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Hourly variations in planktonic larval concentrations on the inner shelf: Emerging patterns and processes

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ABSTRACT

Planktonic larvae are unlikely to be randomly distributed over time or in space. Fluctuations in larval density may result from a variety of physical and biological processes. To identify relatively high-frequency patterns of larval variation for an inner-shelf environment, zooplankton were sampled hourly for 3 d using an automated plankton pump. Moored ~80 cm above bottom, the pump was located in 8 m of water on the Outer Banks of North Carolina. Densities of all larval groups were highly variable: 5–746 m⁻³ for barnacle cyprids, 0–668 m⁻³ for polychaetes, 0–516 m⁻³ for bivalves, 6–414 m⁻³ for gastropods, and 0–86 m⁻³ for bryozoan cyphonautes. Moreover, maximal and submaximal peaks were nearly coincident for all taxa. One hypothesis to explain these results involves passive larval transport by wind-driven cross-shelf flows (upwelling and downwelling). Larval concentrations were persistently low in warm, downwelled water and highest during a period of cool, upwelled water. During upwelling, however, maximal and submaximal peaks for each taxon corresponded with brief relaxation events, dominated by downwelling-favorable winds. Thus, larvae tracking with cool water would have been moved upslope then offshore at the surface by upwelling currents or to the bottom by downwelling flows. A second hypothesis involves active diel vertical migration (DVM). During the cool-water period, peaks in near-bottom larval density occurred near noon, consistent with daytime descent. Daily peaks were not always separated by 24 h, however, probably due to modulation of DVM by physical processes (e.g., cross- or alongshelf advection or mixing). These relatively simple patterns of variation in larval abundance are surprising, given the complex hydrodynamic processes that typically operate on the inner shelf.

1. Introduction

On temperate continental shelves, most benthic invertebrates have a planktonic larval stage that disperses for weeks to months before settling onto suitable adult habitat. The inner shelf (roughly 5–30 m depth) is a vital link between the wave-dominated nearshore and wind-dominated offshore, with characteristics of both environments (Lentz et al., 1999). Thus, various physical processes, such as wind-driven cross-shelf flows (upwelling/
downwelling), thermal fronts, eddies, tides, internal and surface waves, tidal bores, and storms (Boicourt, 1988; Powell, 1989), potentially distribute larvae within this region. Plankton patchiness also may be determined by active vertical migrations (Forward, 1976; Scrope-Howe and Jones, 1986), predator/prey interactions (Rumrill, 1990; Johnson and Shanks, 1997), food limitation (Tremblay and Sinclair, 1990; Raby *et al*., 1994), and spawning events (Morgan, 1995; Shanks, 1998).

The research objectives were to identify (1) short-term temporal variability in larval concentrations at an inner-shelf site, and (2) the most plausible mechanisms to explain the results. The null hypothesis is that larvae are transported like passive particles; deviations from passive predictions may be attributed to other (e.g., biological) processes. Samples were collected hourly for 3 d, and thus, pattern could be resolved at targeted frequencies of 1 cycle per 2 h to 3 d (Diggle, 1990). Physical processes operating over these scales include the diel light/dark cycle, the semi-diurnal tidal cycle, and synoptic wind-driven flows.

2. Field site

The study took place in July 1993 on the inner shelf of the Outer Banks at Duck, North Carolina, USA (Fig. 1), where the U.S. Army Corps of Engineers operates a Field Research Facility (FRF; Birkemeier *et al*., 1985). The Duck site was ideally situated on a coastline that is straight and featureless for >50 km in both directions. Moreover, the FRF routinely collects physical-oceanographic and meteorological data from the end (8-m depth) of a 561-m-long pier. This research was invaluable for designing the subsequent, Coastal Ocean Processes (CoOP94) study of cross-shelf larval transport conducted within the same region (Butman, 1994).

On the Duck inner shelf, alongshore winds produce the cross-shelf flows observed under stratified conditions (Boicourt, 1973; Birkemeier *et al*., 1985; Lentz *et al*., 1999). Winds blowing toward the north/northeast set up classical upwelling (Smith, 1968), where surface water advected seaward is replaced by offshore bottom water (cooler, more saline) that ascends at the coast. Conversely, winds blowing toward the south/southwest result in downwelling, where surface water (warmer, less-saline) moves shoreward, descends and is advected offshore at the bottom. Wind-driven cross-shelf flows are typically of order 5 cm s$^{-1}$, increasing to 20 cm s$^{-1}$ during upwelling (Lentz *et al*., 1999; Rennie *et al*., 1999).

3. Materials and methods

a. Larval time series

A time series of larval concentrations was collected using a moored, automated, serial zooplankton pump (Doherty and Butman, 1990; Butman, 1994), which has a sample storage mechanism fashioned after the towed Longhurst Hardy Plankton Recorder (Hardy, 1936; Longhurst *et al*., 1966). Animals between 100 and 1415 µm were collected on Nitex
mesh and preserved (buffered 3.7% formalin with Rose Bengal stain) in situ. The pump sampled at 1-h intervals over 70 hr, beginning at 1800 on 19 July 1993 and ending at 1500 on 22 July 1993. (All times are reported as Local Mean Time.) Volume filtered was 1000 liters during collections at 0300, 0900, 1500, and 2100, and 500 liters at all other times. The volume flux was 25 liters min$^{-1}$, and thus, the 500- and 1000-liter samples were collected in about 20 and 40 min, respectively. The pump was attached to a tripod so that the intake was 83 cm above bottom. For deployment and recovery, the tripod was lashed to one “leg” of the 10-m-tall Coastal Research Amphibious Buggy (CRAB; Birkemeier and Mason, 1984). The CRAB drove through the surf to the 8-m-deep site (~1-km from shore), where divers secured the tripod in place.
Upon recovery, pump samples were transferred to 80% ethanol with Rose Bengal stain. Larvae were sorted into major taxa (bivalves, polychaetes, gastropods, bryozoan cyphonautes and barnacle cyprids). Most planktonic larvae, particularly the smallest ones, were not sufficiently differentiated to permit species identifications using morphological criteria alone (see also Garland et al., 2002). Classifications were often uncertain even to genus and family. Other identification 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, thus far, are impractical for large samples.

b. Hydrographic and meteorological time series

Most of the hydrographic and meteorological data used in this study were taken by the FRF (e.g., Birkemeier et al., 1985; Field Research Facility, 1993). Sea-surface temperature and salinity were measured daily at the end of the FRF pier (8-m depth), within 350 m horizontally of the plankton pump. A thermistor on the instrument housing recorded temperature at the depth of the pump intake. Wind speed and direction were measured (2 Hz) using a Skyvane anemometer mounted on top of the FRF, 20 m above sea level, within 725 m horizontally of the pump location. The FRF regularly maintains moored current meters along the 8-m isobath, but they were inoperative during July 1993. Tide data from the end of the FRF pier were available from National Oceanic and Atmospheric Association’s National Ocean Service.

Biological and physical time series were cross correlated with 1-h lags in both directions. Degrees of freedom (df) for estimating significance of the cross correlations were calculated as \( df = N\Delta t/DT \), where \( N \) = number of samples, \( \Delta t \) = sampling interval (i.e., \( N\Delta t \) = record length), and \( DT \) is the decorrelation time, estimated from the autocorrelations as the shorter of the two first (positive and negative) zero crossings (Emery and Thomson, 1997).

4. Results

a. Physical and meteorological measurements

During July 1993, there were striking oscillations in sea-surface temperature and salinity: periods of cooler (<15°C), more saline (>33 ppt) water alternated with warmer (>20°C), less saline (<28 ppt) intervals (Fig. 2a). The cool, salty water occurred during north/northeastward winds (Fig. 2b). When winds diminished or reversed direction, warmer, fresher water prevailed.

At the start of the pump sampling period, winds blew toward the northeast (Fig. 3b) and there was relatively cool water at pump depth (Fig. 3a). Short (6–10 h) pulses of southwestward winds occurred near noon each day. A precipitous temperature rise at pump depth occurred just after noon on 21 July (Fig. 3a), coinciding with the second pulse of
southwestward wind. The pump was then bathed in warm water until the end of the study period.

b. Time series of larval concentrations

Time series of larval concentrations showed high temporal variability with remarkably distinct signals (Fig. 4). There were two large density peaks for each taxon, with very low concentrations in between. Ranges in larval densities were similar for most groups, including hard- (barnacle cyprids, 5–746 m⁻³; bryozoan cyphonautes, 0–86 m⁻³) and soft-substrate (polychaetes, 0–668 m⁻³; bivalves, 0–516 m⁻³; gastropods, 6–414 m⁻³) organisms. In most cases, maximal concentrations represented a 100-fold change over
several hours. Decorrelation times were about 5 h for bivalves (Fig. 7a), 6 h for cyprids and cyphonautes, and 7 h for gastropods (data not shown). The polychaete time series was not significantly autocorrelated (Fig. 7b).

Larval concentrations for each taxonomic group peaked within a few hours of one another (Fig. 4). Except for polychaetes, all biological cross correlations were significant at ≥95% confidence level (e.g., Fig. 5), suggesting synchronous larval transport within a single patch. Maximal and submaximal peaks occurred within the cooler (<15°C) water mass (1200 on 20 July to 1200 on 21 July; Fig. 4), and low concentrations of all taxa were associated with warmer (>15°C) water (after 1200 on 21 July; Fig. 4).

For bivalves, gastropods and cyprids, cross correlations were significant between time
series of larvae and the alongshore component of wind velocity (Fig. 6). A significant negative correlation occurred at 0 lag, indicating that larval densities increased in immediate response to southwestward winds. In fact, maximal and submaximal peaks occurred
when subsiding northeastward winds were followed by short bursts of southwestward winds (Fig. 4f).

c. Limitations

This study was an initial foray into collecting time series of larval densities at a near-bottom inner-shelf site. The moored pump offers improved measurement frequency

Figure 5. Cross-correlations between bivalve and barnacle cyprid concentrations \( r = 0.793, p < 0.01 \). The length of each bar indicates the size of the correlation at each hourly lag, and the thin horizontal curves are the 99% confidence intervals. Positive lags relate larval bivalve concentration to subsequent values of barnacle cyprid concentration, and vice versa for negative lags. All other cross-correlations (except those involving polychaetes) were also significantly correlated at the 95% confidence level, or higher (data not shown).

Figure 6. Cross-correlation between alongshore component of wind velocity and bivalve concentration time series \( r = -0.579, p < 0.05 \). See Figure 5 for explanation. All other groups (except polychaetes and cyphonautes) were also negatively correlated with wind velocity at the 95% confidence level, or higher (data not shown).
and duration relative to shipboard techniques (Mann, 1985; Farrell et al., 1991; Shanks et al., 2000). Although a single station was sampled here, the CoOP94 study (11–30 August 1994) involved 9 pumps in 3 vertical arrays that spanned the inner shelf (Butman, 1994). Collection interval (3 h) and water volume (250 L) were dictated by the findings of the present study. Results for the middle station (3 pumps, 21-m depth) of CoOP94 are presented in Garland et al. (2002).

The 3-d larval time series from July 1993 was sufficient to show a detectable signal with a nascent scale (defined by DT) for each taxon, yet inadequate for statistically evaluating causation. Congruence between time series of larval density and temperature or wind velocity—proxies for upwelling and downwelling events—implicate the role of wind-driven cross-shelf transport. Yet, such trends cannot be tested statistically in this 70-h record, because there were too few upwelling and downwelling episodes. A much longer sampling program (2–6 mos) would be confounded, however, by larval availability, which is unlikely to remain constant.

5. Discussion

a. Oceanographic setting

Winds and waves are the dominant physical processes driving currents in this inner-shelf region (Fedderson et al., 1998; Lentz et al., 1999). The weak, semi-diurnal tide (Fig. 2c) cannot produce appreciable, net, cross-shelf flows (Shay et al., 1998; Lentz et al., 2001). Storm waves breaking near shore can generate strong (of order 100 cm s\(^{-1}\)) along- and cross-shelf flows (Fedderson et al., 1998; Gallagher et al., 1998), but winds were relatively weak (<10 m s\(^{-1}\)) and wave amplitude small (<0.3 m) during July 1993 (Fig. 2b).

The large temperature and salinity fluctuations observed at the site (Fig. 2a) were due to intermittent upwelling and downwelling. The extensive physical measurements taken during CoOP94 revealed that alongshore wind velocity singularly drives up- and downwelling in this inner-shelf region, and that temperature and salinity reliably predict these cross-shelf flows (Austin, 1999; Austin and Lentz, 1999; Lentz et al., 1999). Alongshore transport of intermittent, low-salinity plumes from Chesapeake Bay could cause the salinity, but not the temperature oscillations (Fig. 2a) (Boicourt, 1973; Rennie et al., 1999; S. J. Lentz, pers. comm.).

Upwelling conditions existed at the start of the sampling period, with relatively cool temperature throughout the water column (Fig. 3a). Short pulses of downwelling-favorable winds occurred during the first two days, but were insufficient to transport the thermocline to pump depth until midday on 21 July (Fig. 3b). The abrupt temperature increase at 7-m depth (i.e., just after noon on 21 July; Fig. 3a) signifies the passage of the downwelled thermocline.

b. Temporal variation in larval concentrations

Time series of larval concentration for five taxa had markedly similar characteristics. Maximal and submaximal peaks in larval density were nearly coincident (Fig. 4). The
resemblance among time series may reflect hydrodynamic processes or larval characteristics that maintained the organisms within a patch of water over 3 d, despite other phenomena (e.g., physical mixing or taxon-specific behaviors) that would tend to segregate or disperse them. Within a taxon, amplitudes of the two large peaks were similar, suggesting modest mixing or dilution over a day. The interval between peaks, phase lag, and peak width differed slightly (a few hours) among groups, however, implying spatial separation among taxa within the larger patch of organisms. Autocorrelations revealed that a sampling frequency \((DT/2)\) of about 3 h would capture the dominant temporal variabil-

![Figure 7](image_url)

**Figure 7.** Autocorrelations for time series of bivalve concentration (a), and polychaete concentration (b). The length of each bar indicates the size of the correlation at each hourly lag, and the thin horizontal curves indicate the 95% confidence intervals. The time point where the autocorrelation function crosses the t-axis (autocorrelation = 0) indicates the decorrelation time scale of the series (5 h for bivalves, but unspecified for polychaete larvae that were not significantly autocorrelated).
ity in larval densities for all groups, except perhaps the polychaetes. Thus, samples were taken every 3 h in CoOP94, which extended the record length to 20 d (pumps collect 160 samples per deployment) (e.g., Garland et al., 2002).

c. Hypothesized larval-transport mechanisms, and implications for settlement

Similarity among biological time series suggest that larvae of all five taxa were transported by the same process(es). Two mechanisms are proposed to explain the observations. The first hypothesis involves physical transport of a passive larval patch. The second hypothesis entails a behavioral response of larvae to an environmental signal, as modified by a perturbation.

The two most plausible physical hypotheses are passive sinking during the relaxation of upwelling, or advection by cross-shelf flows, which have a strong vertical component near shore. According to the first hypothesis, larvae would be stratified within the water column based on their passive sinking rates. Thus, the heaviest (e.g., most calcified) larval types—bivalves, gastropods, and barnacle cyprids—should be the first to reach near-bottom waters. In fact, these were the first groups to appear in the second set of density peaks, but not in the first set (Fig. 4). The second hypothesis is more consistent with the larval data and physical dynamics at the site (Fig. 8). Peaks in larval concentrations occurred within a relatively cool (10.5–12.5°C), saline (>33 ppt) water mass. Prolonged upwelling would result in shoreward advection of this larval patch (Fig. 8a and c). Relaxation of upwelling or the onset of downwelling would transport larvae down slope, past the pump (Fig. 8b and d). Larval peaks occurring within the cool water mass, coincidental temporal variations among diverse taxa, and significant cross-correlations between larval densities and the alongshore component of wind velocity support this hypothesis.

An alternative biological hypothesis involves vertically migrating larvae, coupled with a physical perturbation. In all five taxa, the first peaks in near-bottom concentration occurred shortly after local noon, perhaps the result of downward larval migration during periods of peak solar radiation. This behavior is consistent with diel vertical migration (DVM) (i.e., daytime descent; Forward, 1976). The second set of peaks were not only staggered from one another, but also occurred before noon in all groups except polychaetes, which peaked near noon. Strictly speaking, DVM is supported only if abundance peaks are 24 h apart (Forward, 1976). Furthermore, there were no peaks in concentration at noon on the last day (22 July) of the time series. However, the pump thermistor indicated that the downwelled thermocline, with a gradient of ~5°C, passed by the site sometime between 1300 and 1400 on the second day (Fig. 4). This advective perturbation may have disrupted temporarily the natural vertical migrations exhibited by larvae. Downwelling transport of relatively weak swimmers would have delivered larvae to the bottom prematurely, relative to a diel cycle. Thus, a combination of larval behavior and physical transport would explain the observed patterns of temporal variation.

Larval availability is a necessary condition for settlement. If larvae are competent and
Figure 8. Diagrammatic representation of a hypothesized physical mechanism for generating observed maximal and submaximal peaks in near-bottom larval concentrations, as observed in this study (Fig. 4). A single patch is considered in this scenario. Scales of depth and distance offshore were chosen for illustrative purposes and do not reflect the exact vertical and horizontal scales of thermal variability at the study site. (a) The water column is thermally stratified. The pump samples few or no larvae because they are being transported elsewhere by upwelling currents. Temperature of cool, upwelled surface waters begin to match the temperature of water near the pump intake. (b) Upwelling relaxes and a larval patch is advected to the pump location, but current strength (or duration) is insufficient to advect the downwelling temperature front to the pump. (c) Downwelling-favorable winds diminish or change direction and upwelling resumes. Larvae are transported to surface waters. (d) Upwelling again relaxes and the same patch of larvae is advected past the near-bottom pump (as in b). Subsequently, the downwelling temperature front reaches the pump as nearshore waters are advected offshore.
the habitat suitable, maximal near-bottom larval densities would predict settlement peaks. Based on the hypothesized larval-transport mechanisms, relaxation from upwelling or downwelling conditions would transport larvae to the seafloor, with DVM potentially modulating this process. At larger spatial scales, patterns of recruitment into adult populations have been attributed to upwelling relaxation (e.g., Farrell et al., 1991; Roughgarden et al., 1991; Wing et al., 1995) or downwelling (Connolly and Roughgarden, 1999). Moreover, using moored pumps and settlement trays, Ma (2001) recently demonstrated a direct relationship between the magnitude of bivalve settlement and downwelling events on the inner shelf of the Mid-Atlantic Bight.

d. Emerging patterns and processes

The distinctive temporal variations in larval concentrations observed in this study are surprising given the complex hydrodynamic processes that typically operate on the inner shelf. This short time series may have fortuitously occurred during an unusually calm period of relatively uncomplicated flow. Thus, the hypothesized mechanisms of wind-driven cross-shelf transport and DVM are supported by the hourly data. Relative to the 1993 observations, the longer time series of CoOP94 displayed, to first order, similar patterns that could be explained by the same processes (Garland et al., 2002). The 1994 data showed striking low-frequency variations in larval densities and water temperature that were consistent with wind-driven cross-shelf transport, and higher-frequency variations suggestive of DVM. In contrast to the present study where all larvae appeared to move as a group, larvae collected in 1994 showed taxon-specific water-mass associations and patterns of vertical migration. Other discrepancies between the 1993 and 1994 studies may be attributed to differences in the timing (July versus August), duration (3 versus 20 d), mooring heights (0.8 versus 3.2, 8.7 and 12.2 meters above bottom) and water depth (8 versus 21 m).

Within the energetic waters of the inner shelf, invertebrate larvae are transported long distances in strong (e.g., 20 cm s\(^{-1}\) mean, with peaks of 60–100 cm s\(^{-1}\)) shore-parallel flows. Cross-shelf transport must be viewed within the context of these swift alongshore currents. A working hypothesis for larval transport, incorporating the major processes discussed herein, involves benthic adults that spawn larvae into the overlying water column. These larval assemblages may show affinity for the natal water mass, which is transported by wind-driven along- and cross-shelf currents. Such low-frequency advection may be modulated by diel vertical migration. This brief study thus provides a glimpse of larval patterns and suggests potential transport processes for future study on the physically complex inner shelf.

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