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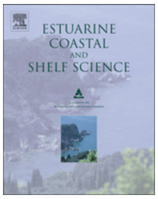

Short Communication

Vertical distribution of barnacle larvae at a fixed nearshore station in southern California: Stage-specific and diel patterns

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ABSTRACT

Patterns of vertical distribution in marine invertebrate larvae interact with coastal hydrodynamics to determine cross-shore distributions, dispersal ranges, and scales of connectivity among populations. We present observations on the vertical distribution of barnacle larvae from southern California, collected from 3 depth intervals every 2 h and over a 48-h period at a fixed nearshore station. Larvae were identified to species and stage of development, and their vertical distributions were tested for day/night and between-stage differences within each species, as well as for correlations with environmental variability. Stage-specific patterns of vertical distribution were distinct and consistent across species. Nauplii were most abundant near the surface at all times, and were numerically dominated by *Chthamalus* spp. (78% of $N_n = 1835$). Cyprids were substantially less abundant than nauplii in our samples ($N_c = 146$) and corresponded mostly to the subtidal barnacle *Balanus nubilus* (84%). Despite the lower counts and different species composition, our data suggest that cyprids remain within the mid-depth and bottom layers, and that changes in their mean depth of distribution (MDD) may track changes in pycnocline depth. Temporal changes in nauplii MDD were not correlated with water-column variability, wind forcing, or tidal height. The apparent vertical segregation of nauplii and cyprids may be related to previously documented differences in the cross-shore distribution of these stages.

1. Introduction

Many invertebrate life cycles include planktonic larval stages (Thorson, 1950), which may disperse over 100s to 1000s of kilometers (Scheltema, 1986) and often settle in adult habitats far from their parental populations (Gaines et al., 2007). Larval dispersal and transport are thus the mechanisms by which disjunct populations of benthic invertebrates are demographically and genetically connected (DiBacco et al., 2006; Pineda et al., 2007). The spatial scale of such exchange of individuals is relevant for understanding recruitment variability (Sponaugle et al., 2002) and for the design of marine reserves (Gaines et al., 2003). Furthermore, planktonic larval dispersal also allows sedentary species to re-colonize and invade coastal habitats (e.g. McQuaid and Phillips, 2000). Therefore, the characterization of factors that control the horizontal distribution and dispersal of larvae is critical to understanding geographic patterns and population dynamics of benthic species.

Swimming speeds range from less than 1 cm s^{-1} in ciliated larvae to a maximum of 2–8 cm s^{-1} in some crustaceans (Chia et al., 1984; DiBacco and Pineda, unpublished data), whereas typical velocities of alongshore currents may fluctuate between 10 and 50 cm s^{-1} (e.g. Largier, 2003; Kaplan et al., 2005), hence most invertebrate larvae are unable to determine their position by horizontal swimming. However, invertebrate larvae may take advantage of vertical shear to determine their horizontal position (e.g. Nelson, 1912). Larvae may swim vertically either to remain in a small region or to enhance their dispersal (e.g. Nelson, 1912; Rothlisberg et al., 1995; DiBacco et al., 2001; Poulin et al., 2002), suggesting that differences in vertical distribution and swimming behavior may result in different patterns of larval dispersal for species developing in the same region and under apparently similar advective regimes (e.g. Bousfield, 1955; Rothlisberg and Miller, 1983; North et al., 2008). Although the relevance of larval behavior and vertical distribution for larval transport is well understood (Pineda et al., 2007), there are surprisingly few field studies on vertical distributions of invertebrate larvae and their temporal variability in open coastal waters (e.g. Barnett and Jahn, 1987; dos Santos et al., 2007).

Recent observations in southern California (Tapia and Pineda, 2007) revealed striking differences in the stage-specific nearshore

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distribution of intertidal barnacle larvae. Late, planktotrophic naupliar stages and the non-feeding cyprid – the stage that settles onto hard substrata and metamorphoses into a juvenile barnacle – exhibited contrasting horizontal distributions within the first kilometer from shore (Tapia and Pineda, 2007). These results were consistent for both *Chthamalus* spp. and *Balanus glandula*, and suggested that cross-shore transport of nauplii and cyprids is driven by different sets of larval behaviors and advective forces in the inner-shelf environment. It was hypothesized that differences in the vertical distribution of late nauplii and cyprids may interact with physical phenomena that force cross-shore transport at local scales (e.g. sea breeze, internal tidal bores), and explain their horizontal segregation in the inner shelf. In the present study, we describe observations on vertical patterns of larval distribution gathered during the same season and in close proximity (ca. 8 km) to the area studied by Tapia and Pineda (2007). The objective of this study was to test for (1) between-stage differences in the vertical distribution of barnacle larvae and (2) diel changes in vertical distribution. Our results indicate that nearshore vertical distributions of barnacle nauplii are heavily skewed towards the surface, and that this pattern does not change between day and night. Although very few cyprids were collected, our data suggest that within a few kilometers from the shoreline they might remain away from the surface at all times. We suggest that this apparent vertical segregation of nauplii and cyprids may be connected with previously documented differences in the cross-shore distribution of these stages.

2. Materials and methods

Sampling was conducted in June 2003 onboard the R/V Robert Gordon Sproul of the Scripps Institution of Oceanography (SIO). The ship was anchored for 48 h, starting on 8 June at 23:00 Pacific Daylight Time (PDT), at a coastal station (30 m depth) located approximately 2 km off Del Mar (32°55.91′N, 117°16.79′W) in southern California, USA (Fig. 1). Plankton samples were collected every 2 h from 3 depth intervals (0.5–9, 11–19, and 21–29 m) using a submersible semi-vortex AC pump designed to push water without driving it through the impeller (Ebara DVS, Ebara Corp.) so that mechanical damage to the plankton is minimized. Volume of water filtered was measured with an inline digital flow meter attached to the pump hose. To insure an even sampling of each depth interval, the pump was hauled up and down within each depth interval at ca. 1 m s^{-1} for approximately 20 min, until 6 m^3 of water were filtered through a 110-μm mesh net. This mesh size was chosen to ensure that all larval stages of *Chthamalus* spp. and other common barnacle species in the region (see below) would be retained if present in the plankton at the time of sampling. Plankton samples were preserved onboard using buffered 4% formaldehyde and sorted using a dissecting microscope in the laboratory. A Conductivity–Temperature–Depth sensor (CTD Seabird SBE9) equipped with a Seatech fluorometer was lowered to 29 m immediately after a plankton profile was collected. Additional environmental data were obtained from the SIO Coastal Data Information Program website (http://cdip.ucsd.edu). Hourly data recorded at the SIO pier (32°52.00′N, 117°15.42′W), located ca. 8 km SE of the ship's position (Fig. 1), were used to compute alongshore and cross-shore components of wind. Winds were first rotated and aligned with the principal axis of variability, which lied 35° west of true North.

All barnacle larvae in our samples were counted and identified. Whenever possible, nauplii and cyprids were identified to species. Species identification and staging of nauplii were based on morphological criteria given by Lewis (1975), Standing (1980), Brown and Roughgarden (1985), Miller et al. (1989), and Miller and Roughgarden (1994). Chthamalid larvae collected during this study were probably those of *Chthamalus fissus*, a species that occurs between San Francisco and Baja California (Newman and Abbott, 1980) and that dominates the high to upper middle intertidal in La Jolla. However, we refer to the larvae in our samples as *Chthamalus* spp. because the geographic distribution of *C. fissus* occasionally overlaps with that of *Chthamalus dalli*, a northern species with a southern limit that fluctuates between Point Conception and San Diego (Newman and Abbott, 1980; Wares, 2001). Adult *C. fissus* and *C. dalli* can be identified upon dissection and microscopic examination, but their larvae are morphologically identical (Miller et al., 1989).

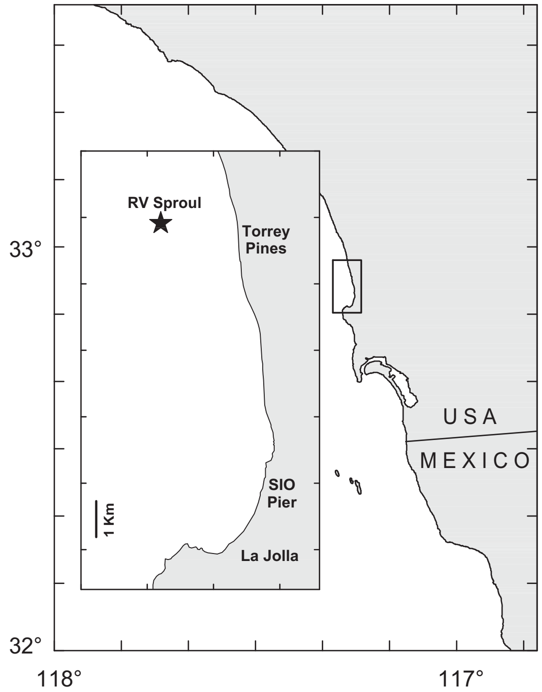

Fig. 1. Sampling area in southern California and detailed view of the ship's position with respect to shore (star), and to the Scripps Institution of Oceanography (SIO) pier, south of which the study by Tapia and Pineda (2007) was conducted in March 2003.

Vertical distributions of larvae were compared with those observed for temperature and chlorophyll-*a* through the water column by estimating mean depth distributions (MDDs) of each larval group. MDD were calculated for each plankton profile *j* as the weighted average

$$\mathrm{MDD}_j = \frac{1}{N_j}\sum_{i=1}^{3} z_i n_{ji} \tag{1}$$

where z_i is the mean depth of interval *i*, n_{ji} is the number of nauplii or cyprids collected within that interval, and N_j is the total number of nauplii or cyprids sampled at time *j*.

For each species, larval counts were used to test for between-stage differences in vertical distribution, as well as day/night differences within stages. We used a statistical test that allows for comparisons of vertical plankton distributions in the presence of patchiness and when multiple replicates are available (Beet et al., 2003). Samples taken at different times were pooled into two sets of observations, daytime and nighttime (12 and 9 profiles, respectively) and considered as replicates. Three plankton profiles collected at transition times (i.e. dawn or dusk) were left out of the analysis. We tested the null hypothesis that means of larval

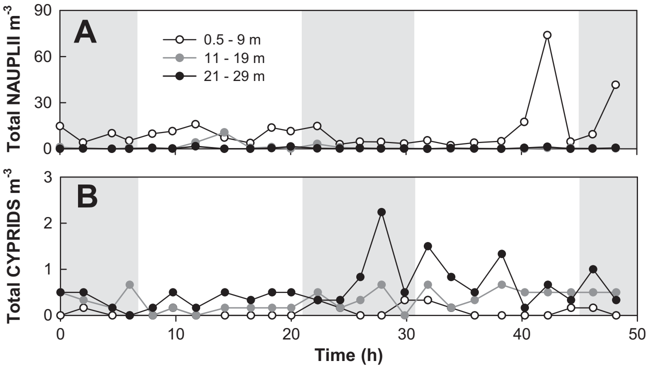

Fig. 2. Temporal variability in the concentration of barnacle (A) nauplii and (B) cyprids sampled from three depth intervals at a coastal station in southern California (32°55.91′N, 117°16.79′W). Concentrations were computed from total counts of larvae found in each plankton sample and standardized per volume (6 m^3) of water sampled. Shading indicates nighttime samples. The series started at 23:00 (PDT) on 8 June 2003.

abundance at each depth under one condition (i.e. daytime) are the same as the means under another condition (i.e. nighttime), using the test statistic

$$B = n\sum_{i=1}^{2}\sum_{j=1}^{3}\frac{\left(\overline{Y}_{ij}-\hat{\mu}_{ij}\right)^{2}}{\hat{\mu}_{ij}\left(1+\hat{c}\hat{\mu}_{ij}\right)} \tag{2}$$

where $\overline{Y}_{ij}$ is the average count of n replicates for condition i and depth j, and $\hat{\mu}_{ij}$ and $\hat{c}$ are maximum likelihood estimates of the mean (μ_{ij}) and dispersion coefficient (c_{ij}) of a negative binomial distribution, which is recommended to describe count data with a variance to mean ratio greater than one (Hayek and Buzas, 1997). The log-likelihood function and details on the procedure used to obtain the maximum likelihood estimates are given by Beet et al. (2003).

To correct for potential effects of autocorrelation within groups (i.e. day and night, nauplii and cyprids), statistical comparisons of vertical distributions were performed for subsets of 6 daytime and 6 nighttime plankton profiles selected at random and without replacement from the pooled datasets. This procedure was repeated 10 times for each comparison, and ranges of values obtained for the test statistic B and its corresponding probability under the null hypothesis (i.e. p-values) are reported here.

3. Results

Differences in the abundance of nauplii and cyprids with depth were observed throughout the sampling period (Fig. 2). Nauplii were consistently more abundant near the surface (Fig. 2a), with 89% of total nauplii ($N_n = 1835$) collected within the top 10 m. This vertical pattern did not change when two profiles with the highest counts of nauplii (last and fourth to last in Fig. 2a) were removed from the data series. Cyprids were less abundant than nauplii by an order of magnitude ($N_c = 146$) and tended to occur away from the surface (Fig. 2b), with 34% and 59% of total cyprid counts collected within the mid-depth and near-bottom layers.

Differences in vertical distributions of nauplii and cyprids became more apparent when total counts were used to compute mean depths of distribution (MDD) for each stage (Fig. 3a). Cyprids remained below the surface mixed layer and, with the exception of one profile, nauplii MDDs did not overlap with high chlorophyll concentrations (Fig. 3a). There was a positive and significant zero-lag correlation ($r = 0.86$, $p < 0.01$) between depth of maximum chlorophyll concentration and pycnocline depth, which cyprid MDDs appeared to track with a 4-h lag ($r = 0.66$, $p < 0.05$). A similar correlation with pycnocline depth was not found for nauplii. Finally,

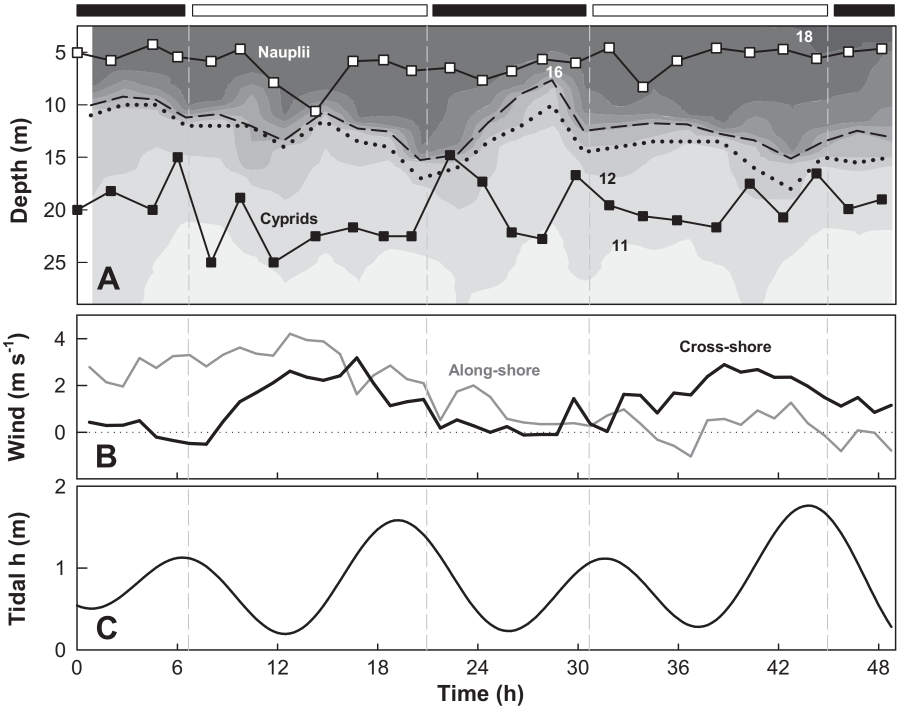

Fig. 3. Mean depth distributions (MDDs) of barnacle larvae and environmental variability. (A) MDDs are superimposed on temperature contours from CTD data collected after each plankton station, and plotted together with the pycnocline and chlorophyll maximum depths (dashed and dotted line, respectively). (B) Hourly winds and (C) tidal height were measured at a site ca. 8 km SE of the sampling station (see Fig. 1). Horizontal black and white bars indicate nighttime and daytime, respectively. Dashed vertical lines correspond to official times of sunrise and sunset.

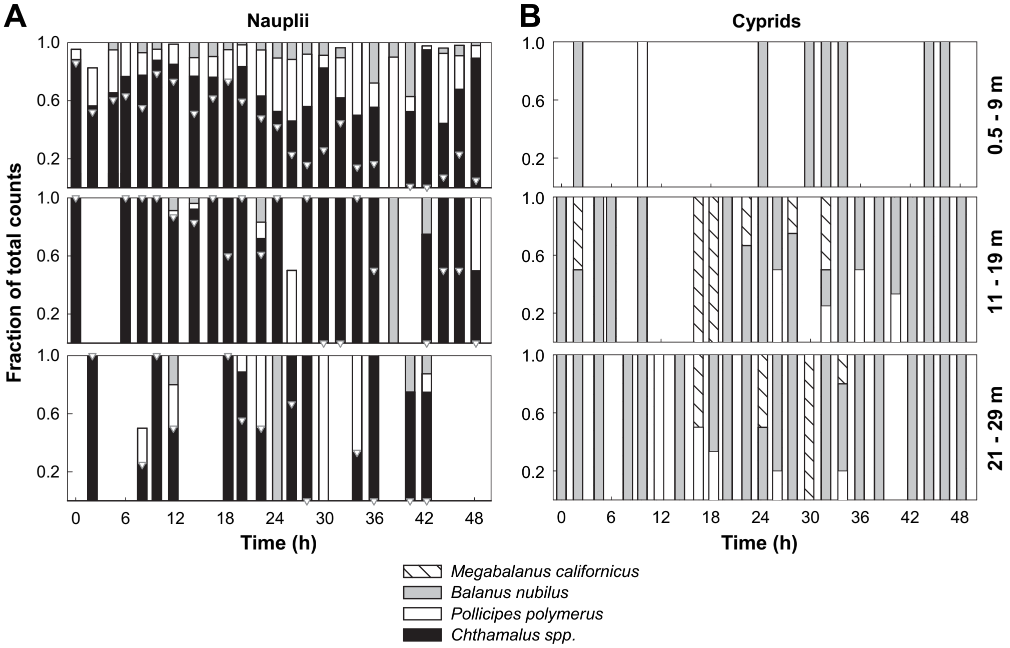

Fig. 4. Species composition of (A) nauplii and (B) cyprids at three depth intervals. The four most abundant species are shown. The symbols in (A) indicate the fraction of *Chthamalus* spp. nauplii that corresponded to stages IV, V and VI. Gaps correspond to plankton samples where no specimens of a given stage were found.

neither nauplii nor cyprid MDD were correlated with variability in nearshore winds (Fig. 3b) or tidal height (Fig. 3c).

The species composition of nauplii and cyprids differed markedly. While *Chthamalus* spp. accounted for 78% of total nauplii sampled from all depth intervals combined (Fig. 4a), cyprids of this species were not found in our samples. Instead, most cyprids (84.2% of total counts from all depth bins combined) corresponded to the subtidal *Balanus nubilus* (Fig. 4b). Nauplii of *B. nubilus* and the intertidal gooseneck barnacle *Pollicipes polymerus* occurred in low numbers and mostly near the surface (Fig. 4a). The stage composition of *Chthamalus* spp. nauplii, on the other hand, changed over the sampling period from a dominance of late stages (nauplius IV–VI) to a greater abundance of early stages (nauplius II–III) throughout the water column (Fig. 4a).

Mean fractions of nauplii and cyprids computed for each depth bin and within species showed no day/night differences in the vertical distribution of either group, and indicated a consistent pattern across species (Fig. 5, Table 1). Vertical profiles of nauplii and cyprids were significantly different from each other at all times (Table 1).

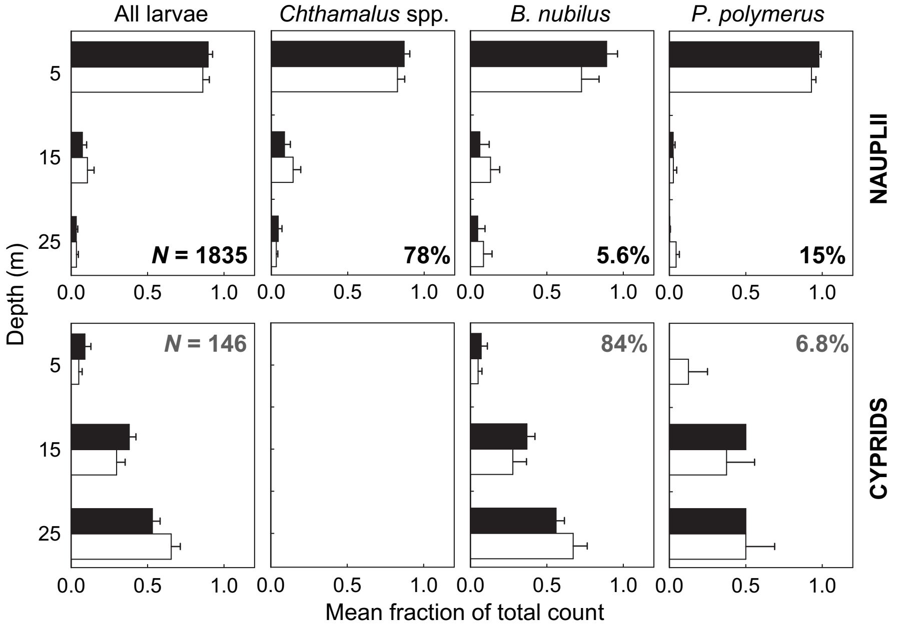

Fig. 5. Mean vertical distributions of barnacle nauplii and cyprids during daytime (white bars) and nighttime plankton collections (black bars) at a coastal station in southern California (32°55.91′N, 117°16.79′W). Fractions of total counts were computed separately for nauplii and cyprids in each plankton profile, and averaged for each depth interval across daytime and nighttime samples. Error bars are standard errors. Percentages do not add up to 100% because a small fraction of unidentified nauplii and *Megabalanus californicus* cyprids were not included in the figure.

Table 1
Comparisons of vertical distributions for species-specific and total counts of barnacle larvae. The test statistic B (Beet et al., 2003) and its corresponding p-value were computed 10 times for each comparison. The range of observed values is reported. Asterisks indicate comparisons where significant differences were found ($\alpha = 0.05$).

Comparison	B	p
Balanus nubilus		
Nauplii day vs. nauplii night	0.0000–2.9288	0.2312–1.0000
Cyprids day vs. cyprids night	0.0976–1.6367	0.4412–0.9524
Nauplii day vs. cyprids day*	9.6415–15.666	0.0004–0.0081
Nauplii night vs. cyprids night*	15.589–21.426	0.0000–0.0004
Pollicipes polymerus		
Nauplii day vs. nauplii night	0.4864–2.4200	0.2982–0.7841
Nauplii day vs. cyprids day*	14.630–19.584	0.0000–0.0007
Chthamalus spp.		
Nauplii day vs. nauplii night	0.3087–3.1196	0.2102–0.8570
Total counts		
Nauplii day vs. nauplii night	0.8009–4.3161	0.1156–0.6700
Cyprids day vs. cyprids night	0.0002–1.2561	0.5336–0.9999

4. Discussion

Contrary to recent evidence of diel migrations in barnacle larvae (e.g. dos Santos et al., 2007), vertical distributions observed in this study did not change between daytime and nighttime collections for any of the three species that were most abundant in our samples (*Balanus nubilus*, *Chthamalus* spp., *Pollicipes polymerus*). Between-stage differences were persistent in *B. nubilus* and *P. polymerus*, the two species for which both nauplii and cyprids were collected. However, the low cyprid counts and absence of *Chthamalus* spp. cyprids from our samples, together with the short duration and lack of spatial replication, preclude generalizations regarding ontogenetic changes in vertical distribution.

The observed vertical segregation of barnacle nauplii and cyprids is consistent with previously reported observations for inner-shelf waters in California. Over 4 years of monitoring a site ca. 50 km north of our sampling station, Barnett and Jahn (1987) found that total cyprids (species not identified) were consistently more abundant near the bottom and within 4 km from shore, whereas Pineda (1991) observed greater cyprid abundance (species not identified) near the bottom in shallow waters (4–16 m) off La Jolla (but see Pineda, 1999 for transient inversions of this pattern). Off the Oregon coast, observations conducted along a ca. 30 km transect by Shanks and Shearman (2009) indicated that barnacle nauplii remain close to shore ($\sim$5 km) throughout the summer, but within a sub-surface layer (10–20 m depth). This apparent discrepancy with the vertical patterns reported here may be partly due to a 2-fold difference in the mesh size used to sample the water column. It is likely that the 202 μm mesh used by Shanks and Shearman (2009) did not retain early stages of *Chthamalus* spp. larvae with the same efficiency as our 110 μm mesh net. Stage II nauplii of both *Chthamalus dalli* and *Chthamalus fissus* are <200 μm in width (Miller et al., 1989). Early stages of *Chthamalus* spp. accounted for up to 99% of nauplii collected in our 0–10 m samples (Fig. 4a) and shaped the near-surface segment of vertical distributions observed during the second half of our study.

4.1. Ecological implications of between-stage differences in vertical distribution

Ontogenetic changes in buoyancy, swimming abilities, and feeding behavior may produce distinct patterns in the vertical distribution of nauplii and cyprids. It has been suggested that early nauplii spend more time in near-surface waters due to a phototactic response enhanced by starvation (e.g. Singarajah et al., 1967), whereas later stages may remain in deeper waters to avoid visual predators and to conserve energy (e.g. Hays, 1995). The negative buoyancy of barnacle cyprids (De Wolf, 1973) would make it energetically costly for these non-feeding larvae to remain near the surface. Furthermore, lower temperatures in near-bottom waters may reduce the consumption rate of lipid reserves (see McLaren, 1963; Enright, 1977), thus allowing cyprids to remain competent for longer periods of time (see Pechenik et al., 1993; Pineda et al., 2005). At the time of our study, near-bottom temperatures were ca. 7 °C lower than at the surface, and similar vertical gradients have been recorded in the area through spring and summer (e.g. Lennert-Cody and Franks, 2002). Therefore, a near-bottom habitat could increase the chances of successful settlement by increasing the competency period of cyprids.

In a study conducted off La Jolla two months prior to the survey reported here, Tapia and Pineda (2007) found concentrations of *Chthamalus* spp. cyprids that were consistently higher (up to 22 per m^3) within 300 m from the shoreline and dropped to almost zero at 1.1 km offshore (ca. 40 m depth), where higher concentrations of late nauplii were observed. This horizontal separation could be enhanced and maintained by the vertical pattern documented here, combined with the cyprids' swimming response to onshore-moving transient hydrodynamic features (see Helfrich and Pineda, 2003; Scotti and Pineda, 2007). This behavior would allow *Chthamalus* cyprids to reach the shoreline more effectively and to remain near adult habitats until settlement.

In conclusion, we have shown that nauplii of intertidal barnacles occur near the surface at all times, whereas the less-abundant cyprids remain within the bottom half of the water column. The low numbers of cyprids found in our samples preclude any generalization as to their vertical patterns of distribution and diel variability. This limitation notwithstanding, the apparent vertical segregation of nauplii and cyprids raises the possibility of a connection between ontogenetic changes in vertical distribution and previously documented differences in the cross-shore distribution of these stages (Tapia and Pineda, 2007). Future studies with greater spatial–temporal coverage and higher depth resolution will be needed to address this question more definitively.

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