

Stage-specific distribution of barnacle larvae in nearshore waters: potential for limited dispersal and high mortality rates

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ABSTRACT: The stage-specific spatial distribution and mortality of *Balanus glandula* and *Chthamalus* spp. larvae were assessed with a series of daily vertical plankton tows collected from inner-shelf waters in La Jolla, Southern California, in March 2003. Sampling stations were located within 1.1 km of the shoreline, at depths of 10 to 45 m. For both groups, we observed a spatial segregation of naupliar stages and cyprids, although this pattern was statistically significant for *Chthamalus* spp. only. Early nauplii (NII and NIII) were more abundant at the inshore stations, whereas later stages (NIV to NVI) occurred in greater numbers offshore. Cyprids were consistently more abundant at the inshore station. Such striking differences in the horizontal distributions of late nauplii and cyprids suggest limited dispersal of barnacle larvae in nearshore waters. Particle trajectories computed from current velocities measured in the area indicated that changes in vertical distribution may indeed affect dispersal, and, in some cases, enhance the retention of larvae in shallow, inner-shelf waters. Vertical life tables were used to estimate naupliar mortality rates from pooled daily stage distributions. Average estimates (\pm SE) for the instantaneous rate of larval mortality in *B. glandula* (0.33 ± 0.05 larvae d^{-1}) and *Chthamalus* spp. (0.23 ± 0.03 larvae d^{-1}) were substantially higher than previously assumed for these species. We discuss the implications of limited dispersal and high mortality rates for the exchange of larvae among disjunct populations of intertidal barnacles and other coastal benthic invertebrates.

KEY WORDS: Larval distribution · Small scale · *Balanus glandula* · *Chthamalus* spp. · Dispersal · Mortality

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INTRODUCTION

The life cycle of many coastal benthic invertebrates is characterized and shaped by differences between the environments where adults and larvae must survive and develop. Adult individuals with limited or no mobility release their larvae into the planktonic environment, where multiple physical and biological processes determine the balance between mortality, dispersal, and survival to complete development (Morgan 1995). Larvae may be transported over long distances before they reach a stage that is competent to settle onto adult habitats (Scheltema 1968), which

often results in the local decoupling of recruitment and adult abundance. Coastal populations are thus considered open systems in terms of their reproductive output and local demography (Caley et al. 1996). Their persistence, structure, and dynamics are greatly influenced by mesoscale and local physical processes that mediate the dispersal of larvae to and from the shoreline (e.g. Roughgarden et al. 1988, Pineda 1991).

A number of influential studies published in the past 2 decades (e.g. Roughgarden et al. 1988, Alexander & Roughgarden 1996, Gaylord & Gaines 2000) used mathematical models to study the coupling of benthic population dynamics and mesoscale physical pro-

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cesses along the west coast of North America. Such models exemplify the 'supply-side' view that has dominated marine ecology in recent years (Underwood & Fairweather 1989), wherein the renewal of coastal invertebrate populations is seen as largely dependent on the interaction of substrate availability and the occurrence of physical phenomena that transport larvae from an offshore larval pool (Roughgarden et al. 1988). Thus, local populations have been regarded as open subunits that contribute with their reproductive output to an offshore pool of larvae, and field-based research has focused on the physical processes that may transport competent larvae back to adult habitats. Timing and spatial distribution of larval settlement have been linked to the occurrence of phenomena such as linear internal waves (Norris 1963, Shanks 1983), internal tidal bores (Pineda 1991, 1994a), persistent onshore winds (Bertness et al. 1996), and the onshore displacement of surface waters during relaxation of wind-induced upwelling (e.g. Wing et al. 1995). However, comparatively little attention has been paid to the fate of pre-competent larval stages in shallow, inner-shelf waters soon or immediately after they are released by sessile adults (but see Macho et al. 2005), although recent evidence suggests that retention and self-recruitment might be more prevalent than previously thought (Warner & Cowen 2002).

The relevance of determining how much local recruitment is given by local reproductive output, or, alternatively, finding the spatial scales at which reproduction and recruitment do correlate with each other, has been highlighted by a growing interest in marine reserves as a tool to protect habitats and biodiversity, as well as to manage marine resources under exploitation (Shanks et al. 2003). To achieve such goals, the scales of dispersal and rates of mortality experienced by larvae during their planktonic development must be known. Efforts to assess dispersal or retention have focused on the micro-chemistry of hard parts in larval fish (e.g. Swearer et al. 1999), crustaceans (DiBacco & Levin 2000), gastropods (Zacherl et al. 2003), and bivalves (Becker et al. 2005), with varying degrees of success in terms of the spatial and temporal scales of dispersal that can be resolved (see Levin 2006 for a review). More direct approaches based on *in situ* tracking and intensive sampling of planktonic aggregations have been attempted for larval crustaceans (e.g. Natunewicz et al. 2001), bivalves (Arnold et al. 2005), and echinoderms (Lamare & Barker 1999), and provided valuable information on the scales and processes that may shape the distribution of larvae relative to their parental populations.

Spatial scales of larval dispersal, which should also correspond to the scales at which disjunct populations exchange individuals (i.e. scales of connectivity), are

given by the interaction of larval biology (i.e. development rates and behavior) and hydrodynamic processes in the coastal ocean. For instance, ontogenetic and inter-specific differences in vertical distribution and swimming abilities of larvae under the same advective regime may result in very distinct patterns of dispersal (e.g. Rothlisberg & Miller 1983, Hill 1998). Dispersal may also be shaped by changes in larval mortality, with a general reduction in dispersal distances when rates of mortality increase relative to residual current velocities (Lefebvre et al. 2003, Ellien et al. 2004). However, available estimates of larval mortality in benthic invertebrates remain scarce and highly uncertain due to methodological and logistical constraints (Rumrill 1990, Morgan 1995). Mortality of larvae can be estimated directly when aggregations are tracked over time, using the observed change in larval abundance to compute a mortality rate averaged over that period. Although such tracking may be feasible in closed or semi-enclosed environments (e.g. Lamare & Barker 1999), in open coastal waters it requires observations of plankton distribution at spatial and temporal scales that are seldom achieved (but see Natunewicz et al. 2001). Thus, laboratory (Johnson & Brink 1998) and indirect field methods are usually employed to estimate mortality from ratios of local larval production to recruitment (e.g. Connell 1970), or from information on the stage composition of larvae over a given area (Aksnes et al. 1997).

In the present study we examined small-scale (~1 km from shore) patterns of horizontal distribution in larval *Balanus glandula* and *Chthamalus* spp. Our main goal was to assess the potential for early larval dispersal (i.e. shortly after hatching) through the observation of daily stage-specific distributions in shallow, inner-shelf waters. Additionally, we used daily stage structures together with a vertical life table method (Aksnes & Ohman 1996) to estimate instantaneous mortality rates for different stage transitions. We discuss the implications of limited dispersal and high larval mortality for the exchange of propagules among disjunct populations of benthic invertebrates, as well as the limitations of our data in relation to local physical variability and larval behavior.

MATERIALS AND METHODS

Study site and species. The survey was conducted in nearshore waters off the Scripps Institution of Oceanography (SIO) pier in La Jolla, Southern California, between 6 and 13 March 2003 (hereafter Days 1 to 8 of the survey). The study area is flanked by 2 submarine canyons (Fig. 1), which are likely to influence local circulation, for example, by reflecting a substantial frac-

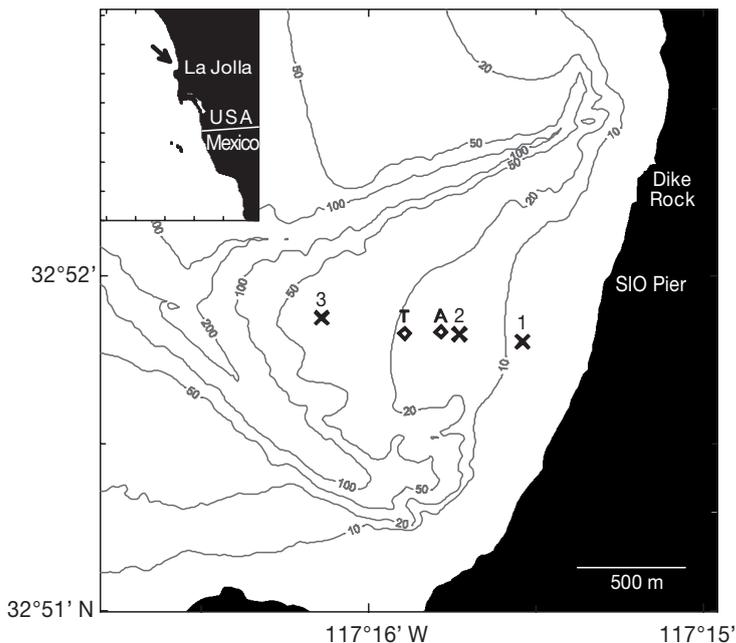


Fig. 1. Study area in La Jolla, Southern California (see inset). Numbered crosses indicate the plankton sampling stations. Diamonds labeled A and T show the location of the Acoustic Doppler Current Profiler ($32^{\circ}51.833'N$, $117^{\circ}15.786'W$) and temperature mooring ($32^{\circ}51.827'N$, $117^{\circ}15.894'W$), respectively. Contour lines indicate depth in meters (bathymetric data courtesy of S. Elgar, Woods Hole Oceanographic Institution)

tion of the infra-gravity wave energy propagating onshore (Thomson et al. 2005). Additionally, local flows may be affected by a large bed of the giant kelp *Macrocystis pyrifera* the northern tip of which reaches up to the marine reserve adjacent to our study area.

The intertidal barnacles on which our study was focused are 2 of the most abundant species found along the United States west coast. The acorn barnacle *Balanus glandula* Darwin, 1854 occurs in the high to middle intertidal zone along the west coast of North America from the Aleutian Islands to Punta Baja, Baja California (Newman & Abbott 1980, authors' pers. obs.). *Chthamalus fissus* is found from San Francisco to Baja California (Newman & Abbott 1980), and dominates the high to upper middle intertidal at La Jolla. Its latitudinal distribution, however, occasionally overlaps with that of *C. dalli*, a northern species found from Alaska to a southern limit that oscillates between Point Conception (Wares 2001) and San Diego (Newman & Abbott 1980). Although adult *C. fissus* and *C. dalli* can be identified by dissection and microscopic examination (Newman & Abbott 1980), their larvae are morphologically identical (Miller et al. 1989). Thus, chthamalid larvae will be referred to as *Chthamalus*

spp., as our larval identification was based solely on morphological criteria (see below).

The timing of our survey was based on the known reproductive cycle of *Balanus glandula* and *Chthamalus fissus*, and aimed at finding larvae of both species in nearshore waters. *Chthamalus* settlers can be found year round at a wide range of tidal heights in Central and Southern California (Hines 1979, Pineda 1994b, authors' unpubl. obs.). Individuals reach sexual maturity ca. 2 mo after settlement, after which up to 16 small broods are continuously produced each year (Hines 1979). Adult *B. glandula*, in contrast, produce 2 to 6 broods over a reproductive season that extends from early winter to late spring (Barnes & Barnes 1956, Hines 1979, Newman & Abbott 1980). Settlement takes place from late winter to early summer (Hines 1979, authors' unpubl. obs.).

Sampling procedure. Plankton samples were collected daily from 3 stations located within 0.3, 0.6, and 1.1 km of the shoreline, at depths of 10 to 40 m (Fig. 1). Plankton was collected by vertically towing a 110 μ m mesh net (0.75 m diameter, 2.75 m length) from bottom to surface. The water volume sampled at each station was estimated using a mechanical flowmeter (General Oceanics 2030). Samples were taken into the laboratory and preserved in 95% ethanol.

The classification of larvae by species and stage was based on the morphological descriptions published for *Balanus glandula* (Branscomb & Vedder 1982, Brown & Roughgarden 1985) and *Chthamalus* spp. (Miller et al. 1989). We only report the abundance of naupliar stages NII through NVI, as NI larvae molt into NII within hours of hatching at the temperatures recorded in our survey (Brown & Roughgarden 1985, Miller et al. 1989).

Spatial patterns in the distribution of different larval stages were analyzed using a 2-way analysis of variance (ANOVA) without replicates, in which tows made on different days at a given station were treated as repeated observations. We tested for homogeneity of variances using Hartley's procedure (Hartley 1950), which is based on the ratio of the largest to smallest sampled variance and is also sensitive to non-normality (Underwood 1997). To reach homogeneity of variances, concentrations of nauplii and cyprids were transformed as $\log(x + 1)$ and $-1/(x + 1)$, respectively.

Concurrently with the plankton survey, we monitored settlement of *Balanus glandula* and *Chthamalus* spp. larvae on collectors deployed within the vertical range of the adult distribution at a nearby intertidal site (Dike Rock, Fig. 1). Collectors were made out of 11 cm long pieces of white PVC pipe (2.54 cm diameter), which were cut in half lengthwise and etched with 3 lengthwise grooves. A hole was drilled in the center, so that the collectors could be attached to the

substrate using stainless steel screws that were cemented into holes drilled in the rock. Settlement collectors were first deployed on Day 1 and recovered/replaced daily during the daytime low tide until Day 8. Tidal height and wave action precluded the recovery of collectors on Day 4. Barnacles on recovered collectors were identified and enumerated using a dissecting microscope. Only larvae that settled within ca. 0.16 mm of the intersection between the groove bottom and wall were counted, since settlement rarely occurs outside this area. Hence, the area of substrate per collector was $\sim 1.9 \text{ cm}^2$ (Pineda 1994b). Settlement rates were calculated as the number of settlers per plate per day of deployment.

Environmental variables. From Day 1, temperature in the water column was recorded at 1 min intervals with Onset Stowaway XTI loggers (response time $< 15 \text{ s}$), located at the water surface and at 1, 2, 4, 6, 8, 10, 12, and 14 meters above the bottom (mab). The string of loggers was deployed at a depth of ca. 18 m (Fig. 1). Current velocities were measured with a bottom-mounted 1200 kHz Acoustic Doppler Current Profiler (ADCP, RD Instruments), deployed on Day 1 near Stn 2 at a depth of ca. 16 m (Fig. 1). Measurements were recorded in 1 m bins at 1 min intervals (60 pings per ensemble). Due to the temporal variability in water depth introduced by tidal fluctuations, surface wave action, and side lobbing, data collected from the surface bins had to be discarded. The uppermost bin with reliable data was at 13 mab, which was on average 3 m below the surface. ADCP data were rotated and aligned with the main axis of variability for horizontal currents (14° with respect to true north), which roughly paralleled the shoreline orientation. The orientation of this axis was given by the major eigenvector of a covariance matrix computed for depth-averaged east and north velocities. The same axis was used to rotate hourly wind observations, which were obtained from the SIO Coastal Data Information Program website (<http://cdip.ucsd.edu>). ADCP and wind data were partitioned into along-shore and cross-shore components.

Assessment of potential dispersal—progressive vector diagrams. We explored the effect that near-shore horizontal flows could have on the distribution of barnacle larvae by means of progressive vector diagrams (PVD). Constructing such diagrams hinges on the assumption that horizontal currents measured at a single point are representative of a larger area. This is clearly a strong assumption given the small-scale heterogeneity that local bathymetry (Fig. 1) may induce on inner-shelf circulation. Keeping these limitations in mind, we used PVD as a first-order approach to project the expected residence of drifting particles in nearshore waters at the study area. Our goal was to assess for how long a passively drifting or actively

swimming larva was likely to remain within a small area in nearshore waters. Near-surface velocities measured by bottom-mounted current meters might fail to predict the trajectory of particles found in the uppermost layer of the water column (Tapia et al. 2004). However, we assumed that the section of the water column for which reliable current meter data were available (1.5 to 13.5 mab, i.e. an average of 3 m below the surface) is representative of the vertical range of larval distribution.

The PVD were computed as predicted (x, y) positions at time t_n :

$$x(t_n) = \Delta t \sum_{i=1}^n u(t_i), \quad y(t_n) = \Delta t \sum_{i=1}^n v(t_i) \quad (1)$$

where $u(t_i)$ and $v(t_i)$ are the east and north current speeds measured by the current meter at a given depth at Time t_i , and Δt is the sampling interval (Emery & Thomson 1998, p. 165). We computed PVD for particles with 4 different types of vertical distribution. First, particles were assumed to be uniformly distributed in the water column; hence, depth-averaged current velocities were used to calculate trajectories from Eq. (1). For the second and third patterns of vertical distribution, it was assumed that larvae remain in the bottom half (i.e. near-bottom) and upper half (i.e. near-surface) of the water column at all times, and trajectories were computed using current velocities averaged over the corresponding depth range. Finally, particles were assumed to perform diel vertical migrations (DVM), so that they occurred near the bottom during the day (here defined as 06:00 to 18:00 h PST) and near the surface at night.

Trajectories for all 4 vertical distributions were computed repeatedly for drifting periods that ranged from 0.5 to 5 d. For each type of vertical distribution and drifting period, 100 starting times were chosen at random from the available dataset. Results are reported as the mean fraction of trajectories whose endpoints fell inside an elliptical area with a major axis of length $a = 5 \text{ km}$ and a minor axis $b = 0.28a$. While the length of this ellipse was arbitrarily chosen, its shape was given by the depth-averaged ratio between the minor and major axes of variability for observed current velocities. As rotated currents were used to compute particle trajectories, the ellipse was rotated accordingly, with its major axis at 14° with respect to true north.

Estimation of larval mortality. Vertical life tables (Aksnes & Ohman 1996) were used to estimate the mortality of nauplius larvae. The method yields estimates of mortality at the transitions between contiguous larval stages, and is recommended for cases where advection is expected to affect the horizontal distribution of larvae (Aksnes et al. 1997). Mortality is estimated from instantaneous stage distributions (i.e. obtained at 1 point in time); hence, it is not necessary

to track a particular larval aggregation. Instead, the stage distribution must be representative of the population under study, and spatial coverage and resolution should be large enough to compensate for the effect of small-scale patchiness.

Below we summarize the derivations of a method presented by Aksnes & Ohman (1996, p. 1462). Three main assumptions are made: (1) daily recruitment (ρ_i) to a given Stage i is constant over the duration of that stage, (2) the duration of a stage (α_i) is constant and equal for all individuals in the same stage, and (3) the mortality over that period (θ_i) is constant. Thus, the number of nauplii in Stage i on Day x can be expressed as:

$$n_i = \rho_i \int_{x-\alpha_i}^x \exp[-\theta_i(x-t)]dt = \frac{\rho_i}{\theta_i} [1 - \exp(-\theta_i \alpha_i)] \quad (2)$$

which is equal to the number of larvae that recruited during the last α_i days and survived (Aksnes & Ohman 1996). If it is also assumed that the mortality rate is constant for a period equal to the duration of 2 consecutive stages i and $i + 1$, then the number of nauplius larvae in Stage $i + 1$ on Day x is:

$$n_{i+1} = \rho_{i+1} \int_{x-\alpha_{i+1}}^x \exp[-\theta(x-t)]dt = \frac{\rho_{i+1}}{\theta} [1 - \exp(-\theta \alpha_{i+1})] \quad (3)$$

The number of cyprid larvae, for which the stage duration α_c is assumed infinite by the analysis, can be expressed as:

$$n_c = \rho_c \int_{-\infty}^x \exp[-\theta_c(x-t)]dt = \frac{\rho_c}{\theta_c} \quad (4)$$

Finally, the rate of recruitment to Stage $i + 1$ is the product of recruitment to the previous Stage i and the stage-specific survival:

$$\rho_{i+1} = \rho_i \exp(-\theta_i \alpha_i) \quad (5)$$

An equation that relates the relative abundance of 2 consecutive stages with their duration and mortality rate can be obtained by combining Eqs. (2), (3), and (5), and by setting $\theta_i = \theta$:

$$\frac{n_i}{n_{i+1}} = \frac{\exp(\theta \alpha_i) - 1}{1 - \exp(-\theta \alpha_{i+1})} \quad (6)$$

Similarly, an equation that relates the number of NVI and cyprid larvae can be obtained by combining Eqs. (2), (4), and (5).

$$\theta = \frac{1}{\alpha_{VI}} \ln \left(\frac{n_{VI}}{n_C} + 1 \right) \quad (7)$$

Eq. (6) was solved iteratively to obtain estimates of the mortality rate at the transition between naupliar stages NII to NV. The estimated mortality of NVI larvae was obtained directly from Eq. (7). Estimates of the number of individuals per stage for each day with

plankton observations (Days 1 to 7) were obtained by pooling larval counts recorded at the 3 stations. An average stage duration of 3 d was used for *Chthamalus* spp. (Miller et al. 1989), whereas durations of 1, 2, 2, 3, and 3 d were used for *Balanus glandula* NII, NIII, NIV, NV, and NVI (Brown & Roughgarden 1985).

RESULTS

Spatial-temporal distribution of larval stages

Patterns of spatial distribution for different larval stages were consistent among species. In general, earlier naupliar stages (NII and NIII) were more abundant at the inshore stations, whereas later stages (NV and NVI) increased in abundance towards the offshore station (Fig. 2). The statistical analysis of stage-specific distributions indicated no significant among-station differences for any but one larval stage in *Balanus glandula* (NII, Table 1). Conversely, the analysis of *Chthamalus* spp. distributions indicated significant spatial differences in all but one case (NII, Table 1). The concentration of *B. glandula* NII larvae at the offshore station was significantly lower than at the inshore stations (Table 1). On the other hand, concentrations of *Chthamalus* spp. NIV, NV, and NVI larvae were significantly higher at the offshore station. Although not statistically significant for *B. glandula*, concentrations of cyprids were higher at the inshore stations (Fig. 2F,L) and resembled the distribution of NII (Fig. 2A,G) rather than the preceding naupliar

Table 1. *Balanus glandula* and *Chthamalus* spp. Results of 2-way ANOVAs used to test for spatial (between-station) differences in the concentration of each larval stage. Different days of the study were treated as repeat observations (df = 2, 6 for all tests). Significant between-station differences are indicated in bold. The results of Tukey pairwise comparisons, performed for each test with a significant between-station effect, are shown in the third column for each species

Species/stage	$F_{2,6}$	p	Pairwise differences
<i>Balanus glandula</i>			
NII	10.973	0.002	Stn 1 > Stn 3, Stn 2 > Stn 3
NIII	3.168	0.082	
NIV	1.254	0.323	
NV	1.872	0.200	
NVI	3.533	0.065	
Cyprids	2.451	0.132	
<i>Chthamalus</i> spp.			
NII	3.120	0.089	
NIII	6.508	0.015	Stn 2 > Stn 1
NIV	25.373	0.000	Stn 3 > Stn 1, Stn 2 > Stn 1
NV	32.301	0.000	Stn 3 > Stn 1, Stn 2 > Stn 1
NVI	28.256	0.000	Stn 3 > Stn 1, Stn 2 > Stn 1
Cyprids	10.326	0.004	Stn 1 > Stn 3

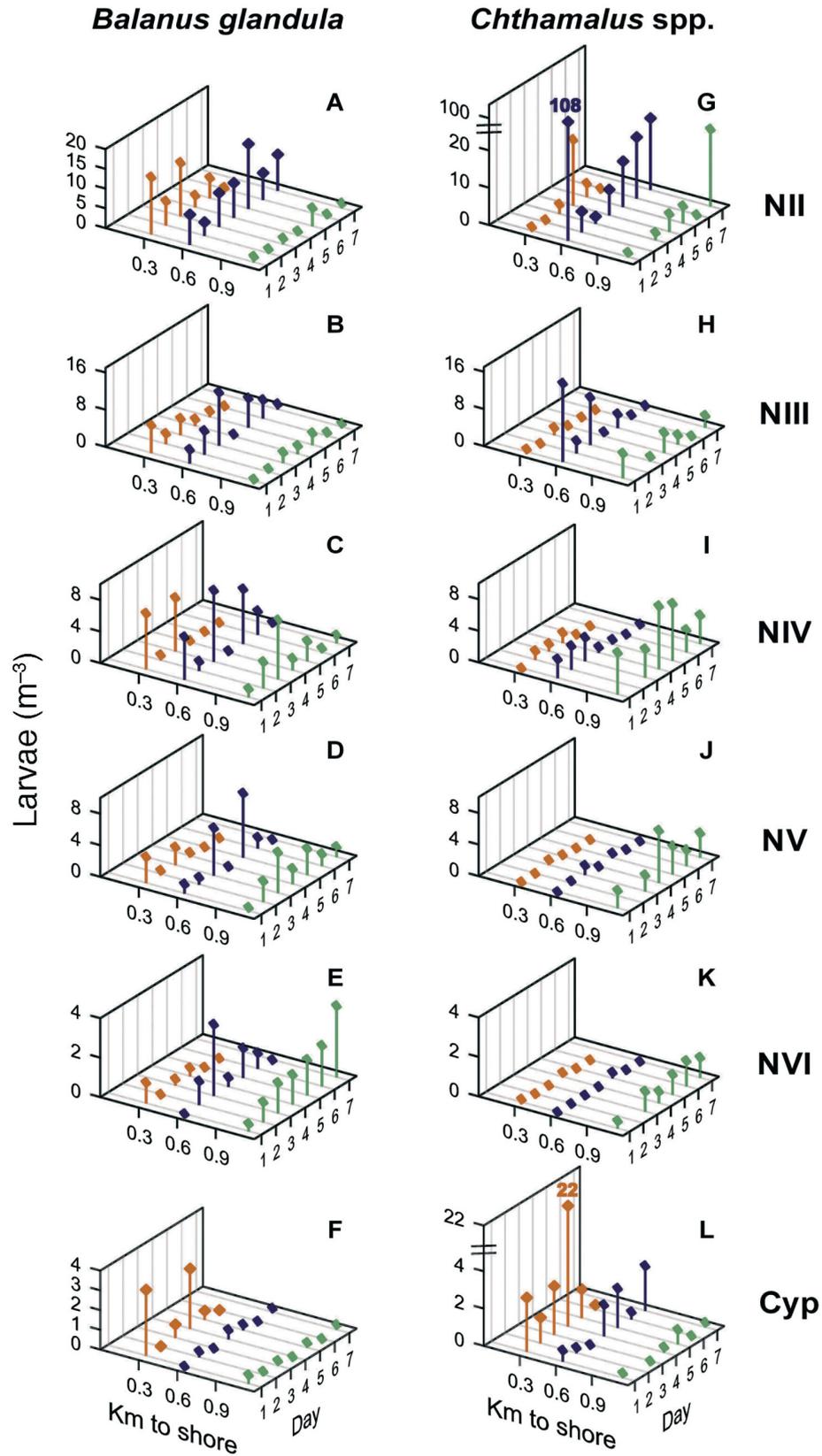


Fig. 2. (A–F) *Balanus glandula* and (G–L) *Chthamalus* spp. Temporal variability in the stage-specific spatial distribution of naupliar (NII to NVI) and cyprid (Cyp) larvae in shallow, inner-shelf waters off La Jolla, Southern California

stage (i.e. NVI). Patchiness in larval distribution appeared to be species specific. For example, on Day 1, the concentration of *B. glandula* NII decreased steadily from 14.5 to 1.5 ind. m⁻³ between the inshore and offshore stations (Fig. 2A), whereas *Chthamalus* spp. NII peaked at Stn 2, with 108 ind. m⁻³, i.e. 2 orders of magnitude higher than concentrations observed at the other 2 stations (Fig. 2G).

Temporal variability in stage distribution

Daily stage distributions for *Balanus glandula* and *Chthamalus* spp. (Fig. 3A–G and H–N, respectively) were obtained by pooling larval counts from the 3 sampling stations. All stages of larval development in *B. glandula* were observed on all but one day of the survey (Fig. 3F). Stage distributions of *B. glandula*

were dominated by NII and NIV during the first 3 d of the survey (Fig. 3A–C). NII larvae were numerically dominant on subsequent days (Fig. 3D–G), suggesting a constant input of newly hatched larvae either released by local adults or advected into the study area from adjacent populations. Stage distributions of *Chthamalus* spp. larvae were dominated by NII on 5 out of 7 d of observations (Fig. 3H–N), but most notably on Days 5 to 7 (Fig. 3L–N). This suggests a continuous input of larvae released locally or at a site from which these larvae can be advected within the time it takes for the NII to NIII transition to occur (~3 d; Miller et al. 1989). Finally, on Days 3 to 5 we observed a high abundance of *Chthamalus* spp. cyprids relative to the abundance of NVI larvae (Fig. 3J–L), which suggests that cyprids are either accumulated over time or transported into the study area from an external source (see 'Discussion').

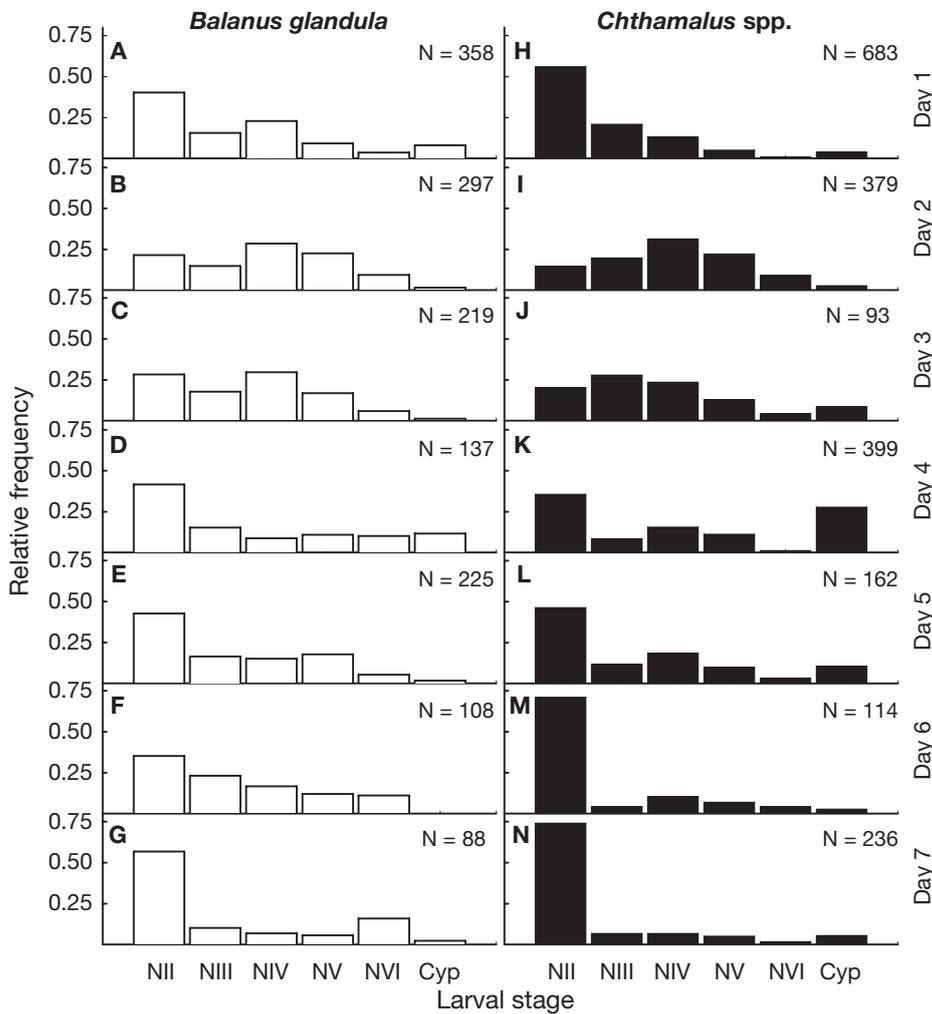


Fig. 3. (A–G) *Balanus glandula* and (H–N) *Chthamalus* spp. Stage distributions of larvae for each day of the survey (Day 1 = 6 March 2003). Relative stage frequencies were computed from total counts of larvae (N) at the 3 sampling stations

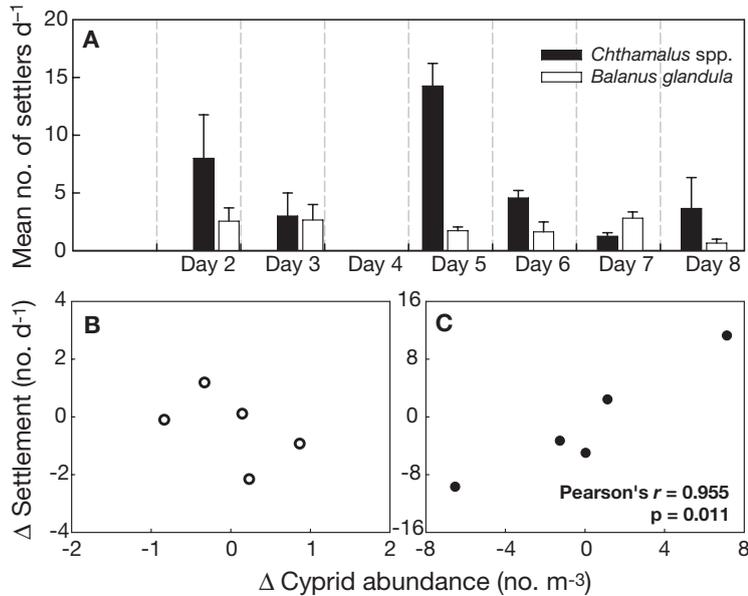


Fig. 4. *Balanus glandula* and *Chthamalus* spp. (A) Larval settlement at Dike Rock, and the correlation between daily changes in settlement and daily changes in nearshore cyprid concentration for (B) *B. glandula* and (C) *Chthamalus* spp.

Settlement and environmental variables

Settlement of both species was observed at Dike Rock throughout the survey (Fig. 4). In general, and consistent with their higher abundance in the plankton (Fig. 2L), settlement rates of *Chthamalus* spp. cyprids were higher than those observed for *Balanus glandula* (Fig. 4A). Settlement of *Chthamalus* spp. cyprids peaked on Day 5 of our study (Fig. 4A), 1 d after their maximum nearshore abundance was observed (Fig. 2L). Finally, while the timing of settlement in *B. glandula* was not correlated with changes in cyprid abundance at the inshore station (Fig. 4B), daily changes in the rate of settlement of *Chthamalus* spp. larvae were positively correlated with daily changes in their concentration at the inshore station (Fig. 4C).

With the exception of Day 4, all of our plankton collections were conducted during periods of relative calm that coincided with the transition from nighttime to daytime winds (Fig. 5A). On several days (1 and 2, 6 to 8), the diurnal pattern of wind variability resembled that shown by the summertime daily sea breeze, with afternoon winds blowing onshore at velocities of up to 3.5 m s^{-1} (Fig. 5A). Nighttime winds showed greater variability, and occasionally blew offshore with intensities similar to those recorded during the day. There was a change in the regime of wind variability on Days 4 and 5, with afternoon and evening winds blowing persistently towards the southeast (Fig. 5A). Local hydrodynamics during the survey were dominated by along-shore barotropic flows (Fig. 5B), which

were more energetic (up to 17 cm s^{-1}) than cross-shore currents (up to 10 cm s^{-1} ; Fig. 5C) and explained an average of 80% of the total variability between 2 and 13 mab (i.e. range of usable bins). Periodicity in the along-shore flow was dominated by the barotropic tide, with semi-diurnal changes in current direction throughout the water column (Fig. 5B). The vertical structure of cross-shore flows, on the other hand, was consistent with the structure of Mode 1 internal motions, often showing 2 layers of variable thickness and opposite flow directions (Fig. 5C). Temperature measurements showed a stratified water column, with differences between the surface and the bottom that reached ca. 5°C on Day 7 (Fig. 5D). Semidiurnal fluctuations in temperature distribution, associated with the tidal cycle were observed throughout the survey. An internal tidal bore warm front was detected in the afternoon of Day 3 (Fig. 5D). The occurrence of this bore coincided with an increase in the velocity of onshore currents throughout the water column, especially near the bottom (Fig. 5C), as well as a change in the vertical structure of along-shore velocities (Fig. 5B). Unfortunately, a high tide made it impossible to record settlement on Day 4, following the occurrence of such feature; maximum *Chthamalus* spp. settlement was nevertheless recorded on Day 5 (Fig. 4A).

Progressive vector diagrams

Trajectories obtained from our PVD calculations confirmed the notion that vertical distribution of larvae may greatly affect their dispersal in nearshore waters (Fig. 6). When PVD were calculated with horizontal velocities measured at the study site, nearly 20% of near-surface and uniformly distributed particles were retained for up to 2 d within a 5 km ellipse, whereas all near-bottom and vertically migrating particles had left the same area by then (Fig. 6). Results of the same calculations for data gathered at another station (ca. 5 km NW) in 2004 also revealed that vertical position influenced drifting times (results not shown).

Mortality estimates

The high variability observed in daily stage distributions (Fig. 3) precluded estimation of mortality for all stage transitions. A number of estimates that were >1 or <0 were obtained when such an approach was used

(results not shown), most likely as a result of differential advection of larval stages and the consequent violation of a basic assumption of the vertical life table method. We pooled larval counts for the contiguous stages NII/NIII and NIV/NV and obtained mortality estimates for the transitions NII + NIII → NIV + NV, NIV + NV → NVI, and NVI → C (Table 2). Average mortality rates estimated by stage transition ranged between 0.298

and 0.396 larvae d⁻¹ for *Balanus glandula* and between 0.176 and 0.309 larvae d⁻¹ for *Chthamalus* spp. There was no apparent tendency in the average values, or in the variability of mortality estimates, to decrease towards later stage transitions (Fig. 7). Average mortality rates (±SD) computed across stage transitions and days were 0.329 (±0.197) larvae d⁻¹ for *B. glandula* and 0.232 (±0.143) larvae d⁻¹ for *Chthamalus* spp.

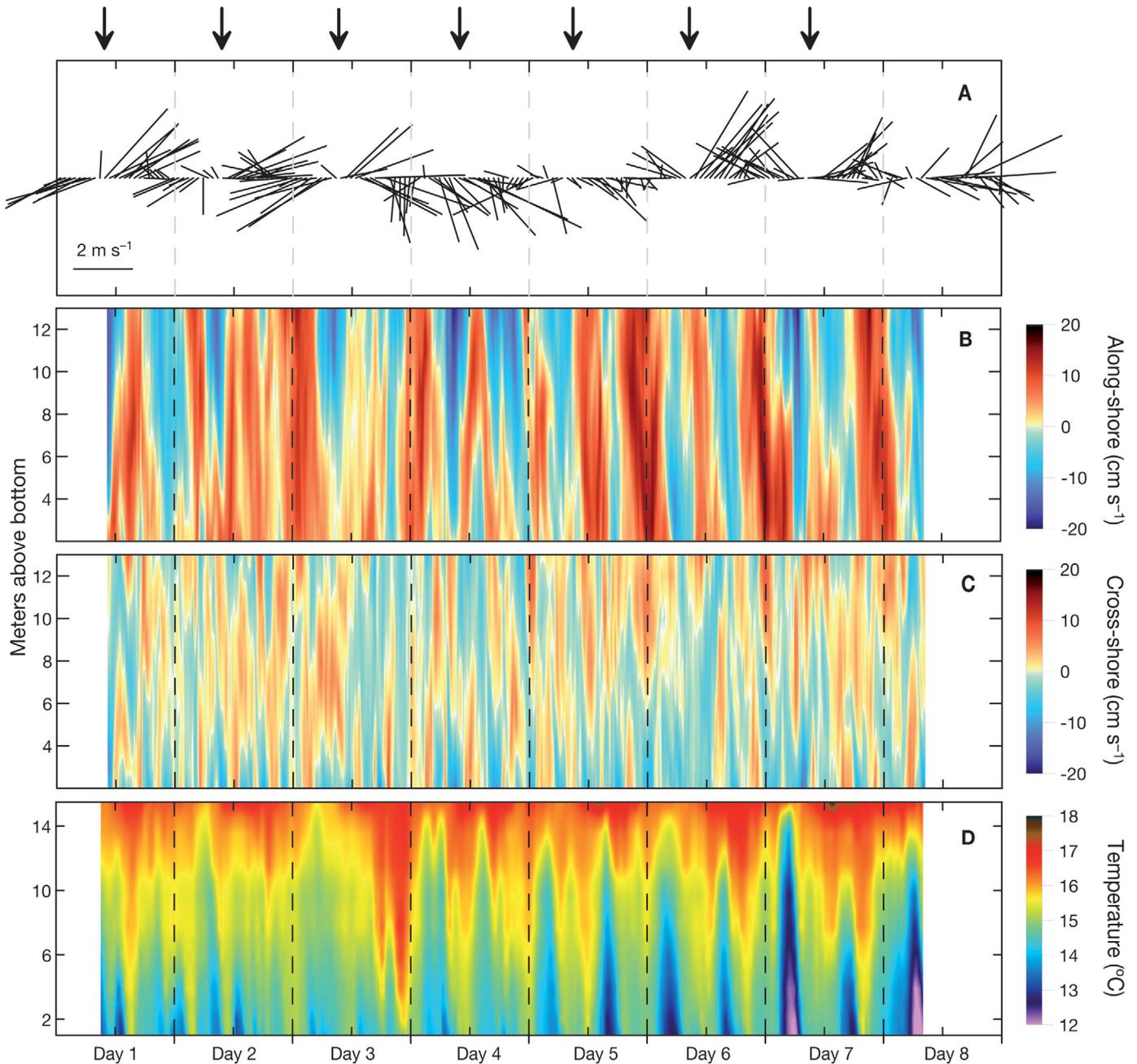


Fig. 5. Time series of environmental variables measured at the study area. Arrows indicate the times at which plankton collections were conducted. (A) Hourly observations of wind velocity were gathered at the Scripps Institution of Oceanography pier. The series of (B) along-shore and (C) cross-shore horizontal currents (both in cm s⁻¹) and (D) temperature distribution were plotted using low-pass-filtered series of 10-point (i.e. 10 min) running means

DISCUSSION

Prior to this study, we expected all larval stages to be well mixed (i.e. exhibit similar horizontal distributions) within the small area encompassed by our nearshore plankton survey. Instead, we have found persistent stage-specific patterns of larval distribution that suggest a potential for limited dispersal in nearshore waters. At the same time, we obtained estimates of larval mortality rates that are substantially higher than previously assumed (see Gaylord & Gaines 2000, p. 774). However, large daily fluctuations in the stage structure of *Balanus glandula* and *Chthamalus* spp. larvae indicated that the spatial coverage and resolution of our sampling were insufficient to compensate for nearshore advection and small-scale patchiness; hence, a central assumption of the mortality estimation method was probably not met. Despite the apparent effect of advection on the pooled stage structures, the consistent finding of late naupliar stages within ca. 1 km from shore suggests that a fraction of these intertidal barnacle larvae may complete their development in shallow, inner-shelf waters. The generality of our observations, however, must be tested at sites with different coastal configurations and bathymetries, as 2 submarine canyons flanking the area (Fig. 1) may affect local circulation in a way that promotes larval retention. Indeed, horizontal flows and their alongshore and cross-shore variability at scales of 0.1 to 10 km, together with stage-specific patterns of vertical distribution, must be better described in order to assess the chances of dispersal versus retention faced by benthic invertebrate larvae in nearshore environments.

Table 2. *Balanus glandula* and *Chthamalus* spp. Estimates of mortality (ind. d⁻¹) obtained for each day and stage transition. Empty cells correspond to days/transitions for which the estimated mortality rate was zero or negative

Species/ day	Mortality estimates per stage transition		
	NII + NIII → NIV + NV	NIV + NV → NVI	NVI → C
<i>Balanus glandula</i>			
1	0.279	0.393	0.123
2	0.043	0.282	0.629
3	0.128	0.366	0.558
4	0.421	0.036	0.210
5	0.288	0.311	0.462
6	0.322	0.108	–
7	0.603	–	0.693
<i>Chthamalus</i> spp.			
1	0.239	0.441	0.082
2	–	0.224	0.501
3	–	0.300	0.135
4	0.083	0.475	0.015
5	0.119	0.315	0.086
6	0.243	0.149	0.327
7	0.320	0.262	0.089

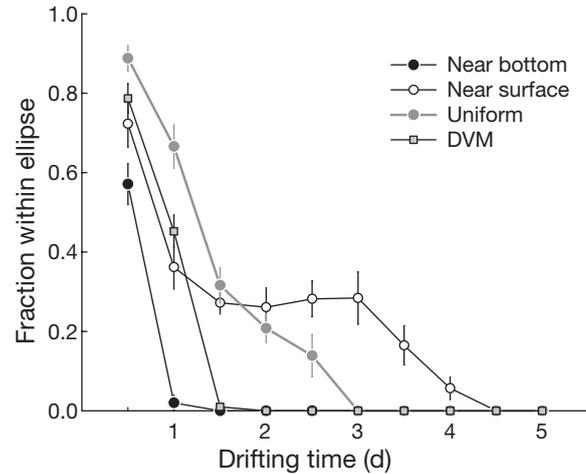


Fig. 6. Expected residence in the nearshore for drifting particles with different patterns of vertical distribution: near bottom, near surface, uniform, and diel vertical migration (DVM). Values correspond to the mean fraction of 100 simulated trajectories that remained within an elliptical area defined by a major axis of length $a = 5$ km and minor axis of $b = 0.28a = 1.4$ km. Trajectories were calculated from horizontal current velocities measured at the study area in March 2003. Error bars = SD

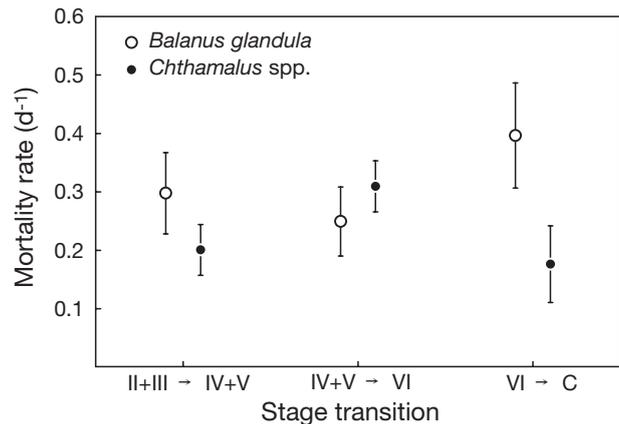


Fig. 7. Average estimates of the instantaneous rate of larval mortality (\pm SE) for 3 stage transitions in *Balanus glandula* and *Chthamalus* spp.

Spatial distribution of larvae

The daily changes we observed in larval stage distributions suggest that there was a continuous input of early nauplii (NII) into nearshore waters, especially after Day 4. A change in the pattern of local wind forcing observed on Days 4 and 5, blowing persistently towards the southeast, may have had a role on the change observed in nearshore stage distributions and settlement rates of *Chthamalus* spp. larvae. Additionally, the persistent spatial pattern observed for early nauplii, with higher concentrations of NII at Stns 1 and

2, suggests that larvae produced by local adults were hatching at the time of our study. Recently hatched barnacle larvae have a positive phototactic response (Lang et al. 1979) and sustained onshore wind forcing may promote the nearshore retention of surface waters and suspended material (McQuaid & Phillips 2000, Tapia et al. 2004). Local topography and shoreline orientation may have further promoted the retention of early stages in shallow, inner-shelf waters at the study area. As for later stages, unpublished observations conducted every 2 h and over a 48 h cycle near the study area in May 2003 (F. Tapia, J. Pineda, C. DiBacco & J. Jarett unpubl. data) indicate that ca. 90% of all barnacle nauplii are found near the surface at any given time. Thus, it seems feasible for a larva to be retained throughout its planktonic development at areas where local hydrodynamics and external physical forcing promote the nearshore retention and/or accumulation of surface waters. The Southern California Bight, where upwelling-favorable atmospheric forcing tends to be weak (Winant 1983), or smaller areas located in what has been termed 'upwelling shadows' (Graham & Largier 1997), are expected to provide such conditions and hence to exhibit higher rates of larval arrival to adult habitat. Recent observations conducted during 5 consecutive seasons indicate that *Chthamalus* spp. settlement rates at La Jolla are over 100 times greater than at a site located 100 km to the south (Pineda & López 2002). At smaller spatial scales, comparisons of invertebrate settlement rates among 16 sites that span 120 km of active-upwelling shoreline in the southeastern Pacific (Lagos et al. 2005) have shown consistently higher settlement at a site that appears to be located in an upwelling shadow (Narvaez et al. 2004). Observations of stage-specific nearshore larval distributions were not gathered during these studies.

Larvae of both *Balanus glandula* and *Chthamalus* spp. settled at Dike Rock throughout the survey, indicating that cyprids found in our inshore plankton samples were competent to settle. Cyprid concentrations at the inshore station were higher than those of NVI larvae, suggesting that cyprids did not settle immediately after molting from a NVI larva and were accumulated over an undetermined number of days, or that they were advected into our study area from an external source of late-stage nauplii, including those located further offshore than our external station (1.1 km). Despite such limitation in spatial coverage, our observations suggest that cross-shelf distributions of cyprids and NVI larvae are dictated by different sets of physical and behavioral factors. Nauplii and cyprids are likely to exhibit different behaviors, especially in terms of their swimming capabilities, and cyprids might be able to respond to transient hydrodynamic features that could transport them onshore (Helfrich & Pineda

2003). Our measurements of current velocities and previous descriptions of physical scales of variability in the region (Winant & Bratkovich 1981) indicate that nearshore larval distributions should be greatly influenced by alongshore flows, which were barotropic and explained an average of 80% of the total variability in nearshore horizontal velocities. This implies that all larval stages are likely to experience passive dispersal on the alongshore axis, and that higher concentrations of cyprids at the inshore station must have resulted from the interaction of stage-specific behavior, duration of the cyprid stage, and the dynamics of cross-shore flows. The vertical distribution of cyprids and their responses to transient hydrodynamic features must be determined in order to further investigate this question.

Assessing larval dispersal in nearshore waters

As larvae develop in the plankton, they acquire behaviors that could either increase dispersal or facilitate retention near their natal sites (e.g. Bousfield 1955). Mortality and dilution, on the other hand, cause a decrease in the abundance of larvae in nearshore waters to an extent that is currently unknown for most species (but see Ellien et al. 2004). Because tagging larvae to estimate mortality and dispersal through a mark-recapture approach has numerous disadvantages and logistical limitations (see Levin 1990), especially for larvae that are as small and abundant as the larvae of intertidal barnacles, natural tags such as environmentally induced chemical signatures have become a promising tool to assess dispersal of fish and invertebrate larvae over scales of days to months (e.g. Swearer et al. 1999). However, the applicability of this approach to tracking crustacean larvae is very limited, given the loss of hard structures during ecdysis. For instance, NI larvae of *Balanus glandula* and *Chthamalus* spp. molt into NII within hours of hatching (Brown & Roughgarden 1985, Miller et al. 1989). Therefore, in order to assess the dispersal of crustacean larvae over periods of days to weeks we must either find natural tags that are conserved throughout planktonic development or resort to a high frequency characterization of nearshore plankton distribution and circulation patterns (e.g. Natunewicz et al. 2001, Arnold et al. 2005).

The results of our PVD analysis illustrated the effect that differences in vertical distribution can have on expected retention times, but also highlighted the importance of measuring horizontal flows and characterizing their variability at appropriate spatial and temporal scales. Supposing that flows measured at 1 point are representative of a larger area is a critical assump-

tion that becomes more critical in nearshore environments, where small-scale changes in bathymetry, shoreline orientation, and features such as the 2 submarine canyons flanking our sampling area could play an important role for the retention and/or aggregation of larvae. Thus, future attempts to assess the generality of our observations must involve measurements of horizontal flow variability at a variety of nearshore environments. Finally, hypotheses regarding vertical migration behavior and ontogenetic changes in the range of vertical distribution, as well as swimming responses to transient hydrodynamic features, remain to be tested in the field.

Mortality estimates

Using vertical life tables to estimate mortality at every transition between larval stages yielded a large number of estimates that were negative, zero, or >1 (results not shown). Such values are clearly outside the range of values expected for a closed system, or for a stage distribution that is representative of the larval population. Although it would not be correct to use these values, for instance, to parameterize a population model, it is possible to use them to infer how open the area was in terms of larval dispersal over the duration of our study. On 4 out of 7 d the mortality estimates for the NII to NIII transition in *Balanus glandula* were >1 , suggesting that an input of NII and/or a loss of NIII larvae had occurred. Negative or zero estimates obtained for the transitions from NII to NIII (2 out of 7) and NIII to NIV (5 out of 7) in *Chthamalus* spp. also suggest that there was a loss of NIII, and probably of NII, during the first 2 d. This might be related to ontogenetic differences in swimming abilities and vertical distribution, as NII/NIII larvae are less able to determine their position within the water column (DiBacco, Pineda & Helfrich unpubl. data), and therefore more prone to entrainment in along-shore flows (see also Yule 1982, Table 7.6, for a summary of sustained swimming performances in cyprids [6 cm s^{-1}] vs. nauplii [0.7 cm s^{-1}]).

Our estimates of larval mortality rates were probably affected by an insufficient spatial and temporal coverage of our sampling. Although the vertical life table method does not require the tracking of individual larval aggregations, instantaneous stage structures utilized in the estimation of mortality are assumed to represent the population's stage distribution (Aksnes & Ohman 1996). Daily stage distributions observed in this study were highly variable, and suggested that our plankton survey lacked the spatial coverage and replication needed to compensate for small-scale patchiness and advection of early naupliar stages. Fur-

thermore, the assumption of constant and equal development time for all larvae in a given stage (Aksnes & Ohman 1996) could be unrealistic for the larvae of *Balanus glandula* and *Chthamalus* spp., which have shown an increase in the variability of stage duration between early and late naupliar stages (Brown & Roughgarden 1985, Miller et al. 1989). These limitations notwithstanding, our results suggest that the average mortality of barnacle nauplii in nearshore waters fluctuates around 20 to 40% larvae d^{-1} , which is substantially higher than previously assumed for *B. glandula* and *Chthamalus* spp. (Gaylord & Gaines 2000, p. 774), but within the range of mortality estimates found in the literature for other benthic invertebrate larvae (Rumrill 1990, Morgan 1995, Lamare & Barker 1999). A nominal mortality rate of 0.05 larvae d^{-1} has been used repeatedly in modeling studies that describe the distribution and population dynamics of *B. glandula* and *Chthamalus* spp. from Northern California and Oregon (see Gaylord & Gaines 2000, p. 774). This estimate was reportedly obtained from stage-specific counts of *Semibalanus balanoides* larvae, collected on 3 occasions over a period of 20 d from a pier in Millport, Scotland (Pyefinch 1949). Despite the caveats mentioned above, we believe that the characteristics of our survey, in terms of target species and sampling design, make the data presented in this contribution more likely to provide a realistic estimate for the nearshore mortality of *B. glandula* and *Chthamalus* spp. larvae.

A 4- to 6-fold increase in the mortality rate would have a substantial effect on the number of larvae completing their planktonic development. When constant mortality rates of 20 to 40% larvae d^{-1} are used together with a simple exponential decay function to project the numbers of larvae in a closed system after 2.5 wk (average development time for barnacle larvae at $\sim 15^\circ\text{C}$), the numbers of larvae expected to complete their development are 15 to 450 times smaller than the number expected with a 5% larvae d^{-1} mortality. Thus, differences in the mortality rates used to parameterize a model of larval dispersal could affect the predicted travel distances, the relevant larval transport mechanisms, population openness, and ultimately change the expected scales of connectivity among populations (e.g. Lefebvre et al. 2003, Ellien et al. 2004).

Results presented in this paper have implications for the currently dominant view of population openness and connectivity in coastal marine invertebrates. If the potential for limited larval dispersal and high mortality rates inferred from our data are a general feature of similar coastal regions, then populations of sedentary benthic invertebrates with planktonic larvae may be disconnected at small spatial scales, as suggested by recent observational (McQuaid & Phillips 2000, Porri et

al. 2006) and modeling studies (Verdier-Bonnet et al. 1997). Future efforts to model the relationship between coastal oceanography and benthic population dynamics must shift from an emphasis on mesoscale processes to a better description of inner-shelf variability and its effect on dispersal and self-recruitment.

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LITERATURE CITED

- Aksnes DL, Ohman MD (1996) A vertical life table approach to zooplankton mortality estimation. *Limnol Oceanogr* 41: 1461–1469
- Aksnes DL, Miller CB, Ohman MD, Wood SN (1997) Estimation techniques used in studies of copepod population dynamics—a review of underlying assumptions. *Sarsia* 82:279–296
- Alexander SE, Roughgarden J (1996) Larval transport and population dynamics of intertidal barnacles: a coupled benthic/oceanic model. *Ecol Monogr* 66:259–275
- Arnold WS, Hitchcock GL, Frischer ME, Wanninkhof R, Sheng YP (2005) Dispersal of an introduced larval cohort in a coastal lagoon. *Limnol Oceanogr* 50:587–597
- Barnes H, Barnes M (1956) The general biology of *Balanus glandula* Darwin. *Pac Sci* 10:415–422
- Becker BJ, Fodrie FJ, McMillan PA, Levin LA (2005) Spatial and temporal variation in trace elemental fingerprints of mytilid mussel shells: a precursor to invertebrate larval tracking. *Limnol Oceanogr* 50:48–61
- Bertness MD, Gaines SD, Wahle RA (1996) Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Mar Ecol Prog Ser* 137:103–110
- Bousfield EL (1955) Ecological control of the occurrence of barnacles in the Miramichi Estuary. *Bull Natl Mus Can Biol Ser* 137:1–65
- Branscomb ES, Vedder K (1982) A description of the naupliar stages of the barnacles *Balanus glandula* Darwin, *Balanus cariosus* Pallas, and *Balanus crenatus* Bruguière (Cirripedia, Thoracica). *Crustaceana* 42:83–95
- Brown SK, Roughgarden J (1985) Growth, morphology, and laboratory culture of larvae of *Balanus glandula* (Cirripedia: Thoracica). *J Crustac Biol* 5:574–590
- Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. *Annu Rev Ecol Syst* 27: 477–500
- Connell JH (1970) A predator–prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecol Monogr* 40:49–78
- DiBacco C, Levin LA (2000) Development and application of elemental fingerprinting to track the dispersal of marine invertebrate larvae. *Limnol Oceanogr* 45:871–880
- Ellien C, Thiebaut E, Dumas F, Salomon JC, Nival P (2004) A modelling study of the respective role of hydrodynamic processes and larval mortality on larval dispersal and recruitment of benthic invertebrates: example of *Pectinaria koreni* (Annelida: Polychaeta) in the Bay of Seine (English Channel). *J Plankton Res* 26:117–132
- Emery WJ, Thomson RE (1998) Data analysis methods in physical oceanography. Pergamon Press, New York
- Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by flow. *Am Nat* 155:769–789
- Graham WM, Largier JL (1997) Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. *Cont Shelf Res* 17:509–532
- Hartley HO (1950) The maximum *F*-ratio as a short-cut test for heterogeneity of variance. *Biometrika* 37:308–312
- Helfrich KR, Pineda J (2003) Accumulation of particles in propagating fronts. *Limnol Oceanogr* 48:1509–1520
- Hill AE (1998) Diel vertical migration in stratified tidal flows: implications for plankton dispersal. *J Mar Res* 56: 1069–1096
- Hines AH (1979) The comparative reproduction ecology of three species of intertidal barnacles. In: Stancyk SE (ed) Reproductive ecology of marine invertebrates. University of South Carolina Press, Columbia, SC, p 213–234
- Johnson KB, Brink LA (1998) Predation on bivalve veligers by polychaete larvae. *Biol Bull (Woods Hole)* 194:297–303
- Lagos NA, Navarrete SA, Veliz F, Masuero A, Castilla JC (2005) Meso-scale spatial variation in settlement and recruitment of intertidal barnacles along the coast of central Chile. *Mar Ecol Prog Ser* 290:165–178
- Lamare MD, Barker MF (1999) *In situ* estimates of larval development and mortality in the New Zealand sea urchin *Evechinus chloroticus* (Echinodermata: Echinoidea). *Mar Ecol Prog Ser* 180:197–211
- Lang WH, Forward RB Jr, Miller DC (1979) Behavioral responses of *Balanus improvisus* nauplii to light intensity and spectrum. *Biol Bull (Woods Hole)* 157:166–181
- Lefebvre A, Ellien C, Davoult D, Thiebaut E, Salomon JC (2003) Pelagic dispersal of the brittle-star *Ophiothrix fragilis* larvae in a megatidal area (English Channel, France) examined using an advection/diffusion model. *Estuar Coast Shelf Sci* 57:421–433
- Levin LA (1990) A review of methods for labeling and tracking marine invertebrate larvae. *Ophelia* 32:115–144
- Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. *Integr Comp Biol* 46:282–297
- Macho G, Molares J, Vázquez E (2005) Timing of larval release by three barnacles from the NW Iberian Peninsula. *Mar Ecol Prog Ser* 298:251–260
- McQuaid CD, Phillips TE (2000) Limited wind-driven dispersal of intertidal mussel larvae: *in situ* evidence from the plankton and the spread of the invasive species *Mytilus galloprovincialis* in South Africa. *Mar Ecol Prog Ser* 201: 211–220
- Miller KM, Blower SM, Hedgecock D, Roughgarden J (1989) Comparison of larval and adult stages of *Chthamalus dalli* and *Chthamalus fissus* (Cirripedia: Thoracica). *J Crustac Biol* 9:242–256
- Morgan SG (1995) Life and death in the plankton: larval mortality and adaptation. In: McEdward L (ed) Ecology of marine invertebrate larvae. CRC Press, Boca Raton, FL, p 279–321
- Narvaez D, Poulin E, Leiva G, Hernandez E, Castilla JC, Navarrete SA (2004) Seasonal and spatial variation of nearshore hydrographic conditions in central Chile. *Cont Shelf Res* 24:279–292

- Natunewicz CC, Epifanio CE, Garvine RW (2001) Transport of crab larval patches in the coastal ocean. *Mar Ecol Prog Ser* 222:143–154
- Newman WA, Abbott DP (1980) Cirripedia: the barnacles. In: Morris RH, Abbott DP, Haderlie EG (eds) *Intertidal invertebrates of California*. Stanford University Press, Palo Alto, CA, p 502–535
- Norris KS (1963) The function of temperature in the ecology of the percid fish *Girella nigricans* (Ayres). *Ecol Monogr* 33:23–62
- Pineda J (1991) Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* 253:548–551
- Pineda J (1994a) Internal tidal bores in the nearshore: warm-water fronts, seaward gravity currents and the onshore transport of neustonic larvae. *J Mar Res* 52:427–458
- Pineda J (1994b) Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Mar Ecol Prog Ser* 107:125–138
- Pineda J, López M (2002) Temperature, stratification and barnacle larval settlement in two Californian sites. *Cont Shelf Res* 22:1183–1198
- Porri F, McQuaid CD, Radloff S (2006) Spatio-temporal variability of larval abundance and settlement of *Perna perna*: differential delivery of mussels. *Mar Ecol Prog Ser* 315: 141–150
- Pyefinch KA (1949) Short-period fluctuations in the numbers of barnacle larvae, with notes on comparisons between pump and net plankton hauls. *J Mar Biol Assoc UK* 28: 353–369
- Rothlisberg PC, Miller CB (1983) Factors affecting the distribution, abundance, and survival of *Pandalus jordani* (Decapoda, Pandalidae) larvae off the Oregon coast. *Fish Bull* 81:455–472
- Roughgarden J, Gaines SD, Possingham H (1988) Recruitment dynamics in complex life cycles. *Science* 241: 1460–1466
- Rumrill SS (1990) Natural mortality of marine invertebrate larvae. *Ophelia* 32:163–198
- Scheltema RS (1968) Dispersal of larvae by Equatorial ocean currents and its importance to the zoogeography of shallow-water tropical species. *Nature* 217:1159–1162
- Shanks AL (1983) Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Mar Ecol Prog Ser* 13: 311–315
- Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecol Appl* 13:159–169
- Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402:799–802
- Tapia FJ, Pineda J, Ocampo-Torres FJ, Fuchs HL, Parnell PE, Montero P, Ramos S (2004) High-frequency observations of wind-forced onshore transport at a coastal site in Baja California. *Cont Shelf Res* 24:1573–1585
- Thomson J, Elgar S, Herbers THC (2005) Reflection and tunneling of ocean waves observed at a submarine canyon. *Geophys Res Lett* 32:L10602, doi:10.1029/2005GL022834
- Underwood AJ (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, New York
- Underwood AJ, Fairweather PG (1989) Supply-side ecology and benthic marine ecology. *Trends Ecol Evol* 4:16–20
- Verdier-Bonnet C, Carlotti F, Rey C, Bhaud M (1997) A model of larval dispersion coupling wind-driven currents and vertical larval behaviour: application to the recruitment of the annelid *Owenia fusiformis* in Banyuls Bay, France. *Mar Ecol Prog Ser* 160:217–231
- Wares JP (2001) Patterns of speciation inferred from mitochondrial DNA in North American *Chthamalus* (Cirripedia: Balanomorpha: Chthamaloidea). *Mol Phylogenet Evol* 18:104–116
- Warner RR, Cowen RK (2002) Local retention of production in marine populations: evidence, mechanisms, and consequences. *Bull Mar Sci* 70:245–249
- Winant CD (1983) Longshore coherence of currents on the Southern California shelf during the summer. *J Phys Oceanogr* 13:54–64
- Winant CD, Bratkovich AW (1981) Temperature and currents on the Southern California shelf: a description of the variability. *J Phys Oceanogr* 11:71–86
- Wing SR, Botsford LW, Largier JL, Morgan LE (1995) Spatial structure of relaxation events and crab settlement in the northern California upwelling system. *Mar Ecol Prog Ser* 128:199–211
- Yule AB (1982) The application of new techniques to the study of planktonic organisms. PhD thesis, Marine Sciences Laboratory, University of Wales, Bangor
- Zacherl DC, Manriquez PH, Paradis G, Day RW, Castilla JC, Warner RR, Lea DW, Gaines SD (2003) Trace elemental fingerprinting of gastropod statoliths to study larval dispersal trajectories. *Mar Ecol Prog Ser* 248:297–303

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