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ONSHORE-OFFSHORE PATTERN AND VARIABILITY IN DISTRIBUTION AND ABUNDANCE OF BAY ANCHOVY, ANCHOA MITCHILLI, EGGS AND LARVAE IN CHESAPEAKE BAY

by

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ABSTRACT

The spatial pattern and daily variability of the onshore-offshore distribution of bay anchovy Anchoa mitchilli eggs and larvae were determined in four days of repetitive sampling on a transect in mid-Chesapeake Bay. The 13-km transect ran from nearshore to the most offshore area of the Bay, passing through a river plume front. Most spawning occurred offshore. Eggs and recently-hatched larvae were 30-200 times more abundant offshore than at inshore and frontal stations. Few eggs and larvae occurred below the pycnocline where oxygen levels often were too low for survival or normal development. Mean larval lengths and relative (but not absolute) abundances of large (≥5.5 mm SL) larvae increased in an offshore to inshore direction. Larval mortality rates were both size and area-specific. Mortality was highest offshore and higher for small length classes. There was no indication that anchovy eggs or larvae were concentrated in the frontal region, but gelatinous predators and zooplankton suitable as larval prey tended to increase at the front. Significant transport of larvae from offshore to inshore may occur, but most larvae of all sizes remain offshore, indicating that juvenile recruitment of anchovy is most dependent on offshore processes.

INTRODUCTION

Year-class abundances of bay anchovy, Anchoa mitchilli, have varied more than ten-fold during the past 30 years in Chesapeake Bay (Horwitz 1987; Newberger and Houde in press). Daily spawning during summer produces cohorts of eggs and larvae which experience high and variable mortality (Dorsey 1993; Houde et al. in press). Few anchovy live beyond age 1 (Newberger and Houde in press) and most annual production occurs in the larval stage (Wang and Houde in press), indicating that prerecruit dynamics drive year-class fluctuations and variability in production.

In a conceptual model, Dovel (1971) proposed that bay anchovy spawned primarily in the mesohaline, shoal regions of the estuarine Chesapeake Bay and that larvae subsequently were advected or migrated up-Bay and into low-salinity tributaries which served as juvenile nurseries. Recent research has demonstrated that spawning actually is widespread (Olney 1983; Dorsey 1993), is most intense offshore (Dalton 1987; MacGregor 1994), and results from individual females spawning repeatedly during an approximate three-month peak period (Luo and Musick 1991; Zastrow et al. 1991). The pelagic eggs develop rapidly and hatch in 20-24 h. Some larvae, presumably by selective tidal transport, migrate into tributaries (Loos and Perry 1991). But, most larvae of all sizes occur offshore (MacGregor 1994). Trawl catches of juvenile recruits do indicate a selective up-Bay transport of larvae and juveniles (Wang and Houde in press).

The Chesapeake Bay is a large estuary, approximately 200 km long and averaging >15 km in width (Figure 1). It can be divided into inshore (shoal), offshore (Bay channel region), and frontal regions associated with its many tributaries. Tidal and river-plume fronts are obvious features that are hypothesized to promote plankton production and perhaps enhance recruitment potential of bay anchovy. Convergent properties or eddies resulting from secondary currents in such fronts could mark regions of distinctly higher productivity or organism accumulation (Pingree 1978; Seliger et al. 1981; Mackas et al. 1985; Richardson 1985; LeFevre 1986; Largier 1993). Fronts, with their convergent properties, are zones where fish larvae may accumulate and experience growth rates, mortality rates, and stage durations that differ significantly from non-frontal regions (Munk et al. 1986; Kiorboe et al. 1988; Govoni et al. 1989; Munk 1993).

Objectives of this research were to estimate cross-Bay abundance patterns of bay anchovy eggs and larvae on a transect that began nearshore, crossed a river-mouth front and extended offshore to the channel region of Chesapeake Bay. We examined the temporal (daily) and spatial variability in distributions and abundances of bay anchovy eggs, larvae, microzooplankton and gelatinous predators of eggs and larvae. We estimated and compared the apparent mortality rates of anchovy larvae in the offshore, frontal and inshore regions along the transect.

METHODS

Study Area

Ichthyoplankton sampling was conducted at 8 stations on a transect extending approximately 13 km from the mouth of the Patuxent River offshore (Figure 1).

Sampling

Ichthyoplankton surveys were conducted on 4 days in July 1988. Surveys were carried out on 2 ebb (12 and 13 July) and 2 flood (14 and 15 July) tide cycles during daylight hours. Depth profiles of temperature, salinity and oxygen concentration at each station were obtained from CTD casts and water samples pumped at specified depths.

Ichthyoplankton was collected on 12, 13 and 15 July in a 60-cm bongo net sampler with 280-μm mesh. Two pairs of one-minute oblique tows were made at each station. The first replicate pair was from near-bottom to the pycnocline and the second was from the pycnocline to surface. At stations with no obvious pycnocline, the water column was divided in half for each set of oblique tows.

The sampling plan differed on 14 July. On that day, a single bongo-net tow of one-minute duration was made at each station from near-bottom to surface, with no division at the pycnocline. In addition, a two-minute oblique tow of a 2 m^2-mouth, Tucker trawl with 700-μm mesh was made from the pycnocline to surface to supplement collections of larger (>8.0 mm) larvae. Flowmeters in the mouths of both the bongo net and Tucker trawl allowed volumes filtered to be calculated from which densities (number m^{-3}) and abundances (number under 1 m^2) of eggs and larvae were estimated. Ichthyoplankton samples were fixed immediately in buffered 5% seawater formalin.

Two gelatinous predators, common during the study period, were the lobate ctenophore, Mnemiopsis leidyi, and the scyphomedusa, Chrysaora quinquecirrha. They are important consumers of zooplankton and ichthyoplankton (Cowan and Houde 1993; Purcell et al. in press). Total volumes of the combined gelatinous predators in each plankton-net catch were measured to the nearest 1.0 ml immediately after collection.

Pumped samples of potential microzooplankton prey of anchovy larvae were collected on three of the four sampling days. Fifty liters of water were pumped (approx. 30-l min^{-1}) from each of three discrete depths (bottom, near pycnocline and surface). Each sample was preserved in buffered 5% seawater formalin. Chlorophyll *a* concentration was determined at each depth by filtering 400-500 ml of water onto glass fiber filters, which were frozen and brought to the laboratory for analysis.

In the laboratory, anchovy eggs, larvae and other ichthyoplankton were removed from samples under a binocular microscope. Subsamples of 100 anchovy larvae were randomly selected from each sample (or all larvae if there were fewer than 100 larvae) and standard lengths (SL) were measured to nominal 0.01 mm SL using JAVA (Imaging Technology, Inc.) software. Three 1-ml aliquots of zooplankton samples were examined and counted to estimate densities (number l^{-1}). Organisms were identified to broad taxonomic or size categories: copepods, copepodites, copepod nauplii, cirripede nauplii, polychaete larvae, and veliger larvae.

Data and Analysis

Temperature, salinity and dissolved oxygen data were analyzed and contour-plotted using SURFER (Golden Software). Ichthyoplankton numbers were converted to mean abundances by date, station, depth stratum (i.e., below or above pycnocline) and replicate.

Larval abundances were adjusted for extrusion of small larvae through the bongo net's 280-μm meshes (MacGregor 1994). The adjustment was applied to larvae $\leq$5.5 mm SL.

Stations within three designated regions were grouped to examine possible regional differences. The stations (Figure 1) were grouped as follows: 1 and 2 = Inshore; 7, 8, 9, and 10 = Frontal; 11 and 12 = Offshore.

Abundances or densities of organisms were $\log_{10}$-transformed prior to statistical analyses to homogenize variances, satisfying requirements for analysis of variance (ANOVA). ANOVA was used to test for differences in mean $\log_{10}$ abundances among dates, stations, regions and depth strata. When ANOVA results were significant ($P<0.05$), Tukey's multiple comparison test was applied to compare individual means.

Length-specific mortality rates (Z_1) were estimated by regressing $\log_e$-transformed abundances (number under 100 m^{-2}) of anchovy larvae in 0.5 mm length classes on length. The slopes of the regression lines were estimates of Z_1. A 0.5 mm length increase is approximately equivalent to one day's growth in bay anchovy larvae (Houde and Schekter 1981; Leak and Houde 1987; Cowan and Houde 1990; Castro and Cowen 1991). Thus, Z_1 values (mm^{-1}) could be converted to approximate daily instantaneous mortalities Z_d. ANOVA was used to test if $\log_e$-transformed mean loss rates (Z_1) differed among days, stations, regions or depth strata.

RESULTS

Hydrography

Hydrographic conditions were typical for mid-Chesapeake Bay during July (Figure 2). An oxycline and pycnocline generally coincided at approximately 10 m depth. Subpycnocline water often was hypoxic. In the offshore region, dissolved oxygen values at >20 m depth usually were anoxic or nearly so ($\leq$0.5 mg l^{-1}).

Egg and Larvae Abundances

The mean abundances of bay anchovy eggs and larvae during the 4-d period were 1,143.9 eggs m^{-2} and 194.5 larvae m^{-2}, respectively (Table 1). Mean abundances differed among days (ANOVA, $P<0.05$). Lowest egg and larvae abundances were observed on 12 July ($P<0.05$). Egg and larval abundances were highest on 15 and 13 July, respectively.

Mean abundances of eggs and larvae differed among the eight transect stations (ANOVA, $P<0.0001$). Highest abundances occurred at stations 11 and 12 (Table 1; Figure 3). Among-station mean egg abundances varied by more than 45-fold and mean larval abundances varied more than 200-fold (Table 1; Figure 3) across the 13-km transect.

It was clear that the offshore region egg and larval abundances were very much higher (ANOVA, $P<0.0001$) than abundances in the frontal and inshore regions (Table 2). The mean egg abundances differed between all regions ($P<0.05$). Mean egg abundance in the frontal region, 227.0 m^{-2}, was significantly lower ($P<0.05$) than inshore or offshore mean abundances.

Anchovy eggs and larvae were less abundant below the pycnocline than above it on each sampling day. The above-pycnocline mean egg abundance, 961.7 m^{-2}, was 28 times higher (ANOVA, $P<0.005$) than the below-pycnocline mean, 34.4 m^{-2}. The above-pycnocline mean larval abundance, 167.2 m^{-2}, was 36 times higher (ANOVA, $P<0.005$) than the below-pycnocline mean, 4.6 m^{-2}.

A relatively higher fraction of anchovy eggs and larvae occurred below the pycnocline at inshore stations. Offshore, eggs and larvae were 79 and 89 times less abundant, respectively, below the pycnocline (where the water was hypoxic or anoxic) than above it. Inshore, where water was not hypoxic, egg and larval abundances were only 6 and 4 times less abundant, respectively, in below-pycnocline collections.

Sizes of Larvae

Most bay anchovy larvae were recently hatched. Standard lengths in the bongo net catches ranged from 1.04 to 12.34 mm and the overall mean was 2.91 mm (Table 3). Mean lengths did not differ among days (ANOVA, $P>0.10$). Mean length offshore (2.46 mm) was significantly less ($P<0.05$) than mean length in the frontal and inshore regions (3.00 and 3.19 mm, respectively) (Table 3).

Mean larval length tended to increase in an offshore to inshore direction along the transect (Figure 4). Larvae of longest mean lengths, 3.46 mm and 3.43 mm, were collected at Stations 2 and 9, respectively.

In the offshore and frontal regions, mean lengths of larvae collected below the pycnocline were less than mean lengths above it. At inshore stations, larval mean lengths were longer below the pycnocline (Figure 4a).

The length-frequency distributions of bay anchovy larvae were dominated by recently-hatched larvae in the 2.0 - 2.5 mm length class, but the distributions were multimodal at all stations during the four days. At the offshore Stations 11 and 12, newly-hatched larvae ($\leq$2.5 mm) constituted >98% of the larval catch, a reflection of the high offshore spawning and egg abundance (Table 2).

Size-Specific Abundances of Larvae

The absolute abundances of large anchovy larvae ($\geq$5.5 mm SL) were highest offshore (Figure 5). However, relative abundances of large larvae were higher in the frontal and inshore regions (Figure 6) and were significantly higher ($P<0.05$) inshore than offshore. The proportion of anchovy larvae categorized as "large" peaked at Station 9, in the frontal zone, and was higher there ($P<0.05$) than at Stations 11 and 12 (Figure 6). Absolute abundances of small anchovy larvae (<5.5 mm) always were significantly higher ($P<0.05$) in the offshore region but were nearly equally abundant ($P>0.05$) in frontal and inshore regions.

Apparent Mortality

Mean length-specific mortality rates (mm^{-1}) on the four days ranged from Z = 1.09 to Z = 1.34 (Table 4), which are equivalent to loss rates of 66.4 to 73.8% mm^{-1}. At the assumed 0.5 mm d^{-1} growth rate, the mean percent daily losses ranged from 42.0 to 48.8%. The mean length-specific mortality rate over all days and stations was Z = 1.24 mm^{-1}, which is equivalent to a daily loss rate of 46.2%.

The loss rates tended to decrease from offshore to inshore (Figure 7). The apparent mortality rates were higher ($P<0.05$) offshore (85.0% mm^{-1}) than in the inshore (60.5% mm^{-1}) and frontal (65.4% mm^{-1}) regions (Table 4).

Length-specific mortality rates declined as larvae increased in length. Mean mortality rates in three designated length classes, 2.5 - 4.5 mm, 4.5 - 7.5 mm, and 8.5 - 14.0 mm, differed significantly ($P<0.05$) (Figure 8).

Larvae in the 2.5 - 4.5 mm length class experienced a mean mortality rate of 1.52 mm^{-1} (78.1% mm^{-1}). The rate had declined to 0.60 mm^{-1} (45.1% mm^{-1}) for 5.0 - 8.5 mm larvae and to 0.29 mm^{-1} (25.2% mm^{-1}) for 8.5 - 14.0 mm larvae (Figure 8). Although apparent mortality rates were higher offshore for each length class, the regional difference was minor for the 8.5 - 14.0 mm larvae.

Gelatinous Predators

Two major gelatinous predators of bay anchovy eggs and larvae in the net collections were the scyphomedusa (Chrysaora quinquecirrha) and the lobate ctenophore (Mnemiopsis leidyi). Their combined biovolumes did not differ significantly among days or among stations (ANOVA, $P>0.10$). Mean biovolume during the four days was 148.2 ml m^{-2}. On a regional basis, gelatinous zooplankton tended to have highest biovolumes (but not significant at $P = 0.05$) in the frontal zone. Biovolumes were nearly 5 times higher (ANOVA, $P<0.0001$) above the pycnocline (106.3 ml m^{-2}) than below it (23.1 ml m^{-2}).

Zooplankton Densities

The mean density of zooplankton during the sampling period was 203.8 organisms l^{-1}. Copepod nauplii were the most abundant (ANOVA, $P<0.0001$) organism (163.1 l^{-1}). There were no significant differences ($P>0.05$) in mean combined-taxa zooplankton densities among stations, although the highest observed values were at stations in the frontal zone (Figure 9). Regionally, densities tended to be higher, although not significantly so ($P>0.05$), in the frontal region compared to offshore and inshore. Zooplankton mean density near surface (346.5 l^{-1}) was significantly higher ($P<0.05$) than mean densities at mid-depth and near bottom (169.0 and 102.5 l^{-1}).

Chlorophyll *a*

Mean chlorophyll *a* levels did not differ during the sampling period ($P>0.05$). The overall mean level was 10.2 $\mu g\ l^{-1}$. Mean chlorophyll *a* level, integrated over the entire water column, was significantly higher ($P<0.05$) in the frontal region than offshore and tended to be higher in the front than inshore.

DISCUSSION

Strong gradients were observed in cross-bay abundances of bay anchovy eggs and larvae, and in apparent mortality rates of larvae. Abundances and apparent mortality rates were consistently higher offshore during the four-day study along a 13-km transect. The role, if any, of the ephemeral tidal front near the Patuxent River mouth, with respect to anchovy reproduction and early life dynamics, was unclear. Plankton densities and biovolumes may be elevated in the front relative to inshore or offshore regions (Figure 10). It is clear that anchovy egg abundances were lowest in the frontal region and that larval abundances also were very low compared to the offshore zone. Most spawning occurs offshore, explaining the egg abundance and distribution results, and partly explaining larval distributions and loss rates.

The high abundances of bay anchovy eggs and recently-hatched larvae offshore indicate that it is the primary spawning location in Chesapeake Bay. Because incubation time for bay anchovy eggs is <24 h, currents and transport cannot account for the observed egg distributions. Egg abundances offshore are the result of intensive spawning there, not resultant transport from other regions.

In this study, chlorophyll *a* concentration and densities of microzooplankton suitable as anchovy larval prey were equal to or somewhat lower offshore than in frontal or inshore regions (Figure 10). Consequently, there is no apparent nutritional advantage to larvae from eggs being spawned offshore. In fact, if there were a nutritional advantage for larvae, it potentially was in the frontal region where copepod nauplii densities, an important larval food (Houde and Lovdal 1984), averaged 200 l^{-1}. This density was nearly twice that observed offshore (Figure 10). Like other described river plumes (e.g. Mackas and Luottit 1988; Dagg and Whitledge 1991; Grimes and Finucane 1991; St. John and Pond 1992), chlorophyll *a* and zooplankton densities were higher in the frontal region. But, in our study the abundances of bay anchovy eggs and larvae were low in and near the front.

Jellyfish can be effective predators on fish eggs and larvae (Bailey 1984; Purcell 1985, 1989). Some research has demonstrated that increases in gelatinous predator biovolumes results in increased larval mortality (e.g. de Lafontaine and Leggett 1988; Cowan and Houde 1993). On average, gelatinous predator biovolumes were about 1.5 times higher in the Patuxent River frontal region. This relatively small increase in gelatinous predators seems unlikely to be a possible cause of major increases in mortality rates of anchovy eggs and larvae in the frontal region compared to other regions. If the increase in gelatinous predator biovolume in the front were due only to the scyphomedusa C. quinquecirrha, rather than to the ctenophore M. leidyi, it potentially was a significant factor leading to increased egg and larval mortality (Cowan and Houde 1993; Purcell et al. in press).

Behavior of adult anchovy provides a probable explanation for the low egg abundances in the frontal region. Acoustics and trawling studies have demonstrated that, on a daily schedule, most adults in Chesapeake Bay move onshore during the day and offshore at night (Brandt et al. 1992). Spawning occurs at night (Zastrow et al. 1991). In addition, recent evidence suggests that adult bay anchovy may avoid spawning in areas of high gelatinous predator abundance (Dorsey 1993), which might have reduced egg output in the frontal region.

Subpycnocline water, which was hypoxic or anoxic, contained few anchovy eggs and larvae in the offshore region. Mean anchovy egg and larvae abundances were nearly two orders of magnitude higher above the pycnocline than below it. Inshore, where hypoxia was less severe below the pycnocline, anchovy egg and larval abundances still were six and four times higher, respectively, above the pycnocline.

Anchovy eggs and larvae collected below the pycnocline often were in obviously poor condition. It appeared that many had been dead before they were collected. Laboratory research has demonstrated that bay anchovy eggs can tolerate dissolved oxygen levels as low as 2.0 mg l^{-1} and bay anchovy yolk-sac larvae can tolerate levels of 1.5 mg l^{-1} (Houde and Zastrow 1991). Dissolved oxygen levels below the pycnocline generally were <2.0 mg l^{-1} during this study, which suggests that eggs and newly-hatched larvae below the pycnocline were not viable or alive when collected.

<u>Larval Size Distribution, Apparent Mortality and Transport Mechanisms</u>

The observed increase in mean larval length and in relative abundance of large anchovy larvae in an offshore to inshore direction suggested that anchovy larvae might have been advected shoreward or that size-specific mortality rates differed among regions. Larval mean and modal lengths offshore were <2.5 mm, a length only slightly longer than the approximate 2.0 mm length-at-hatch. It is possible that a net shoreward transport of larvae from the offshore region could have accounted for the 0.73 mm increase in mean larval length between the offshore and inshore regions.

Norcross and Shaw (1984), Kingsford and Choat (1986), Nakata (1989), and Murdoch et al. (1990) reported similar regional trends in mean larval lengths and large-larvae abundances. They attributed these trends to shoreward advection of recently-hatched larvae by currents and tides. In the tidal Patuxent River, Loos and Perry (1991) demonstrated that bay anchovy larval lengths and densities of large larvae increased from the river mouth to the upriver region, indicating that upstream transport or differential mortality between the upstream and downstream regions could explain the results. They favored a transport hypothesis because differential mortality did not reasonably explain how numbers of large larvae, averaged over the spawning seasons, exceeded numbers of smaller larvae in the upriver region.

In our study, the longest mean lengths of anchovy larvae came from catches below mid-depth at the inshore Stations 1 and 2 in the mouth of the Patuxent River. These larvae could have represented large individuals that potentially were susceptible to upriver transport in a two-layered estuarine circulation (Miller et al. 1984; Weinstein et al. 1980; Laprise and Dodson 1989).

A simulation transport model, which we applied to data from the three regions, indicated that offshore-onshore transport was unlikely to have been an important factor affecting the distribution and abundance of bay anchovy larvae along the transect (MacGregor 1994). Under some circumstances, transport losses and gains among regions could partially account for the observed distributions and early-life dynamics, but in most cases it appears that mortality was the primary cause of loss in each of the regions.

The differences among regions in mean larval lengths and large-larvae abundances may have been a consequence of different larval mortality rates. The mean apparent mortality rate offshore was nearly double the rates ($P<0.05$) in the inshore and frontal regions. It also is probable that mortality rates differ among length classes of larvae. If mortality is size-selective or density-dependent, the high abundance offshore of recently-hatched larvae may have been a factor influencing the high estimated mortality rate in that region. Comparing the length-specific larval mortality rates among regions for larvae in three length classes (Figure 8), it was apparent that rates for all lengths were higher offshore than inshore or in the frontal region. This suggests that mortality is size-selective and also that it differs between regions only a few km apart. For the small (2.5 - 4.5 mm) and intermediate size (5.0 - 8.5 mm) anchovy larvae, mortality offshore was significantly higher than mortality inshore. For the 8.5 - 14.0 mm anchovy larvae, the estimated offshore mortality also was slightly, but not significantly, higher than mortality in the other regions.

The processes that led to increases in mean larval length and relative abundance of large larvae inshore may be of minor consequence to recruitment of bay anchovy because of the differences in respective volumes of the regions. The volume of the offshore region, where most eggs and larvae occurred, greatly exceeds that of the inshore and frontal regions, and the standing stock of anchovy larvae of all sizes was many times larger offshore. The standing stock of large anchovy larvae (>5.5 mm; >7 days after hatching) offshore was 12 times higher than in the other regions. If a modest fraction of bay anchovy larvae were advected shoreward from the offshore region, and if the inshore population experienced lower mortality, such processes may have only small effects on regional contributions to recruitment in Chesapeake Bay. Most recruits probably originate from spawning and larval production offshore. The inshore and frontal regions, though only a few km removed from the offshore region, may contribute relatively little to baywide recruitment, despite a tendency for increases in relative abundance of large larvae inshore and a propensity for some larvae to be advected upstream into tidal rivers where substantial recruitment may occur.

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Table 1. Bay anchovy egg and larvae mean abundances (number under 1.0 m^2) on four dates and at eight stations. Stations are indicated on Figure 1. Identical superscripts on mean values indicate no significant difference ($P > 0.05$, Tukey's comparison procedure).

Dates (July 1988)

		12	13	14	15	Grand Mean
Eggs						
	Mean	371.6[b]	955.7[a]	1,587.4[a]	1,660.9[a]	1,143.9
	S.E.	25.0	74.0	747.5	248.3	302.2
Larvae						
	Mean	50.5[b]	305.3[a]	262.2[a]	159.9[a]	194.5
	S.E.	1.9	54.7	171.2	16.0	56.9

Stations

	1	2	7	8	9	10	11	12	Grand Mean
Eggs									
Mean	878.8[abc]	370.3[abcd]	215.7[bcd]	113.7[cd]	99.7[d]	478.8[abcd]	2,310.6[ab]	4,720.1[a]	1,143.9
S.E.	322.4	94.4	43.6	33.3	38.3	283.5	668.0	1,945.1	302.2
Larvae									
Mean	14.4[cd]	18.0[cd]	4.9[d]	14.5[d]	16.7[cd]	99.3[bc]	358.9[ab]	1,013.5[a]	194.5
S.E.	3.0	3.6	1.5	5.1	7.2	48.1	94.8	347.4	113.7

Table 2. Bay anchovy egg and larvae abundances (number under 1.0 m^2) in the offshore, frontal and inshore regions on the sampling transect illustrated in Figure 1. Offshore = Stations 11 and 12; Frontal = Stations 7, 8, 9 and 10; Inshore = Stations 1 and 2. Identical superscripts on mean values indicate no significant difference ($P>0.05$, Tukey's comparison procedure).

	Regions		
	Inshore	Frontal	Offshore
Eggs			
Mean	624.6^{b}	227.0^{c}	$3,515.3^{a}$
S.E.	182.8	76.1	1,055.4
Larvae			
Mean	16.2^{b}	33.9^{b}	686.2^{a}
S.E.	2.3	14.7	207.6

Table 3. Mean standard lengths (mm) of bay anchovy larvae on four days and at eight stations. Stations are indicated on Figure 1. Identical superscripts on mean values indicate no significant difference ($P>0.05$, Tukey's comparison procedure).

	Dates (July 1988)				
	12	13	14	15	Grand Mean
Mean	2.92^{a}	2.70^{a}	3.03^{a}	2.99^{a}	2.91
S.E.	0.04	0.14	0.17	0.08	0.08

	Stations								
	1	2	7	8	9	10	11	12	Grand Mean
Mean	2.91^{ab}	3.46^{a}	2.90^{ab}	3.02^{ab}	3.43^{a}	2.65^{ab}	2.46^{b}	2.46^{b}	2.91
S.E.	0.12	0.09	0.21	0.10	0.33	0.09	0.10	0.21	0.08

	Regions		
	Inshore	Frontal	Offshore
Mean	3.19^{a}	3.00^{a}	2.46^{b}
S.E.	0.13	0.12	0.11

Table 4. Length-specific, apparent mortality rates (mm^{-1}) of bay anchovy larvae on four days and at eight stations. Stations are indicated on Figure 1. Identical superscripts on mean values indicate no significant difference ($P>0.05$, Tukey's comparison procedure).

Dates (July 1988)

	12	13	14	15	Grand Mean
Mean	1.09^{b}	1.34^{a}	1.28^{ab}	1.24^{b}	1.24
S.E.	0.03	0.06	0.23	0.07	0.06

Stations

	1	2	7	8	9	10	11	12	Grand Mean
Mean	0.83^{c}	1.02^{bc}	0.85^{c}	1.21^{abc}	0.88^{c}	1.30^{abc}	1.82^{ab}	1.98^{a}	1.24
S.E.	0.05	0.07	0.09	0.12	0.22	0.21	0.11	0.23	0.06

Regions

	Inshore	Frontal	Offshore
Mean	0.93^{b}	1.06^{b}	1.90^{a}
S.E.	0.06	0.09	0.12

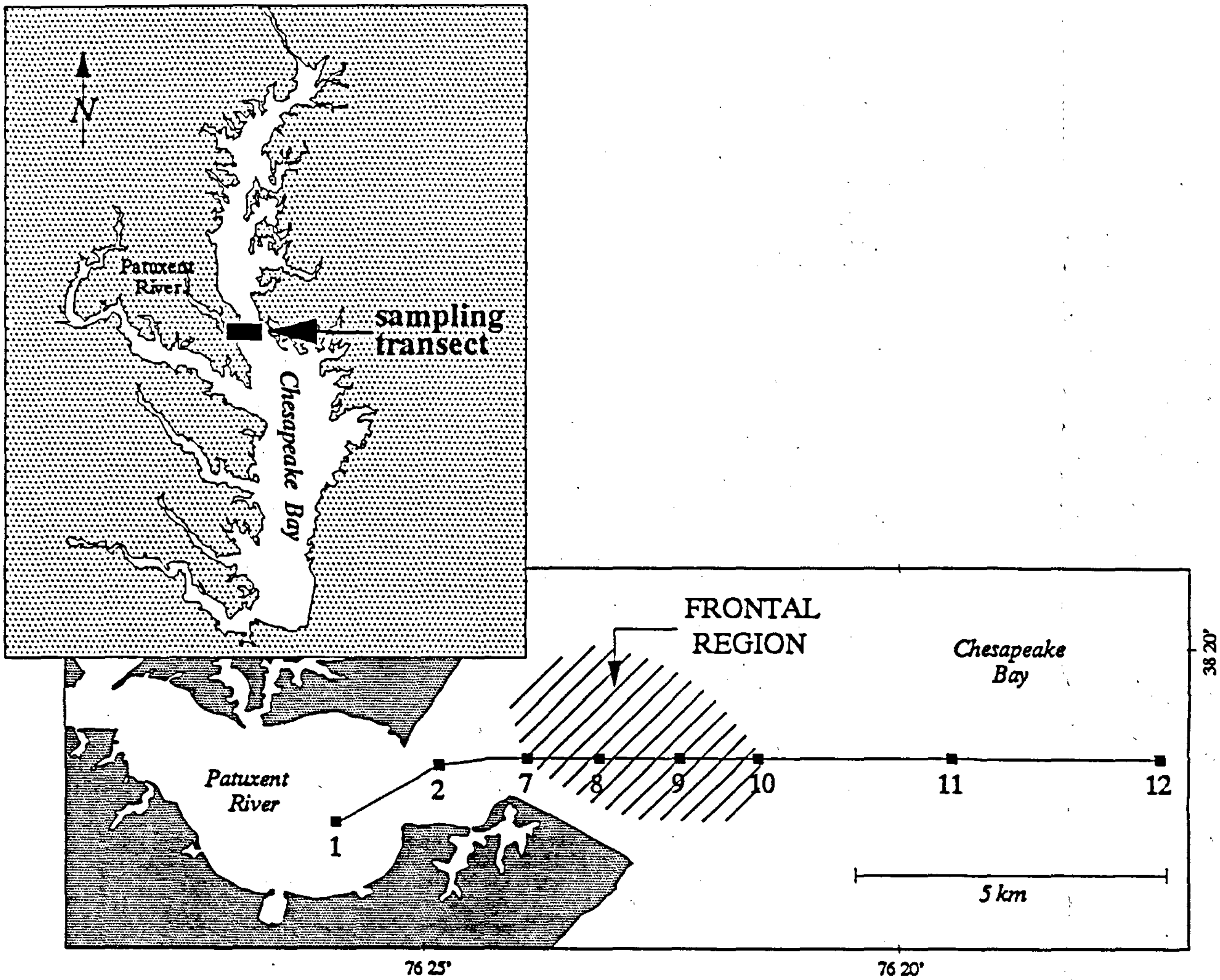

Figure 1. Chesapeake Bay and the sampling transect. The frontal region is indicated. Station numbers: 1 and 2, inshore region; 7 - 10, frontal region; 11 and 12, offshore region.

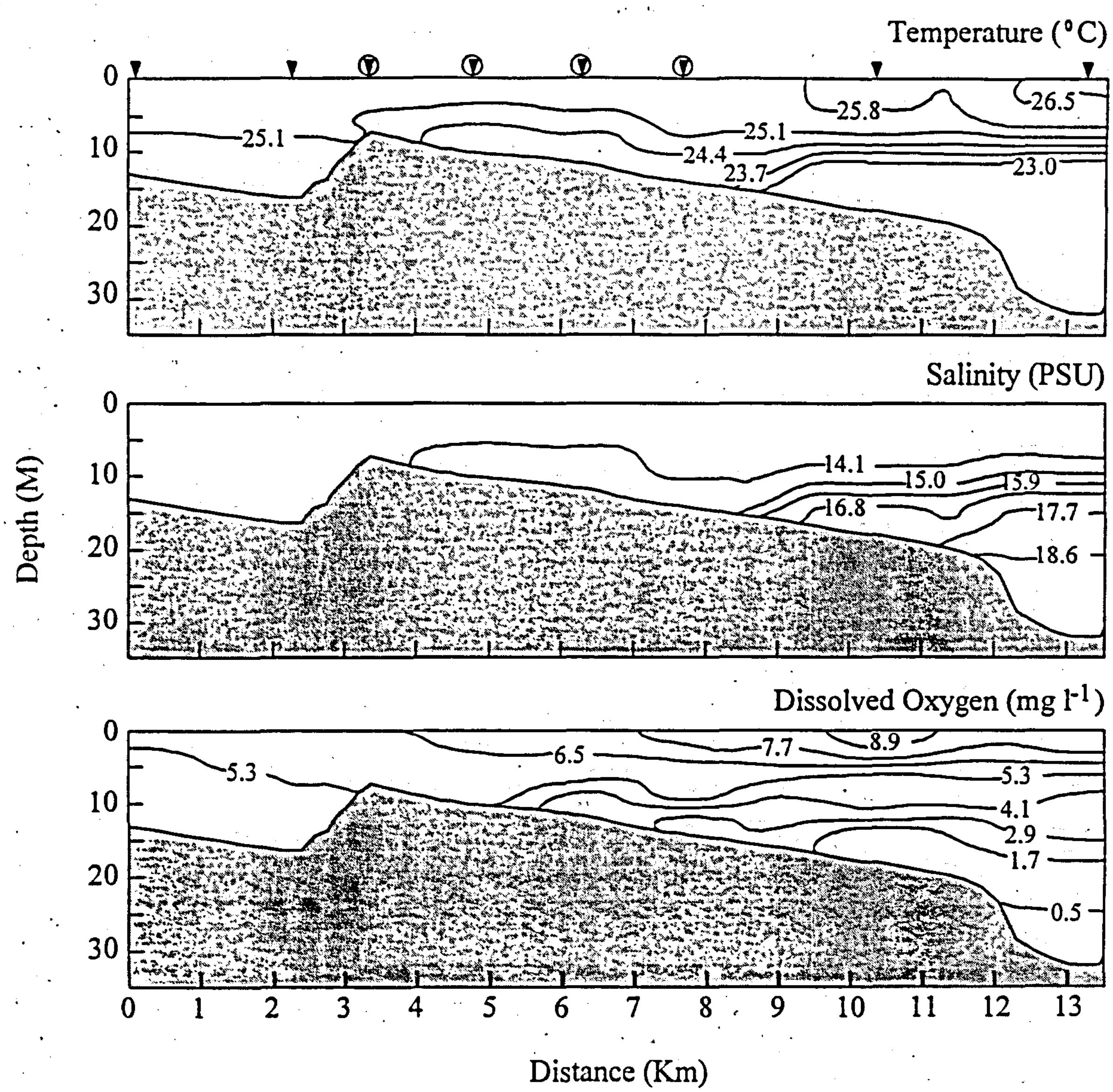

Figure 2. Contour plots of mean temperature (°C) and salinity (PSU) along the sampling transect on four days, 12 - 15 July 1988. Markers (▾) indicate station locations. Encircled markers (ⓥ) indicate frontal zone stations.

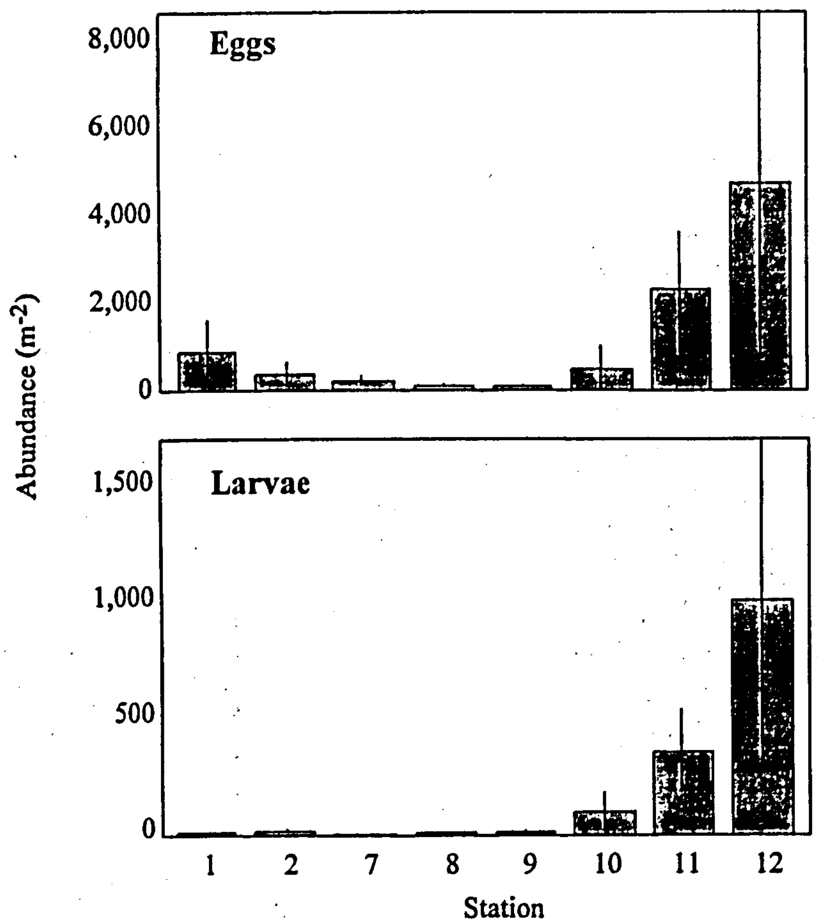

Figure 3. Mean bay anchovy egg and larvae abundances (m^{-2}) at the eight stations indicated in Figure 1 during the 12 - 15 July 1988 period. The eight stations were on a transect of ca. 13-km length. Error bars are ± 2 S.E.

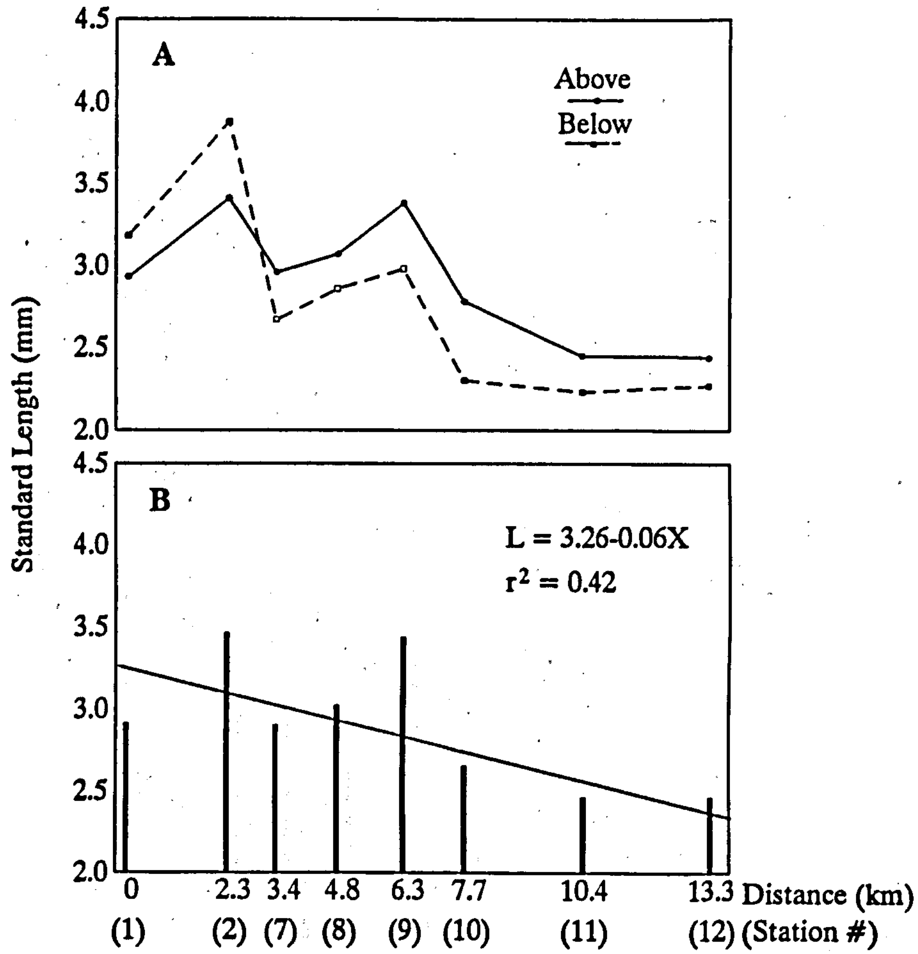

Figure 4a-b. Mean lengths (mm) of bay anchovy at each station during the 12 - 15 July 1988 period. (A) Mean lengths above and below the pycnocline. (B) Mean lengths for entire water column. The regression equation is the relationship between anchovy larval length and distance offshore.

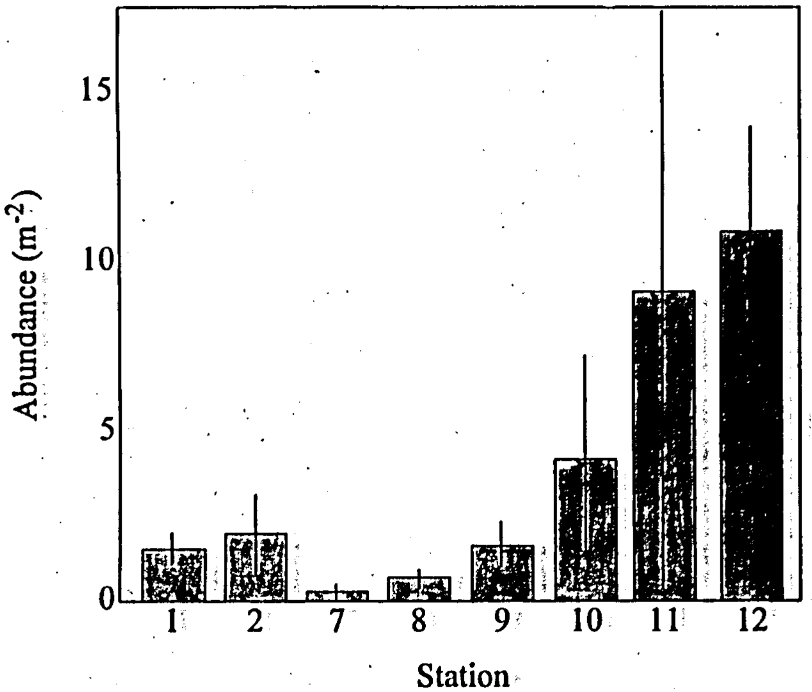

Figure 5. Mean abundances of "large" bay anchovy (m^{-2}) in bongo-net collections at eight stations on a 13-km transect, 12 - 15 July 1988. Large larvae are ≥5.5 mm SL. Error bars are ± 2 S.E.

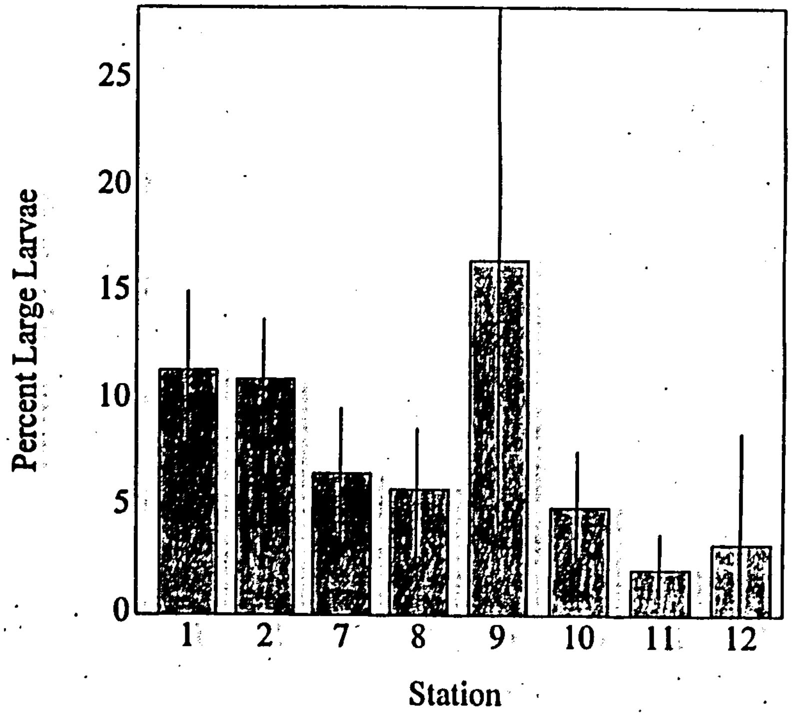

Figure 6. Mean percentage of bay anchovy larvae in the bongo-net collections that were "large" (≥5.5 mm SL) at each station during the 12 - 15 July 1988 period.

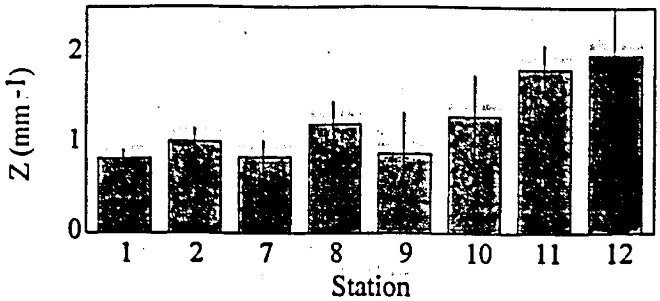

Figure 7. Mean length-specific mortality rates (mm^{-1}) of bay anchovy larvae from 12 - 15 July 1988 at eight stations on a transect in Chesapeake Bay (see Figure 1). Error bars are ± 2 S.E.

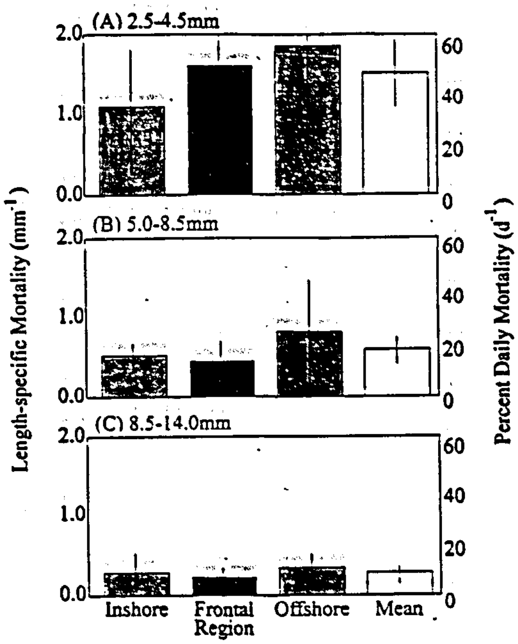

Figure 8. Mean length-specific mortality rates (mm^{-1}) of bay anchovy larvae in three regions of Chesapeake Bay. Mortality rates for (A) 2.5 - 4.5 mm larvae, (B) 5.0 - 8.5 mm larvae, and (C) Tucker-trawl collected 8.5 - 14.0 mm larvae. Percent daily mortality is estimated based upon an assumed 0.5 mm d^{-1} growth rate.

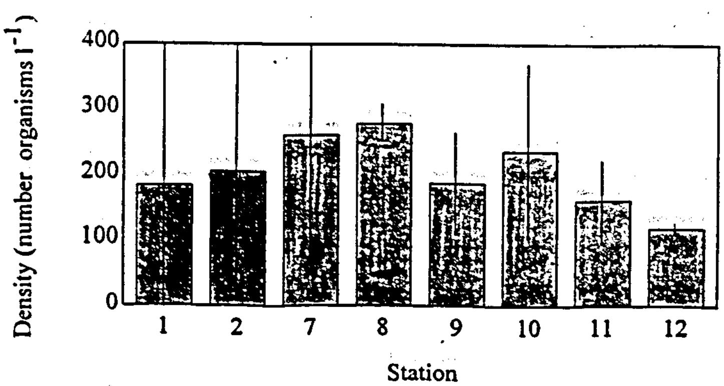

Figure 9. Zooplankton mean densities (number organisms l^{-1}) at eight stations on a 13-km transect sampled during three days in July 1988. Stations are indicated on Figure 1. Stations 7, 8 9 and 10 were in the frontal region. Error bars are ± 2 S.E.

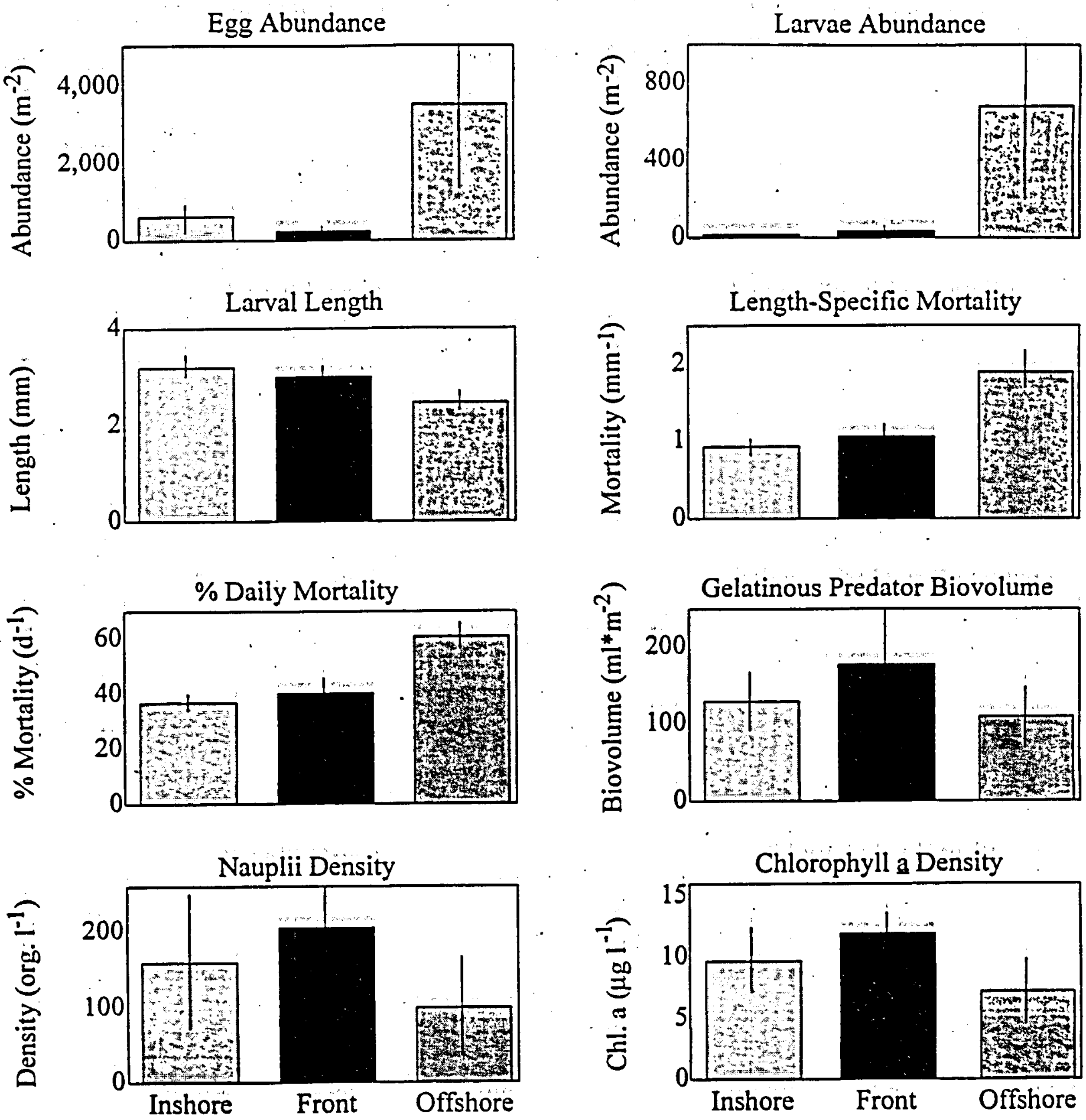

Figure 10. Summary of mean values for each variable in the three regions on a 13-km transect in Chesapeake Bay. Stations and regions are described in Methods.