr=*L. rhomboides*, Lx=*L. xanthurus*, Mu=*M. undulatus*, Mc=*M. cephalus*, Pa=*P. albigutta*, Pd=*P. dentatus*, Pl=*P. lethostigma*. *=$P$<0.05. **=$P$<0.01. ***=$P$<0.001.

| Variable | Bt | Lr | Lx | Mu | Mc | Pa | Pd | Pl |
|---|---|---|---|---|---|---|---|---|
| Amplitude | 0.40*** | 0.19* | 0.12 | 0.08 | –0.24 | –0.02 | 0.20 | 0.08 |
| Pressure | 0.11 | –0.09 | 0.04 | 0.03 | –0.24 | –0.08 | –0.02 | –0.20* |
| Current | 0.29*** | 0.22* | 0.06 | 0.14 | –0.11 | 0.15 | 0.10 | 0.20* |
| Hours | 0.19* | 0.30*** | 0.30** | 0.43*** | 0.01 | 0.24** | 0.17 | 0.22* |
| Salinity | 0.06 | 0.01 | –0.20* | –0.11 | –0.08 | –0.18* | 0.14 | –0.19* |
| Spring tide | –0.26** | 0.04 | –0.22* | –0.24** | –0.00 | 0.00 | –0.19 | 0.09 |
| Temperature | –0.07 | –0.24** | –0.05 | –0.06 | 0.18 | 0.02 | 0.08 | 0.00 |
| Turbidity | –0.28*** | –0.42*** | –0.32*** | –0.29*** | 0.10 | –0.19* | 0.03 | –0.17 |
| Wind velocity | 0.14 | 0.28* | 0.22* | 0.06 | 0.31* | 0.11 | 0.16 | 0.15 |
| (Sample size) | 133 | 116 | 102 | 133 | 61 | 138 | 91 | 125 |

ferent species implies that care must be taken in the interpretation of correlations between these variables and fish densities. For example, temperature may be inappropriate to associate with observed densities owing to the spawning-season periodicities involved with life history strategies of each species. Time of spawning (e.g. early winter) and the arrival at the inlet after a 2–3 month cross-shelf transport time, could result in higher abundance corresponding with rising temperatures. The multiple-regres-

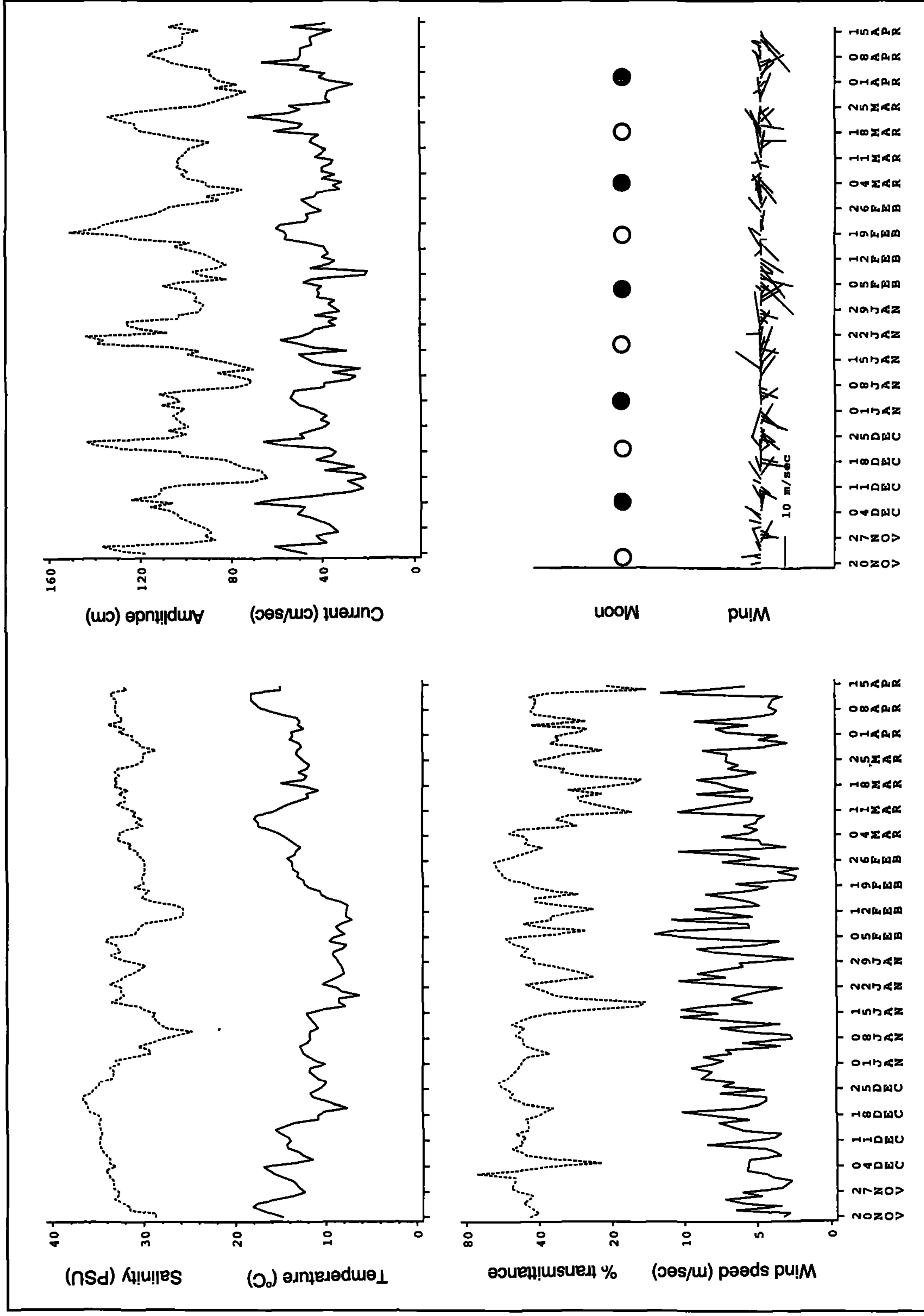

**Figure 8**

Observed environmental conditions during sampling. Upper left: temperature and salinity. Upper right: tidal current speed and amplitude. Lower left: wind speed and water clarity. Lower right: daily wind vectors (speed and direction blowing toward) and moon phase (open circles = full moon; solid circles = new moon).

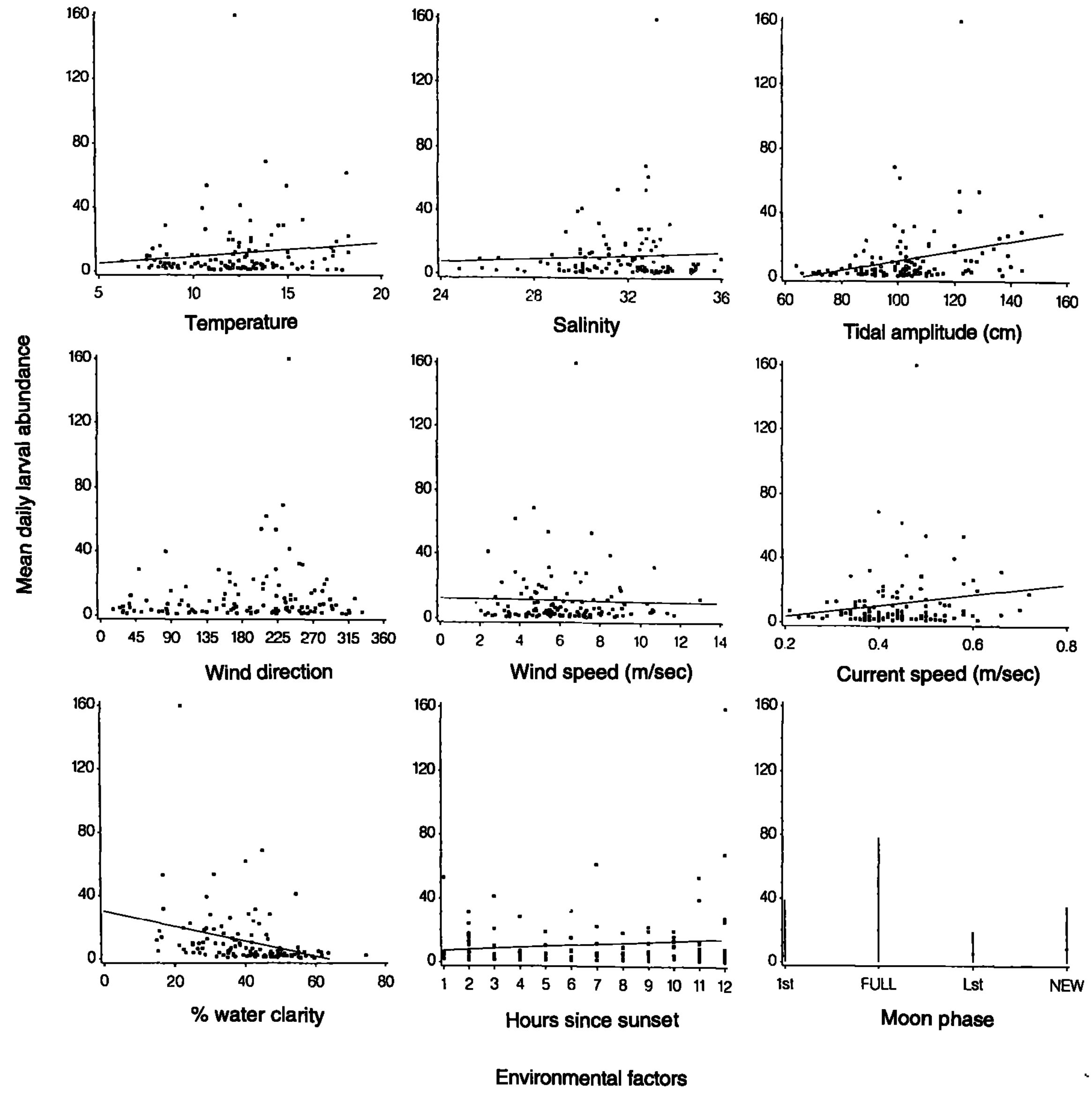

**Figure 9**

Abundance of *B. tyrannus* collected during 138 sampling nights versus nine environmental factors. Wind direction is direction wind is coming from. Vertical axis is abundance (number larvae per 100 $m^3$).

sion analysis and the principal-component analysis suggested that unknown factors on a scale larger than the locally measured environmental conditions are probably more important in causing peaks in abundance of the immigrating larvae. Originating from wide-spread spawning sites during the fall-winter period, larvae of different spawning cohorts arrive near the inlet from many possible transport routes. The most likely factor is onshore displacement of warm Gulf Stream filaments containing patches of larvae (Stegmann and Yoder, 1996). Once under the influence of tidal exchange at the inlet, patches of larvae merge as they ingress the estuary. Variables including temperature, salinity, turbulence, turbidity, odors, and currents differentially affect survival or active transport behavior into the estuary (Boehlert and Mundy, 1988). Larval behavior may have contributed to the fact that some species were more abundant in catches made later in the night (e.g. *L. rhomboides, L. xanthurus, M. cephalus,* and *P. dentatus*), acting to disperse larvae into the water column from the edges and bottom, thus making them more vulnerable to the sampling gear.

Daily ageing of *B. tyrannus* caught during the study revealed that a rapid and distinct shift in larval populations occurred in mid-March (Fig. 7). In early March, the recruiting larvae were primarily from a cohort that was spawned in mid-December, first reached the inlet in mid-January, and suddenly disappeared on 16 March. On 18 March a new cohort, spawned in mid-January, appeared. Its appearance was coincident with the year's highest daily mean density. This change in age structure coincided with a 3-day shift to southwesterly winds and full-moon spring tides. Advanced very high resolution radiometer sea surface temperature (AVHRR-SST) imagery revealed that sea surface temperatures 15 km off Beaufort Inlet warmed to 15°C on 9 March 1992, up from 11°C a week earlier (and down to 12.3°C a week later), possibly bringing in the younger *B. tyrannus* larvae from warmer offshore water to the vicinity of Beaufort Inlet (Stegmann[1]). This warming was also detected by our temperature measurements at the sampling platform, rising to 17.9°C on 9 March followed by a decrease to 12°C on 18 March (Fig. 8), when the large number of younger larvae were caught. Until that date, the average estimated age of larvae caught in Beaufort Inlet increased from about 35 days in late November to about 80 days in mid-March. About 57% of the menhaden captured in the 1991–92 season were spawned in two 2-week periods (mid-December and late January). Although substantial spawning may have occurred at other times, the population from which these larvae were caught contained the survivors of the cross-shelf transport. It appears that size at estimated age was significantly larger, about 3 mm SL, for ages between 40 and 80 days for the 1991–92 collections than the larval size reported by Warlen (1992) for *B. tyrannus* collected mainly offshore of Beaufort Inlet in 1979–80. Because the daily ageing method was the same, this observed difference in growth rates of the 1991–92 ingressing larvae is attributed to a higher growth rate among the larvae that survive to reach the inlet.

Coastal marine environments experience periods of diurnal or semidurnal tidal cycles imbedded within lunar and semilunar cycles, and these have been shown to influence a broad range of organisms and processes (Hutchinson and Sklar, 1993). Cyclical phenomena impose a particular set of requirements for their adequate measurement and for the avoidance of bias arising from aliasing (Kelly, 1976) because the temporal sequence of observations will be autocorrelated. A circannual rhythm is a feature of the life history of most vertebrates, and one manifestation of this is the restriction of reproduction of a species to a season of several weeks or months. If the purpose of a sampling program is to compare recruitment of a species of larval fish from year to year, then it should be designed so that it describes each year's temporal pattern accurately. In this respect it differs from the normal random sampling situation designed to estimate the mean and variance of some statistical population. Because its purpose is to enable description of a temporal pattern, a systematic design is normally chosen to ensure equal (or near equal) spacing of samples. Equal spacing of samples is required for many approaches for the analysis of a time series. However, if there are other, shorter cycles within the seasonal pattern, then care must be taken to avoid spurious results (aliasing) that can arise when the sampling interval is greater than one half the wavelength of a significant component cycle. Sampling to determine a seasonal flux of larvae should be designed to detect temporal patterns, as well as estimate a mean abundance and variance.

The question of sampling frequency may have a lower priority than considerations of sampling costs and vessel availability, and thus it is important to quantify the effect that sampling frequency has on estimates of larval abundance, size, and age. For example, one may be interested in estimating the flux of larvae across a boundary over some unit of time. If one is interested in the strength of a year class, the sampling effort must include the entire season of larval recruitment of that species. If one is interested in evaluating the influence of a meteorological event on larval distribution, then the appropriate sampling interval would be measured in hours. As we shall see, both sampling designs also require due consideration of various physical and biological rhythms that have an important bearing on the number of larvae collected at a given point in space and time (e.g. tidal, circadian, circannual). Prior to establishing sampling protocol for future studies, we attempted to determine a sampling interval that would provide acceptable larval fish abundance estimates. Larval fish surveys have been made in Beaufort Inlet and other North Carolina inlets on different sampling intervals, i.e. weekly (Warlen, 1994), bi-weekly (Lewis and Mann, 1971), every new and full moon period (Hettler and Chester, 1990) and every new moon period (Hettler and Barker, 1993). When we compared the weekly sampling method that has been used for monitoring at Pivers Island for the past 10 years (Warlen, 1994) with our daily sampling experiment, a difference in estimated abundance of *B. tyrannus* was detected. Differences in the two types of nets may have

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[1] Stegmann, P. 1996. Graduate School of Oceanography, Univ. Rhode Island, S. Ferry Road, Narragansett, RI 02882. Personal commun.

been responsible for the differences in catches. The 1-m net is an active gear, retrieved obliquely at a rate of about 1 m/sec through the water column, whereas the 1 × 2 m net is fished passively in the surface current (flowing 0.2–0.5 m/sec, Warlen[2]). Also, the mesh of the 1-m net is 200 m smaller and may have reduced extrusion of larvae. Density estimates derived from sampling one night per week with the 1-m net were similar to estimates derived from sampling every night per week with the 1-m net made on the same night as the 1 × 2 m surface net sets and further support our suspicions regarding the differences in sampling with the two gears. Finally, we have assumed for 10 years (Warlen[2]) that the Pivers Island station serves as a proxy for Beaufort Inlet. An intensive SABRE study conducted in March 1996, during which larval fish were sampled synchronously at seven locations in and near the inlet, including Pivers Island, is under analysis to determine how closely Pivers Island larval fish densities reflect Beaufort Inlet densities.

We conclude that at least one sampling event each week is required for estimating late autumn through early spring seasonal abundance of fish larvae in North Carolina inlets, although more frequent sampling is preferred if the standard error of estimates is to be reduced. Bias may be introduced by sampling only at a specific period of the lunar cycle, because larval abundance appeared to decrease following spring tides. Studies where sampling is done exclusively at the same lunar phase may consistently over or under estimate abundance. This attribute may be acceptable for interannual comparisons, if the same methods are followed from year to year, but would not be acceptable for calculating the flux of larvae through an inlet. Sampling at intervals of 7 days or less can reduce this bias.

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