

## Larval distributions in inner-shelf waters: The roles of wind-driven cross-shelf currents and diel vertical migrations

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### Abstract

To determine how physical processes and biological behaviors influence larval dispersal on the inner shelf, time series of larval concentrations were quantified during August 1994, on the Outer Banks of North Carolina, U.S.A. Zooplankton pumps, moored in 21 m of water at 3.2, 8.7, and 12.2 m above bottom, collected larvae every 3 h for 3 weeks. Physical variables and larvae were sampled at similar time and space scales. Larval concentrations were typically  $10^2$ – $10^4$  m<sup>-3</sup> for polychaetes, bivalves, and gastropods and  $10$ – $10^2$  m<sup>-3</sup> for brachyuran crab zoeae. There were two dominant scales of variability, 3–6 h and 2–10 d. The high-frequency signal is partially explained by diel vertical migrations—nocturnal ascent and daytime descent. This pattern would allow larvae to feed in subthermocline waters while avoiding visual predators. Low-frequency variations tracked with water temperature. Highest concentrations of worm larvae occurred in cool (upwelled) water and of crab zoeae in warm (downwelled) water. At least two larval groups comprised the clam and snail time series, one with fairly high abundances in cool water and the other with peak concentrations in warm water. Wind-driven cross-shelf transport is the most plausible explanation for these low-frequency fluctuations. For example, dense patches of worm larvae overlying parental habitat (offshore muds) would be carried shoreward in cool, upwelling flows. In contrast, brachyuran zoeae in near-surface waters would descend at the coast during downwelling and, together with larvae aloft nearshore sediments, be transported seaward below the thermocline. Thus advected by strong along-shore and weaker cross-shelf currents, larvae zigzag up and down the coast. Vertically traversing the water column while they feed and grow, larvae ultimately seek a suitable habitat in which to settle.

The inner portion of the continental shelf (roughly 5–30 m depth) is a dispersal corridor between intertidal and offshore habitats. Replete with planktonic larvae, it also provides soft sediments for benthic adults. Physical processes, such as wind-driven upwelling and downwelling, thermal fronts, eddies, tides, internal waves, tidal bores, surface waves, and storms, operate over spatial scales of 1 m to  $10^3$  km and temporal scales of hours to weeks (Mann and Lazier 1991). In this high-energy environment, physics should play

an important role in creating or maintaining patchiness of invertebrate larvae that live for weeks to months in the plankton. Moreover, behaviors, such as diel or tidally timed vertical migrations, may also drive variability in larval dispersion patterns (Sulkin 1984; Forward and Tankersley 2001). Because benthic recruitment can be limited by larval supply (Connell 1985, but *see also* Ólafsson et al. 1994), planktonic processes are ultimately linked to population and community dynamics.

There is compelling support for the hypothesis that upwelling and downwelling circulations transport larvae across the inner shelf, ultimately controlling recruitment of intertidal species (Roughgarden et al. 1987). Along eastern shores in the Northern Hemisphere, winds blowing toward the north initiate upwelling, where surface water advected seaward is replaced by offshore bottom water that ascends at the coast (Smith 1968). Winds blowing toward the south produce downwelling, where surface water moves shoreward, descends, and is advected offshore at the bottom. Prolonged upwelling or downwelling conditions result in two-layered cross-shelf circulations, with opposing surface and bottom flows (Lentz 2001). Larval transport by these wind-driven cross-shelf currents depends on their vertical distributions (Kullenberg 1978). For example, larvae move shoreward if they are located below the thermocline during upwelling or near the surface during downwelling. Recruitment pulses of neritic barnacles and crabs have been attributed to onshore larval transport during relaxation of upwelling (Farrell et al. 1991; Roughgarden et al. 1991; Wing et al. 1995) or downwelling (Connolly and Roughgarden 1999).

Vertical stratification of planktonic larvae may result from physical or biological mechanisms. Passive physical pro-

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cesses include vertical flows (e.g., upwelling and downwelling) and depth-dependent variations in turbulent mixing. Biological mechanisms that would, for example, locally increase near-bottom larval concentrations include differential spawning activity of benthic adults or enhanced sinking rates due to calcification of late-stage larval shells. Moreover, stratification of larvae requires vertical larval swimming in response to physical (temperature, salinity, mixing) or biological (food, predators) factors.

The goals of this study were to (1) quantify temporal fluctuations and vertical distributions of planktonic larvae inhabiting inner-shelf waters and (2) develop plausible scenarios involving physical or biological mechanisms to explain observed patterns of variation. The null hypothesis is that larvae are transported like passive particles and, thus, planktonic dispersion patterns are determined by physical processes alone. Deviations from passive predictions may be attributed to biological processes, such as vertical larval swimming in response to physical or biological signals.

In this study, planktonic larvae and physical variables were sampled at similar time and space scales over 20 d, during significant wind-driven cross-shelf flows, energetic along-shore currents, intense wave activity, and intermittent freshwater intrusions. Three vertically moored zooplankton pumps yielded synoptic time series (3-h sampling) of larval concentrations in 21 m of water. Physical-oceanographic instruments were more densely distributed in the vertical and sampled more frequently than the pumps. These moorings were part of a larger cross-shelf array (three sites, nine pumps) for quantifying distributions and evaluating potential mechanisms of cross-shelf larval transport (Coastal Ocean Processes study, CoOP94; Butman 1994). Owing to limited resources, three pumps in one vertical array were processed for the full 20-d deployment and the remainder for an abbreviated 7-d interval. Results for all pumps in the cross-shelf array over this truncated period will be presented elsewhere (C.A. Zimmer and S.J. Lentz unpubl. data).

## Materials and methods

*Inner-shelf study site*—The study site was located on the Outer Banks at Duck, North Carolina, U.S.A., between Cape Henry and Cape Hatteras (Fig. 1 insert). Oriented 340° true, the coastline slopes gently to the east over a 100-km-wide continental shelf. Irregular ridge and swale topography occurs between the 20- and 25-m isobaths (J.C. Church unpubl. data). Sediments are sandy inshore and muddy offshore (Kim et al. 1997), with isolated hard substrate. The inner shelf is a conduit for exchange of water and animals between brackish sounds and the Atlantic Ocean. The Duck site was chosen because of its physical characteristics and its proximity to the U.S. Army Corps of Engineers' Field Research Facility (FRF) (Birkemeier et al. 1985). In 1994, the FRF was the site of two large, multidisciplinary, oceanographic research programs—CoOP94 (Butman 1994) and a near-shore-dynamics study (Duck94; Wakefield 1994).

*Sampling techniques*—Larvae were collected using three moored, automated, serial zooplankton pumps (Doherty and Butman 1990; Butman 1994) that were mounted vertically

at the 21-m isobath, ~5 km from shore. Designed to minimize flow disturbances that may bias collections, the entrance region is formed by two horizontal, circular plates (60-cm diameter, 15 cm apart). Water moving between the plates is pumped up through an intake (center of upper plate) and covered by a 1-mm prefilter along a channel spanned by a 100- $\mu\text{m}$  mesh strip. Larvae >100  $\mu\text{m}$  but <1415  $\mu\text{m}$  (diagonal of prefilter openings) are retained on the mesh. After pumping for a preset interval, the sample is protected with another 100- $\mu\text{m}$  mesh strip and rolled onto a take-up spool residing in a preservative bath (3.7% buffered formalin, stained with Rose Bengal) for in situ long-term storage (Longhurst et al. 1966).

Sampling frequency was constrained by the instrument, which can collect 160 samples per deployment. The goal was to maximize the length of the record while preserving tidal variation, the shortest scale physical process that could be resolved. The pumps sampled at 3-h intervals over 20 d, from 0000 h on 11 August to 2100 h on 30 August, local mean time (LMT). Targeted water volume was 250 L. At a volume flux of ~25 L min<sup>-1</sup>, samples were collected in 10 min. This sampling scheme was stipulated, in part, by results of a smaller scale study conducted at Duck during the previous July (Garland and Zimmer 2002).

The three pumps were positioned 3.2 (bottom), 8.7 (middle), and 12.2 (upper) m above the bottom (mab) (Fig. 1). A fourth pump (top) was located 16.8 mab, but disappeared from its mooring during a storm. Temperature, salinity, and currents were measured within 2 m vertically and 500 m horizontally of comparable pumps (Fig. 1). Meteorological variables (winds, shortwave radiation) were recorded on a surface mooring at the 21-m site, within 500 m of the pump moorings. A bottom tetrapod, recording suspended sediment concentrations and current velocities within 1 m of the bed, was located 0.8 km (11–19 August) or 1.4 km (19–30 August) shoreward of the other moorings (L.D. Wright pers. comm.).

*Sample processing*—Each plankton sample was cut from the mesh strips and transferred to 80% buffered ethanol with Rose Bengal stain. All samples were washed from the mesh over a 90- $\mu\text{m}$  sieve and processed somewhat differently for the upper and bottom versus the middle pumps. Upper and bottom pump samples were split into four fractions using a modified Folsom plankton splitter (Scarola and Novotny 1968). At least one quarter split was sorted under a dissecting microscope, and larvae enumerated to major taxa (polychaetes, bivalves, gastropods, and brachyuran crab zoeae), with the exception of nondescript trochophores. Subsampling error, calculated as the mean coefficient of variation for samples with  $\geq 2$  splits and >5 larvae, was 26% ( $N = 11$ ) for polychaetes, 11% ( $N = 11$ ) for bivalves, and 21% ( $N = 9$ ) for gastropods.

Middle pump samples were processed using density stratification (as adapted from Price et al. 1978) in an exploratory effort to speed up presorting. This procedure streamlined sorting of mollusks, but was not effective for soft-bodied taxa. Samples were concentrated in <25 ml freshwater, layered on top of a colloidal silica solution (25 ml Ludox AM, Dupont Chemicals, 1.2091 specific gravity, 9.0 pH) in a 50-

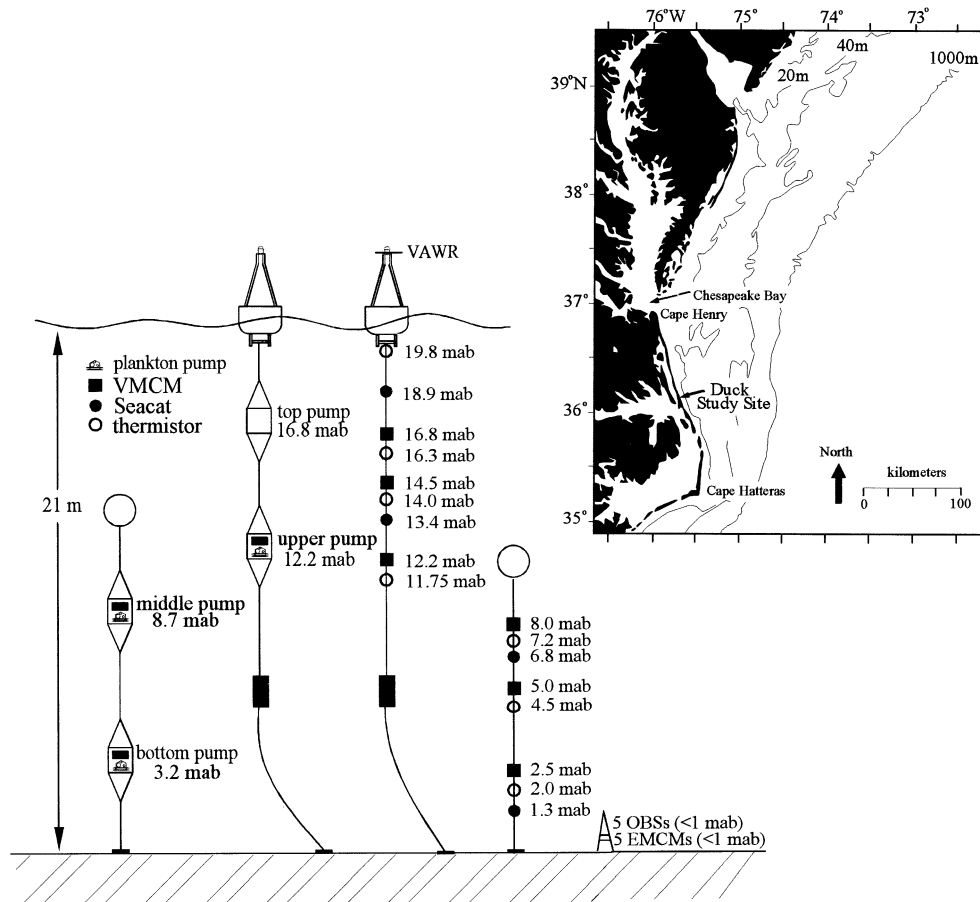


Fig. 1. Configuration of the moored plankton pumps and oceanographic instruments at the 21-m site during August 1994. Heights are given in meters above bottom (mab). Seacats recorded water temperature and conductivity; vector measuring current meters (VMCMs) and electromagnetic current meters (EMCMs) recorded current velocity; the Vector Averaging Wind Recorder (VAWR) package recorded wind speed, wind direction and shortwave radiation; thermistors recorded water temperature; and the optical backscatter sensors (OBSs) recorded suspended sediment concentrations within the bottom boundary layer. Insert: map showing location of study region ( $36^{\circ}10.895'N$ ,  $75^{\circ}45.068'W$ ) off Duck, North Carolina, U.S.A.

ml centrifuge tube and spun at maximal speed for 5 min in a clinical centrifuge. Most crab zoeae and barnacle cyprids were trapped at the air–water interface, and most polychaete larvae, copepods, and debris accumulated at the freshwater–silica solution interface. Everything else, including some taxa mentioned above, settled to the bottom. This bottom fraction was processed for bivalve and gastropod larvae only. The sorting of zoeae and polychaetes was extremely time consuming because they occurred in multiple density fractions.

The goal of this study was to quantify temporal changes in larval distributions relative to physical variables. Yet most larvae were not sufficiently differentiated to enable species identifications using morphological criteria alone. Likewise, in the Shanks (1998) study of the large megalopa larval stage of brachyuran crabs at Duck, only the very common blue crab (*Callinectes sapidus*) larvae were identified to species, and all other individuals only to genus (e.g., *Uca* spp. and *Libinia* spp.). Identifications of the very small larvae collected by the pumps were uncertain even to genus or family.

Other taxonomic methods, such as scanning electron microscopy of bivalve hinge “teeth” (Lutz and Jablonski 1979; Le Pennec 1980) and molecular probes (Bell and Grassle 1998; Hare et al. 2000), apply to only a few species and are impractical for large samples ( $10^2$ – $10^3$  per 1/4 split). Supraspecific categories (e.g., genus, family) are not meaningful for this study because species, not higher taxa, evolve. Thus, only species may have consistent, distinctive behaviors and ecological characteristics.

This coarse taxonomic resolution was balanced by unprecedented temporal (3 h for 20 d) and synchronous vertical (three depths) coverage, which has not been practical using shipboard techniques. In fact, this study required the development of a moored pump that could make frequent larval collections over weeks or longer (Butman 1994). Sorting to higher taxa is sufficient to evaluate the null hypothesis that larvae are transported like passive particles. Within the groups chosen here, larvae are expected to have comparable hydrodynamic characteristics (Butman 1986) and, if spawned from the same population, would transport simi-

larly as passive particles (Gross et al. 1992). But because larval behaviors may vary substantially among closely related species (Mann et al. 1990; Shanks 1995) or even among populations of the same species (Manuel et al. 1996), this study cannot reveal the specifics of behaviorally mediated transport.

*Time-series analysis*—Associations between biological and physical time series were quantified with lagged (3-h steps in both directions) cross correlations. Physical data were averaged over 10 min at 3-h intervals for comparison to pump samples. The decorrelation time (DT) dictated the degrees of freedom ( $df$ ) for estimating the significance of correlations, according to  $df = N\Delta t/DT$ , where  $N\Delta t$  is the record length (20 d) (Emery and Thomson 1997). The decorrelation time was estimated as the first zero crossing of the autocorrelation, and the shorter of the two DTs (positive and negative) was used to estimate  $df$ .

Dominant scales of variability within a given time series were determined from visual inspection of the data and DTs. Most time series have variability at several time scales. There is, however, only one DT, which may be neither the dominant nor the most meaningful scale of variation. The 20-d length of the larval time series was not amenable to spectral analyses.

Diel periodicity was evaluated to determine whether vertical migration behavior could partially account for relatively high-frequency variations. The averages of the 20 daily samples taken at hour 0, at hour 3, and so on, were calculated for each taxon at each pump. The standard errors were ~20% for polychaetes, bivalves, and gastropods and ~40% for crab zoeae.

*Assumptions*—In this study, physical and biological time series taken at one location (three depths) are used to infer mechanisms of cross-shelf larval transport. Embodied in this Eulerian approach are two major assumptions. First, temporal variations in larval concentrations result from patches that move via advection or larval swimming but not from local events, such as spawning or resuspension (*see next section*). Second, cross-shelf (not along-shelf) transport controls low-frequency fluctuations in larval concentrations, as it does temperature variations (Austin and Lentz 1999). Large-scale homogeneity in larval distributions along the coast is implicit in this assumption. Many invertebrates that contribute larvae to inner-shelf waters have broad distributions, from south of Cape Hatteras to north of Cape Cod, Massachusetts (Gosner 1971). Cross-shelf larval transport is complicated, however, by patchy adult populations and spawning that is rarely synchronous within or among species. This study was not designed to track larval cohorts, but rather to explore mechanisms controlling first-order transport of large taxonomic groups. Cross- and along-shelf advection of larvae cannot be separated here. Some spikiness in the time series is undoubtedly due to shore-parallel advection of larval patches.

#### Oceanographic setting at the study site

Winds varying on synoptic time scales of 3–5 d were the dominant influence on inner-shelf dynamics in the Duck re-

gion during CoOP94 (Figs. 2, 3) (Austin 1999; Austin and Lentz 1999; Lentz et al. 2001). Along-shore winds controlled stratification/vertical mixing, initiated cross-shelf flows that drove upwelling and downwelling (Austin 1999; Lentz in press), generated swift along-shore currents (Lentz et al. 1999), and influenced transport of Chesapeake Bay plume water to the site (Rennie et al. 1999). The inner-shelf water column was thermally stratified, with the thermocline at 5–10 m (22–25°C above, 16–20°C below) (Fig. 2; Austin 1999).

Large temporal variations in water temperature resulted primarily from cross-shelf rather than along-shore advection (Austin and Lentz 1999). Intermittent upwelling and downwelling periods occurred on roughly 3–5-d intervals (Austin and Lentz 1999). During this study, atmospheric cold fronts transited the region on 10, 15, 22, and 29 August. These fronts generated strong southwestward winds that drove downwelling conditions observed on 11–12, 15–16, 23–25 August, and briefly on 29 and 30 August (Figs. 2, 3; Austin 1999). Otherwise, upwelling wind conditions prevailed. Sustained downwelling winds (22–26 August) produced a water column homogeneous in temperature for several days.

Salinity variability in the Duck region resulted primarily from wind-forced cross-shelf flows and along-shore transport of the Chesapeake Bay plume (<32 psu) (Boicourt et al. 1987; Rennie et al. 1999). Typically, near-surface water is fresher than near the bottom. Wind-driven cross-shelf currents can further enhance salinity variations. Upwelling transports warmer, fresher, near-surface waters offshore and cooler, saltier near-bottom waters onshore. The opposite occurs during downwelling. Resulting distributions of salinity and temperature are almost indistinguishable. Downwelling winds also transported the Chesapeake Bay plume southward, toward Duck (Fig. 1 insert). The plume was usually <5-km wide and reached the 21-m site only when downwelling winds relaxed and the plume broadened (Fig. 3: 10–11 and 24–25 August) or during upwelling, when the plume moved offshore (Fig. 3: 12, 17, 20–21, 26 August). During 24–25 August, variability in near-surface salinity was likely due to the offshore plume edge moving back and forth past the 21-m site.

The strongest currents over the inner shelf tend to be oriented along shore, in the direction of the wind. Southwestward winds produced shore-parallel currents in excess of 75 cm s<sup>-1</sup> (Lentz et al. 1999). Cross-shelf flows were considerably slower, averaging about 5 cm s<sup>-1</sup> and occasionally exceeding 20 cm s<sup>-1</sup> during strong upwelling and downwelling events (Lentz in press). The semidiurnal tide produced a nominal M2 tidal flow of less than 5 cm s<sup>-1</sup> (Lentz et al. 2001).

Within 1 m of the bed, suspended sediment concentrations were highly variable, reflecting local-scale winds and waves (Kim et al. 1997). Wave-driven flows produced shear velocities that sometimes exceeded the critical value for initiating motion of silt—sediments hydrodynamically similar to larvae (Butman 1986). Local resuspension occurred during high bottom flows generated by intense wave activity or strong downwelling (e.g., 14–16 and 22–24 August, Fig. 3; L.D. Wright pers. comm.). Silts typically were not mixed

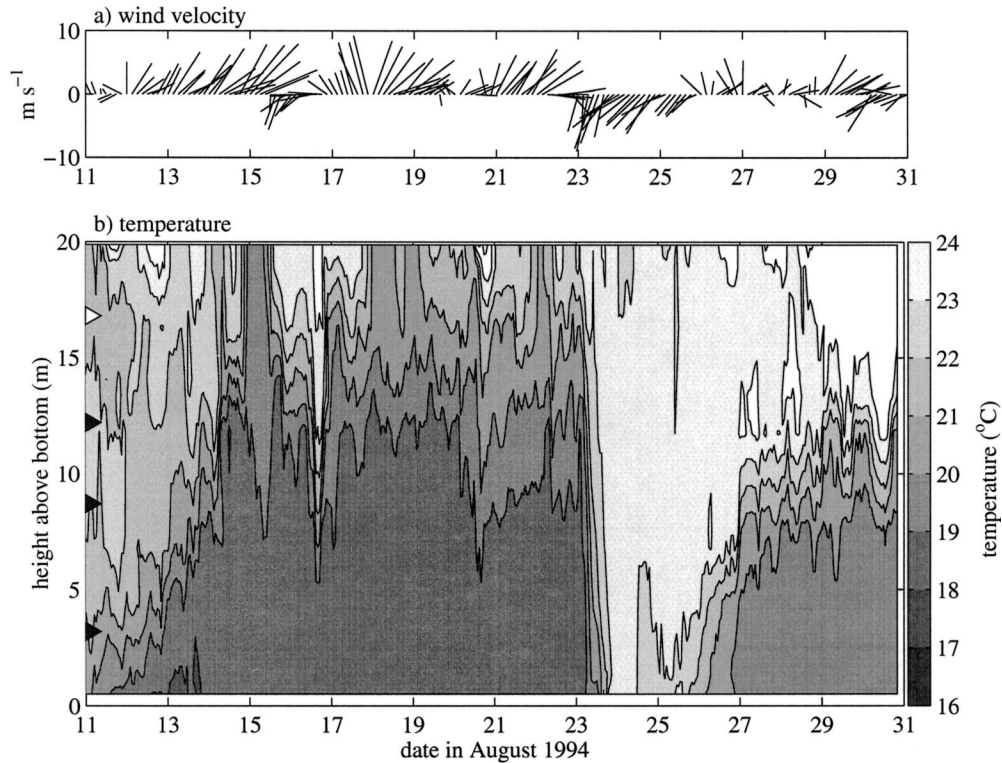


Fig. 2. (a) Stick plot of wind velocity from measurements taken at the FRF pier. A stick pointing straight up from the time axis indicates an along-shore wind toward  $340^{\circ}$  true (i.e., approximately parallel to the coast at the Outer Banks). (b) Water temperature at the 21-m site as a function of time and depth. Solid triangles on depth axis indicate pump locations, with the empty triangle representing the lost pump. Arrows correspond to thermistor depths. All times are local mean time, which was Daylight Savings Time (Eastern Standard Time +1 h) during the study.

beyond 30 cm above the bed (C. Friedrichs pers. comm.), well below the bottom pump.

## Results

Time series of larval concentrations had four general characteristics (Figs. 4–7). (1) Larvae were very abundant (maximal values of  $11,576 \text{ m}^{-3}$  for polychaetes,  $9,780 \text{ m}^{-3}$  for bivalves,  $6,756 \text{ m}^{-3}$  for gastropods, and  $352 \text{ m}^{-3}$  for crab zoeae). (2) Temporal changes varied by as much a factor of 1,000 over 3 h to days. (3) Depth-dependent effects differed among larval groups. (4) Gross patterns of temporal variability tracked with temperature, salinity, and along-shore wind, but there were no significant cross correlations between larvae and physical parameters.

Dominant scales of variability in the larval time series are (1) a relatively low-frequency scale of 2–10 d, related to synoptic meteorology and (2) a higher frequency scale of 3–6 h. Larval availability is a potentially confounding factor in interpreting the correspondence between biological and physical time series. Favorable physical conditions may not be accompanied by high larval concentrations because of the vagaries of larval availability. Thus, inferring causes of the absence of larvae is more ambiguous than of their presence.

*Polychaete larvae*—At the upper and bottom pumps, polychaete larval concentrations were highest ( $10^3$  to  $10^4 \text{ m}^{-3}$ ) during 15–20 August, when temperature was low ( $<19^{\circ}\text{C}$ ), salinity high ( $>34$  psu), and winds blew from the south/southwest, denoting upwelling conditions (Figs. 3, 4). Larval concentrations and low-frequency temporal variations were similar between the two pumps, indicating a vertical scale of over 9 m. For the bottom pump, intermediate concentrations occurred in cool (upwelled) water during 12–14 and 26–31 August. There were much lower values ( $0$ – $10^2 \text{ m}^{-3}$ ) at the upper pump in warm-water periods before and after the extensive, mid-August upwelling and at the bottom pump during the 23–25 August downwelling. Upwelling winds from 26 to 30 August were sufficient to cool the lower water column, but not to the height of the upper pump (12 mab) (Fig. 2). Thus, lowest larval concentrations were associated with warm, downwelled water, irrespective of water depth.

Diel changes in the vertical distribution of polychaetes (Fig. 8) likely contributed to the observed high-frequency variability (Fig. 4). Larvae were concentrated near bottom during the day and were distributed between the upper and bottom pumps at night (Fig. 8). These patterns are suggestive of diel vertical migration, with nocturnal ascent and daytime descent.

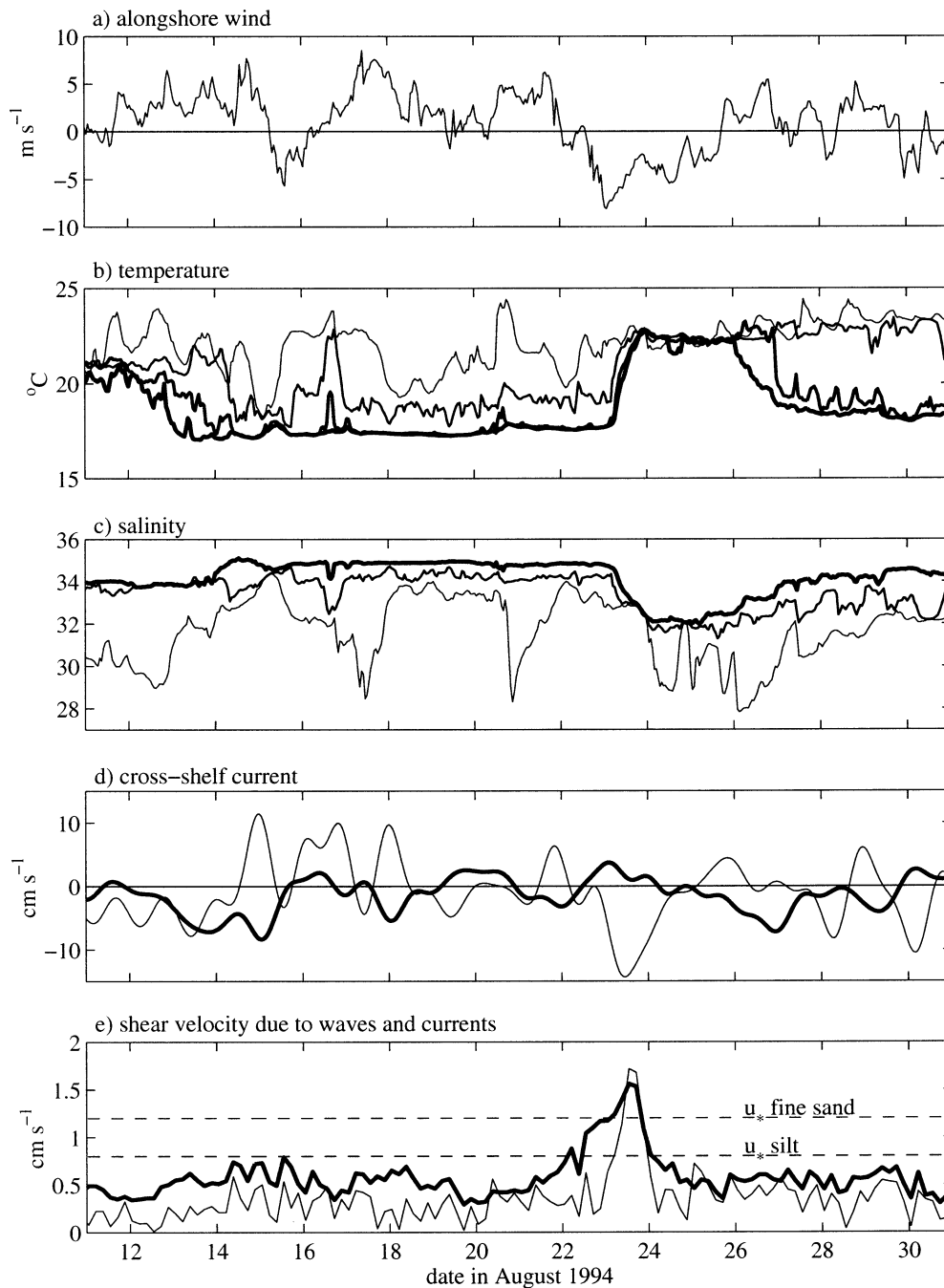


Fig. 3. Time series of oceanographic variables measured at the 21-m site during the 11–30 August study period (Lentz et al. 1999; Austin and Lentz 1999; L.D. Wright unpubl. data). Time series of (a) along-shore winds, (b) temperature, (c) salinity, (d) cross-shelf currents, and (e) near-bottom shear velocities,  $u_*$ , due to waves (bold line) and currents (thin line). Critical shear velocities for initiation of motion of fine sand ( $u_{* \text{fine sand}}$ ) and silt ( $u_{* \text{silt}}$ ) are identified by horizontal lines in (e). Line thickness indicates position of instruments within the water column, with the thinnest line 1.2 m below the water surface and the thickest line at the depth (3.2 mab) of the bottom pump (Fig. 1). All physical data were hourly averaged. Cross-shelf velocities were low-pass filtered.

*Bivalve larvae*—At the upper and middle pumps, bivalve larvae were relatively abundant ( $10^2$  to  $10^3$   $\text{m}^{-3}$ ) under cooler ( $<19^\circ\text{C}$ ), more saline ( $>34$  psu) conditions (14–22 August) (Fig. 5). Concentrations were lower ( $0$ – $10^2$   $\text{m}^{-3}$ ) in warm water (11–14 and 26–30 August), but maximal and submax-

imal peaks (up to  $10^4$   $\text{m}^{-3}$ ) occurred during strong downwelling on 24–26 August (upper) and 25 August (middle). At the bottom pump, larval concentrations were low, except on 25 (downwelling) and 28 August (upwelling). The maximal peak (0600 h on 25 August) was synchronous and sim-

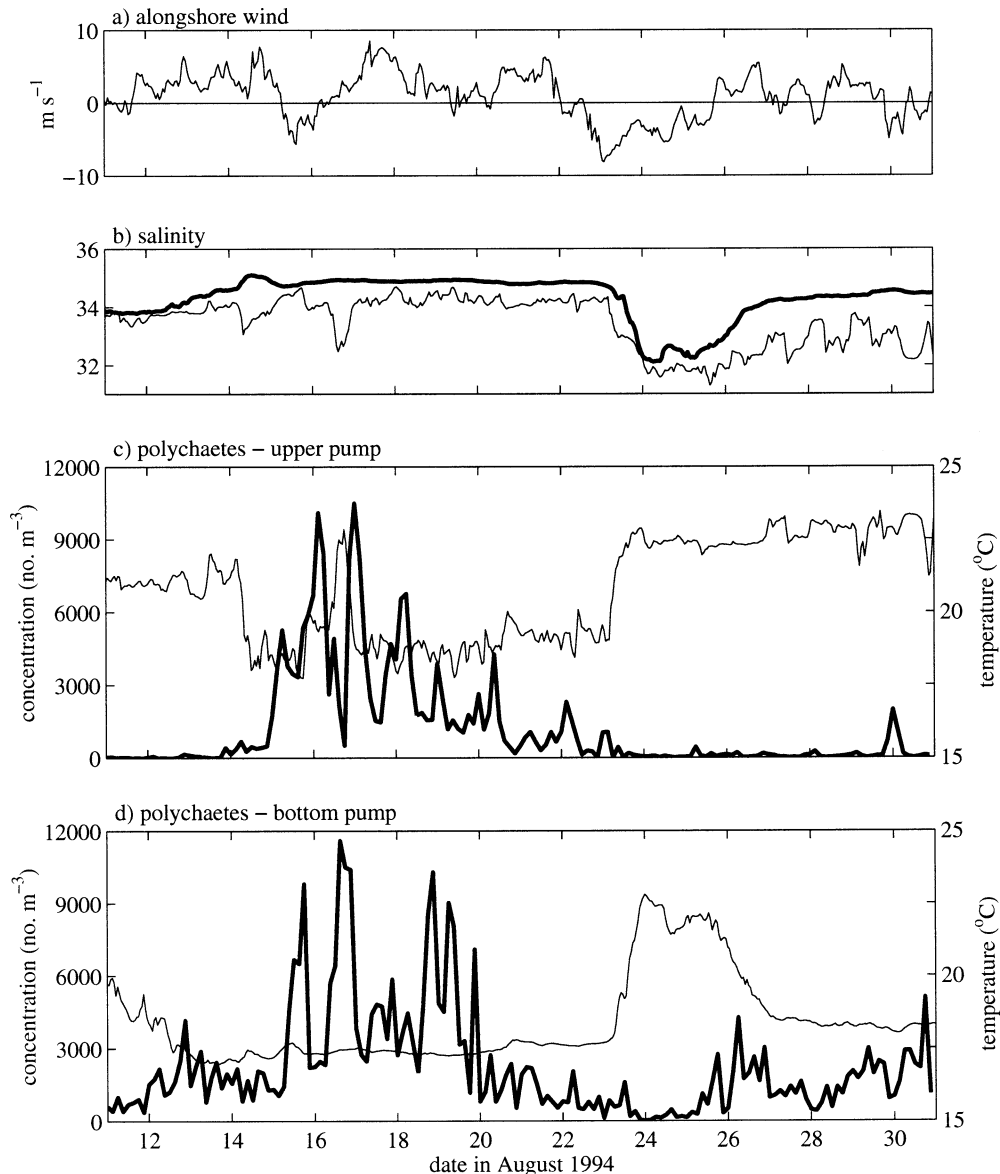


Fig. 4. Time series of the along-shore component of (a) wind velocity and (b) salinity. Larval polychaete concentrations (thick line) and water temperature (thin line) at the (c) upper and (d) lower pumps. Salinity is shown for the upper (thin line) and bottom (thick line) pump locations.

ilar in magnitude at all depths: 9,780  $\text{m}^3$  (upper), 8,756  $\text{m}^3$  (middle), and 8,108  $\text{m}^3$  (bottom). These maxima, plus a subsequent large peak at the bottom pump, occurred during a 2-d downwelling period of minimal salinities ( $\sim 32$  psu).

Larval time series at the upper and middle pumps were significantly correlated ( $r^2 = 0.49$ ,  $P < 0.05$ ). Thus, a large patch with relatively high concentrations of bivalve larvae may have extended between the two upper pumps.

The time series of bivalve concentrations showed evidence of a diel cycle (Fig. 8). Larvae were most abundant in the bottom pump during the day and in the upper and middle pumps at night. Upper pump concentrations were higher at night by a factor of two or more. These patterns suggest nocturnal ascent and daytime descent, as with the polychaetes.

*Gastropod larvae*—Time series of gastropod larval concentrations were similar to those of bivalve larvae (Fig. 6 vs. Fig. 5). In fact, cross correlations between gastropods and bivalves were significant at both the upper ( $r^2 = 0.43$ ,  $P < 0.05$ ) and middle ( $r^2 = 0.20$ ,  $P < 0.05$ ) pumps. The relatively small fraction of the total variance explained by these correlations is not unusual for oceanographic time series, where fluctuations are driven by several concurrent processes. At the upper pump, gastropod concentrations were relatively high ( $10^2$ – $10^3$   $\text{m}^{-3}$ , with major peaks nearing  $10^4$   $\text{m}^{-3}$ ) during the extensive cool-water period (14–23 August), and were generally low ( $0$ – $10^2$   $\text{m}^{-3}$ ) in warm water (11–14 and 26–30 August). Exceptions are the elevated values at the onset of strong downwelling in late August. Larval concentrations were low ( $0$ – $10^2$   $\text{m}^{-3}$ ) at the middle pump during

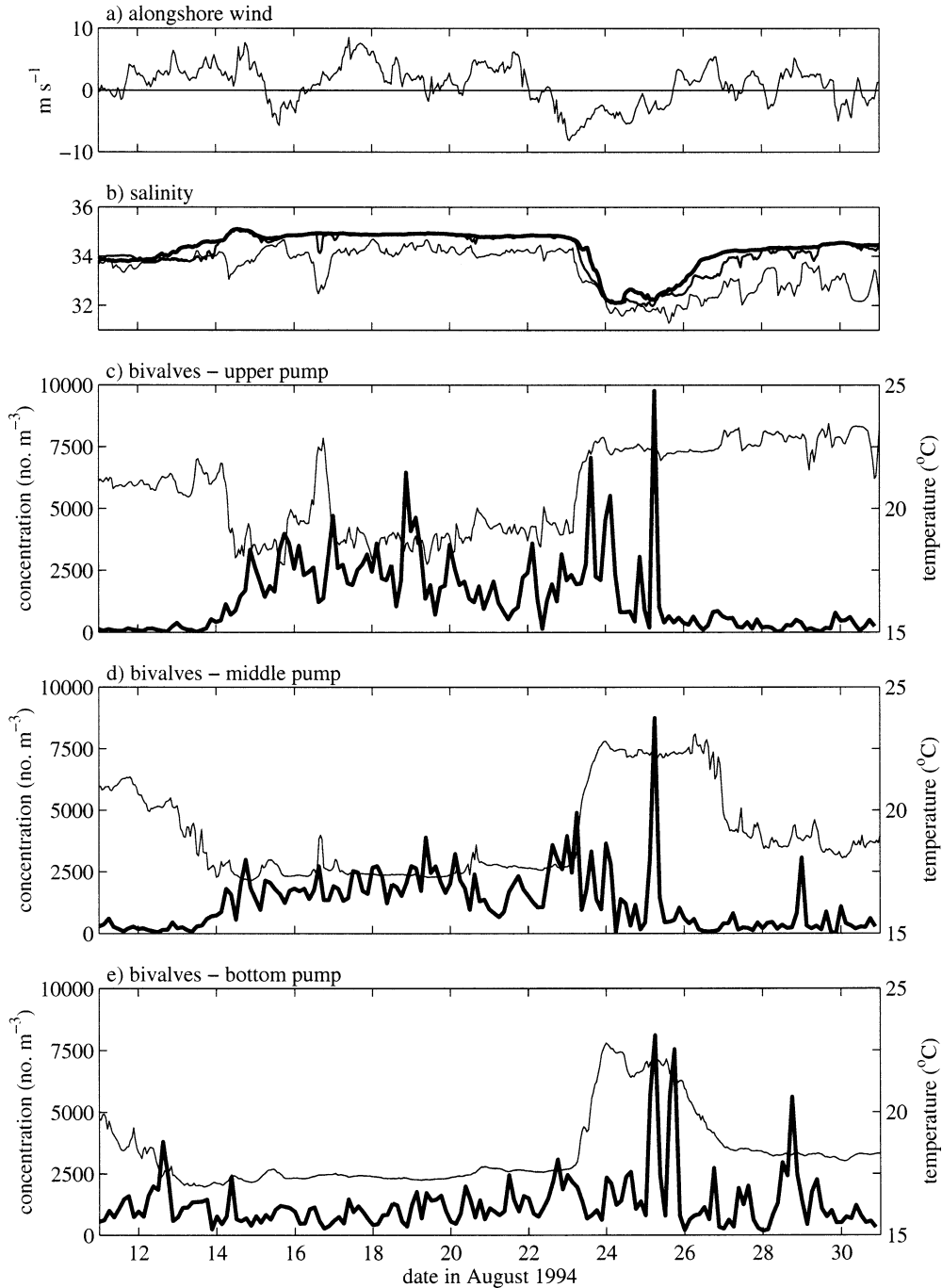


Fig. 5. Time series of the along-shore component of (a) wind velocity and (b) salinity. Larval bivalve concentrations (thick line) and water temperature (thin line) at the (c) upper, (d) middle, and (e) lower pumps. Five samples collected by the middle pump (21 August at 0300, 1500, 2100 h, and 22 August at 0000, 1200 h) were damaged during recovery and processing, so interpolated values are plotted here. Salinity is shown for the upper (thin line), middle (intermediate line thickness), and bottom (thick line) pump locations.

the cool-water (upwelling) period, but increased with the sudden rise in temperature (onset of downwelling) on 23 August. At the bottom pump, highest values also occurred during warm-water periods (12 and 24–25 August).

Coincident large peaks in gastropod larval concentration occurred one day earlier (0300 h on 24 August) than syn-

chronous peaks for bivalve larvae (0600 h on 25 August). For gastropods, coincident peaks lagged by several hours the advance of the downwelled thermocline, and asynchronous peaks preceded the thermocline's retreat by several hours (Fig. 6).

A diel cycle was evident in the time series of larval gas-



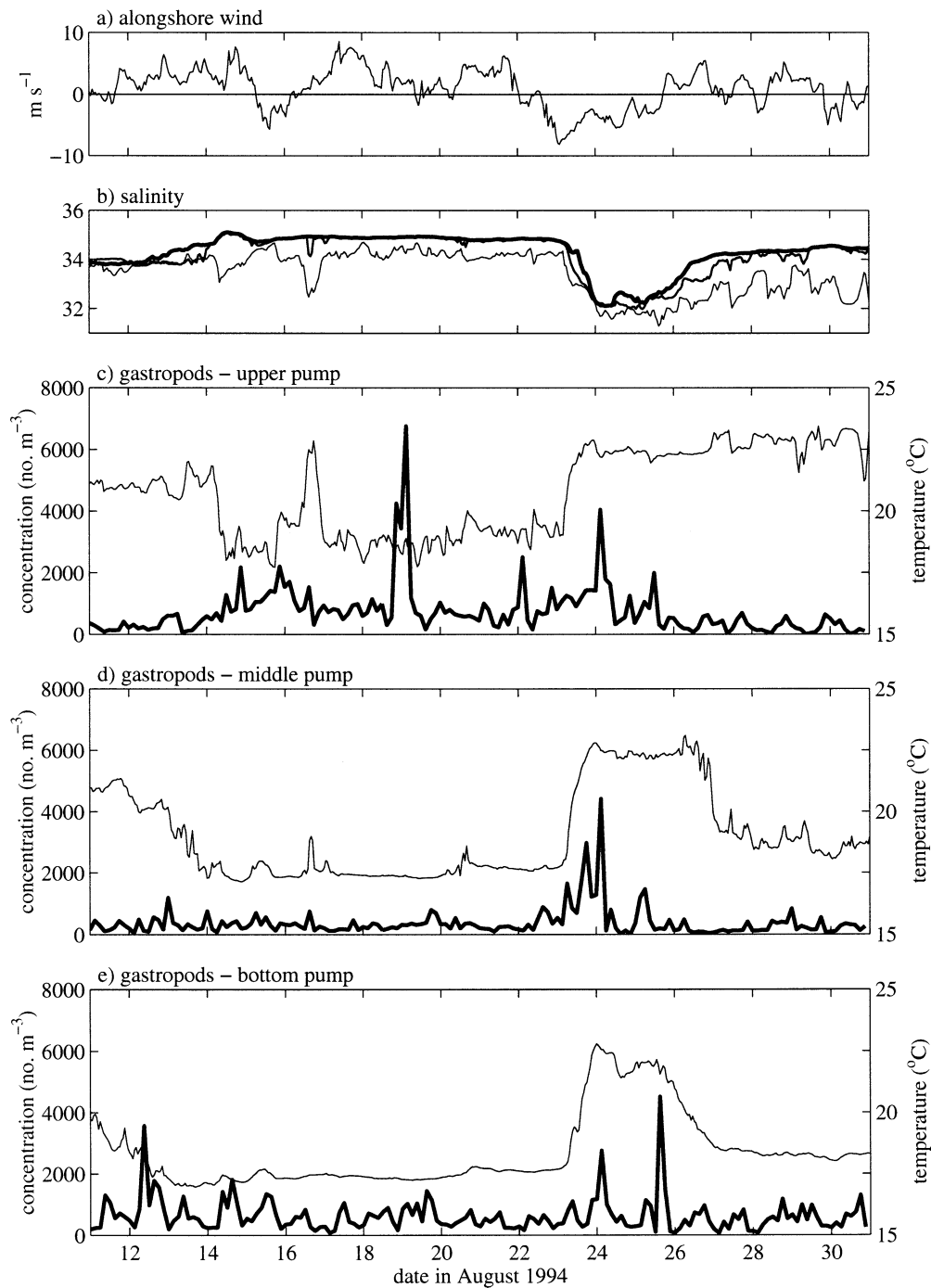


Fig. 6. Time series of the along-shore component of (a) wind velocity and (b) salinity. Larval gastropod concentrations (thick line) and water temperature (thin line) at the (c) upper, (d) middle, and (e) lower pumps. Five samples collected by the middle pump (21 August at 0300, 1500, 2100 h, and 22 August at 0000, 1200 h) were damaged during recovery and processing, so interpolated values are plotted here. Salinity is shown for the upper (thin line), middle (intermediate line thickness), and bottom (thick line) pump locations.

tropod concentration (Fig. 8) at the upper and bottom pumps. Larvae were most abundant in the bottom pump during the day and in the upper pump at night, again suggesting nocturnal ascent and daytime descent.

*Crab zoeae*—Time series of brachyuran crab zoeae showed a striking pattern of very low concentrations ( $0\text{--}10\text{ m}^{-3}$ ) in cool water and high ( $0\text{--}10^2\text{ m}^{-3}$ ) in warm water (Fig. 7). Zoeae concentrations were similar at the two depths,

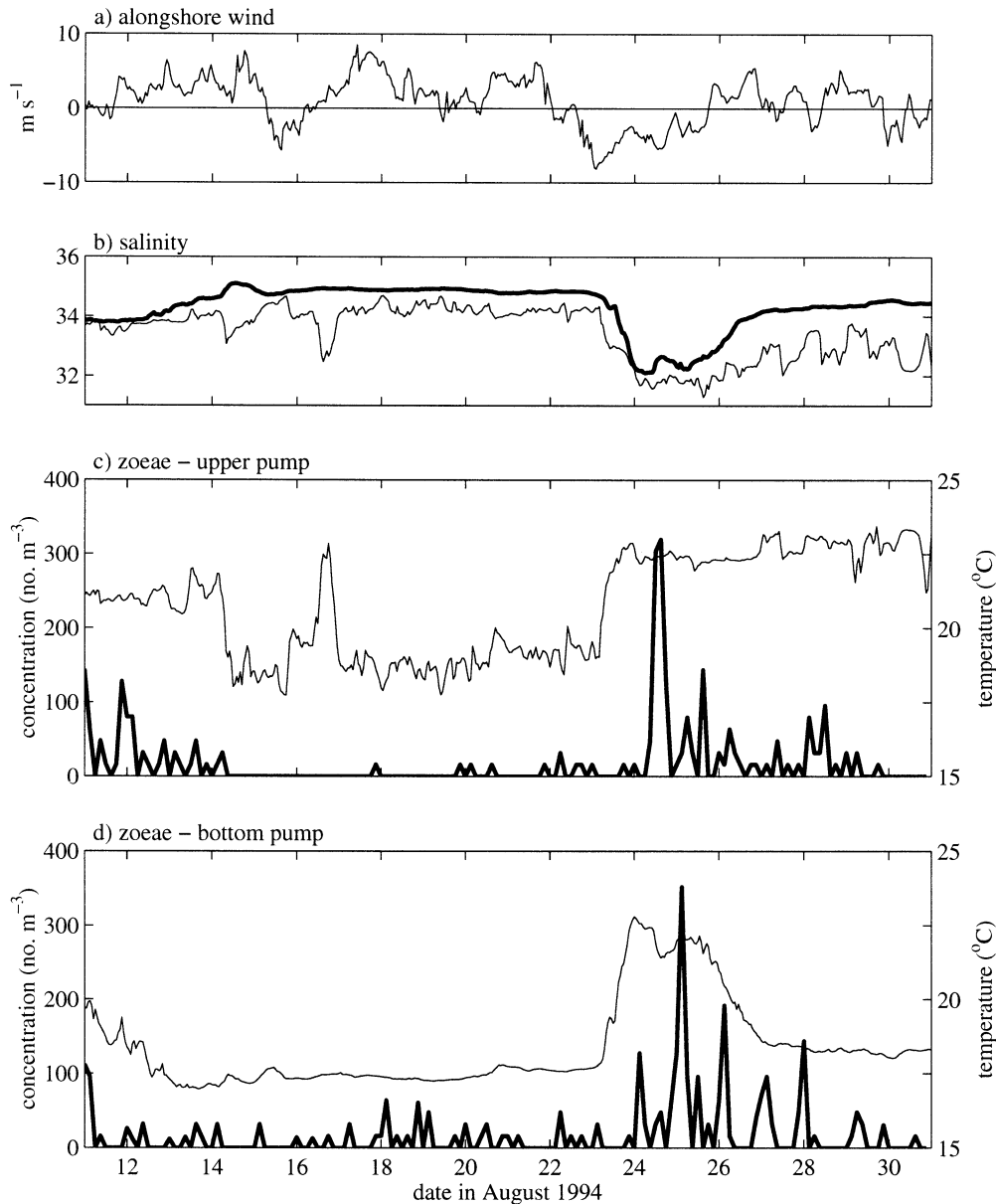


Fig. 7. Time series of the along-shore component of (a) wind velocity and (b) salinity. Brachyuran crab zoeae concentrations (thick line), and water temperature (thin line) at the (c) upper and (d) lower pumps. Salinity is shown for the upper (thin line) and bottom (thick line) pump locations.

peaking during 24–25 August, within hours of the highest peaks for bivalves and gastropods. Diel variation was less distinctive for zoeae as compared to the other three taxa (Fig. 8). At the bottom pump, highest zoeae concentrations tended to occur at night, but there is no evidence of a diel signal at the upper pump.

## Discussion

The inner shelf is a pivotal environment both physically and biologically. Situated between the wave-dominated near-shore and the wind-dominated offshore, it has physical attributes of both regions (Lentz et al. 1999). Transport paths and rates of long-lived larvae moving between intertidal and

offshore waters are influenced by these complex inner-shelf flows. For example, larvae of estuarine and coastal species can behaviorally exploit vertically sheared flows to facilitate transport toward a desirable location (Forward and Tankersley 2001).

The fluctuating, high larval concentrations at Duck exceed the temporal variation and maxima recorded for most other coastal, nonestuarine areas. This 20-d time series, with 3-h resolution, captured spikes in larval concentration of  $10^3$  (bivalves) to  $10^4$  (polychaetes)  $m^{-3}$  (Figs. 4, 5) that are difficult to detect otherwise. In contrast, previously recorded abundances of coastal larvae were typically  $<10^2 m^{-3}$  (Banse 1986; Tremblay and Sinclair 1990), with peaks of  $10^3$  bivalves  $m^{-3}$  (Mann 1985). Concentrations at Duck resemble

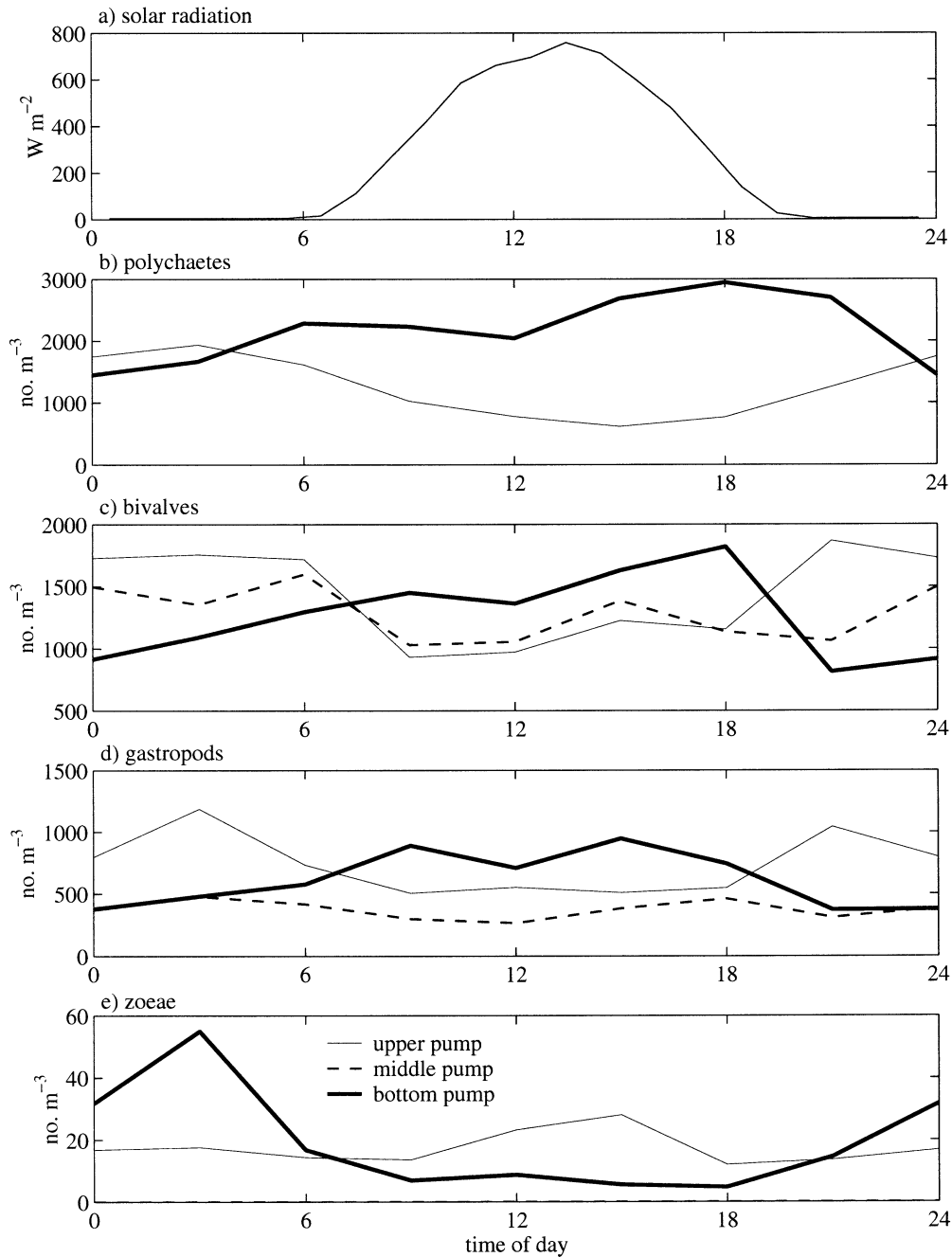


Fig. 8. Average daily variation ( $N = 20$  d) for each larval taxon. See text for description of averaging and error calculations.

higher values measured in bays or estuaries along the eastern seaboard of the U.S.A. (Nelson 1928; Raby et al. 1994).

Larval concentrations measured in this study were highly variable over space and time. Still, prevalent patterns can be explained by several plausible mechanisms: wind-driven cross-shelf transport, southward advection of the Chesapeake Bay plume, and diel vertical migration. These are not the only scenarios that may account for the observations. They are, however, the most parsimonious interpretations based on knowledge of physical/biological coupling in coastal waters and inner-shelf dynamics on the Outer Banks.

*Wind-driven cross-shelf transport*—Comparisons between the larval and temperature time series revealed three general patterns. Larval concentrations were (1) highest when water was cool (i.e.,  $\sim 17$ – $18^\circ\text{C}$ , 13–23 August), as for polychaetes (Fig. 4); (2) highest when water was warm (i.e.,  $\sim 22$ – $23^\circ\text{C}$ , 24–30 August), as for crab zoeae (Fig. 7); and (3) moderately high in cool water, with maximal and submaximal peaks in warm water, as for bivalves and gastropods (with some exceptions) (Figs. 5, 6). The most plausible mechanism to explain these results is cross-shelf transport of larval patches via wind-driven upwelling and downwelling. Be-

cause low-frequency variations in temperature are largely due to cross-shelf advection in this region (Austin and Lentz 1999), the same process would likely drive similar low-frequency variations in larval concentrations. From the 21-m site, larvae transported toward shore in these relatively weak ( $\sim 5 \text{ cm s}^{-1}$  or  $\sim 4.3 \text{ km per day}$ ) cross-shelf currents could reach the beach in a little over a day.

Low-frequency variations were similar in nature for the larval and temperature time series. Cross correlations were not significant, however, because of higher frequency variability in the larval records, presumably associated with biological phenomena such as patchy species distributions, variable spawning times, and planktonic predators. Because larval time series were spikier than the physical series, much longer records (e.g., 6 months to a year) are required to establish statistically significant cross correlations. Yet larval availability is limited to late spring/summer, with planktonic periods of temperate species usually lasting 4–6 weeks. Moreover the stratification required for upwelling or downwelling occurs only during the warm months of the year. Thus, serial sampling of sufficiently long duration to detect significant correlations may be confounded by vastly changing larval composition and physical-transport processes.

The high concentrations of polychaete larvae collected in cool water (Fig. 4) may have arrived via upwelling. Worm larvae should be relatively abundant above offshore muddy sediments that tend to be dominated by polychaete populations on the North Carolina shelf (Day et al. 1971). Larvae would be ferried shoreward during upwelling, when cool, subthermocline water moves inshore, past the pump array, and ultimately ascends at the coast.

In contrast, crab zoeae were most abundant in warm water (Fig. 7) that moved across the pump array during downwelling. Crab larvae in near-surface waters would descend at the coast during downwelling and, together with zoeae overlying nearshore sediments, be transported seaward below the thermocline. Although brachyuran crabs are common in the Duck region, the species are distributed among a wide range of habitat types and water depths (Gosner 1971). The origin of the zoeae collected here is unknown. Moreover, transport mechanism may vary with species or developmental stage. For example, daily abundance of surface-dwelling megalopae correlated with physical measurements at Duck, indicating shoreward larval transport (Shanks 1998). The analysis suggested, however, that *Callinectes sapidus* was carried by tidal flows, *Uca* spp. via surface downwelling currents, and *Libinia* spp. in near-bottom upwelling flows.

The mechanisms that control bivalve and gastropod larval transport may be more complicated. Relatively high concentrations of both groups occurred in cool and warm water, with temporal patterns varying somewhat with depth (Figs. 5, 6). Hypothesized transport scenarios are provided to stimulate future process-oriented research in this area. At least two prevalent mollusk assemblages—differing in species composition, ages, or origins—may have resided on the Duck inner shelf. The larvae in one group were transported in warm downwelled water, like the zoeae, whereas larvae in the other group tracked with cool upwelled water, like the polychaetes. Major peaks in mollusk concentrations occurred

in warm water at all depths, except for gastropods at the upper pump (Figs. 5, 6). Like brachyuran crabs, bivalves and gastropods live in a wide range of benthic habitats and depths. The warm-water mollusk larvae were likely generated from nearshore populations. Moreover, large, nearly synchronous peaks of bivalves, gastropods, and zoeae during 24–25 August (Figs. 5–7) indicate downwelling transport of a multitaxa larval patch. The cool-water mollusk group was most abundant at the upper pump and likely included species living in shallow to shelf depths (e.g., the surfclam *Spisula solidissima*, Merrill and Ropes 1969) or deep-water species (e.g., scallops, Merrill 1962).

Combined, the overall results of the low-frequency analysis suggest that wind-driven cross-shelf currents ferry larvae residing in subthermocline to near-bottom waters. Previous studies have implicated upwelling or downwelling in the transport of surface-dwelling larvae (Farrell et al. 1991; Roughgarden et al. 1991; Wing et al. 1995; Connolly and Roughgarden 1999). The mechanism proposed here is not the only, but seems the most plausible, explanation for low-frequency variations in the biology time series. In summary, dense larval patches may roughly overlie parental habitat. Depending on the cross-shelf location of adult populations, larvae would be carried shoreward by upwelling or seaward by downwelling. Whether larvae actively exploit specific current regimes or are simply at their mercy, the animals would be passively transported horizontally much farther than they can swim.

*Along-shore transport in Chesapeake Bay plume water*—Sustained downwelling winds transport Chesapeake Bay plume water to the Duck region. The plume water may contain larvae of obligate, estuarine species distinct from those living on the inner shelf. Occasionally, the plume may have extended to the 21-m isobath, for example, on 14, 16, and 24–26 August at the upper pump (Fig. 3). The late August event was very intense, and the entire water column became homogeneously warm for several days (Fig. 2). Thus, mollusk larvae that reached maximal and submaximal concentrations in warm water during 24–26 August (Figs. 5, 6) could have been associated with plume water advected along shore; warm, downwelled surface water (see previous section); or a combination of the two water masses.

The plume explanation is not, however, supported by the salinity data (Fig. 3). For example, if the synchronous peaks that occurred at all pumps on 24 August (gastropods) and 25 August (bivalves) contain plume fauna, then the signature of plume water should have been evident at all depths. Plume water rarely exceeds a salinity of 32 psu (Rennie et al. 1999), but this salinity was recorded only briefly at the middle and upper pumps and never at the bottom pump (minimum of 32.2 psu). Otherwise, salinities were much higher. Thus, although the plume occasionally intruded the Duck region, it rarely extended offshore to the 21-m site.

*Diel vertical migrations*—Hourly variations in larval concentrations are consistent with diel vertical migration (DVM). Diurnal advection (caused by sea breeze) is an unlikely mechanism because diurnal winds were very weak during the study:  $\sim 0 \text{ m s}^{-1}$  (day) to  $\sim 1 \text{ m s}^{-1}$  (night) off-

shore. Cross-shelf transport, intermittent intrusions of the Chesapeake Bay plume, and varying species composition would tend to obscure patterns expected for DVM. Thus, the signature of DVM is relatively clear for the polychaetes, but vaguer for the other groups.

Analyses of DVM suggested that larval polychaetes, bivalves, and gastropods moved up at night and down during the day (Fig. 8). Nighttime ascent has been attributed to avoidance of visual predators and ultraviolet light (Pennington and Emlet 1986; Bollens and Frost 1989). In contrast to bivalves and gastropods, the diel cycle was asymmetrical for polychaetes, with relatively high larval concentrations at the bottom pump for  $\sim 18$  h. This period is similar to that of the near-inertial, cross-shelf currents (20-h period,  $15 \text{ cm s}^{-1}$  amplitude) during 15–17 August (authors' unpubl. data) that also may have contributed to high-frequency variability in the polychaete time series.

Evidence of DVM was weaker for brachyuran zoeae than for the other groups, with significant peaks occurring at night in the bottom pump only (Fig. 8). One explanation is that the zoeae were migrating between the bottom pump depth (3 mab) and the seafloor. This rhythm of nocturnal ascent and daytime descent is consistent with that reported previously for brachyuran zoeae in estuaries (Cronin and Forward 1986), albeit lower in the water column.

It is unlikely that differential cross-shelf transport resulted from DVM because subthermocline currents were unidirectional (Fig. 3, Lentz et al. 1999). Under prevailing upwelling conditions, for example, subthermocline larval groups would be moved shoreward whether or not they vertically migrated (Fig. 3). Vertical migrations would, however, determine when larvae occur in near-bottom waters and thus potentially contact the bed. By use of DVM, competent larvae may test the bottom (for settlement) during the day and take advantage of enhanced food resources higher in the water column, especially just below the thermocline, at night.

*The composite picture*—On the inner shelf, invertebrate larvae are advected long distances in strong (mean of  $\sim 20 \text{ cm s}^{-1}$ , with peaks of  $60\text{--}100 \text{ cm s}^{-1}$  in the Duck region), shore-parallel flows. Larval-transport mechanisms must be viewed within the context of these substantial along-shore currents. The present study suggests that invertebrate larvae move shoreward and seaward via wind-driven cross-shelf flows. With few realizations of upwelling and downwelling events over the 20-d larval time series, statistical correlations were not possible between temperature (controlled by upwelling/downwelling) and larval concentrations. That is, resolution of temporal and vertical patterns was achieved at the expense of elucidating variation in the horizontal. Moreover, the small sizes and young stages of larvae prohibited morphology-based species identifications. Such data would expose the finer scale details of larval transport, as well as species-specific effects. Thus, the picture of physical-biological coupling revealed here is a meaningful research increment, but the strokes are broad brush.

The larval-transport mechanisms described in this study are not new. For example, upwelling strength was hypothesized to control recruitment variation in intertidal barnacles well over a decade ago (Roughgarden et al. 1987). This tenet

was supported by field data on long-term (months) recruitment variability as a function of upwelling/downwelling conditions, but planktonic larvae were sampled infrequently (Farrell et al. 1991; Roughgarden et al. 1991) or not at all (Wing et al. 1995; Connolly and Roughgarden 1999). Making oblique tows beside an upwelling front, Roughgarden et al. (1991) collected plankton once only, and Farrell et al. (1991) took twice-daily shipboard pump samples at just one depth (1 m) over 4 d. The temporal and spatial scales of larval sampling were substantially more resolved in the present study, due to the development of the moored automated serial zooplankton pump (MASZP). A decade ago, no larval sampler could be moored at similar depths and be programmed to sample synchronously with physical-oceanographic instruments. To refine further larval distributions at large spatial and fine temporal scales, the next technological challenge is automated sample processing and species identifications. For example, using spatial arrays of MASZPs and molecular probes to definitively identify surfclam (*Spisula solidissima*) larvae, Ma (2001) recently showed that some recruitment pulses are controlled by downwelling transport of competent pediveligers.

Against a backdrop of low-frequency cross-shelf fluctuations due to physical transport, diel vertical migrations contributed to higher frequency variations in the larval time series. A larger scale context also revealed the potential contribution of episodic processes, such as intrusions of Chesapeake Bay plume water during strong downwelling events. Thus, the emerging picture is larval transport along shore via fast currents and cross shelf by slower flows. Zig-zagging up and down the coast, larvae also make daily vertical excursions within the water column while they feed and grow and ultimately search for the right habitat in which to settle.

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