



## Diel vertical migration and cross-shore distribution of barnacle and bivalve larvae in the central Chile inner-shelf



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### ABSTRACT

The vertical and horizontal distribution of larval stages of the most common intertidal barnacle and mussel species were characterized in near-shore waters of central Chile. Paired day/night cruises were conducted on four spring-summer dates between December 2007 and November 2008, under contrasting wind, wave height, and near-shore stratification conditions. Regardless of variability in oceanographic conditions, the highest abundances of barnacle and mussel larvae were found within 1500 m from shore. Non-uniform vertical distributions were observed for chthamalids, balanids and mussel larvae, but patterns of diel variability differed among them. Chthamalid and balanid nauplii, as well as balanid cyprids were more abundant in the upper 20 m of the water column, while the density of chthamalid cyprids was highest near the bottom. Mussel larvae were only found within 20 m of the surface. The Mean Depth Distribution (MDD) of all nauplii (balanid and chthamalid) and chthamalid cyprids was deeper during day than night, suggesting typical diel vertical migration (DVM), but this difference was statistically significant only for nauplii. Mussels did not show diel differences in vertical distribution. The amplitude of DVM, measured as the difference between daytime and nighttime MDD, decreased with increasing wave height in chthamalid and balanid nauplii, but not with along-shore wind stress. Chthamalid nauplii, and to a lesser extent, balanid nauplii were found below the pycnocline during the day and above at night, suggesting that DVM involves daily crossing of this density barrier. In contrast, cyprids of all barnacle species were distributed across the pycnocline with no clear pattern. The results suggest that barnacle and bivalve larvae may exhibit a variety of behavioral responses to position themselves in the water column despite typically turbulent near-shore waters, and that such behavior varies between species and through ontogeny within species. Moreover, some stages of barnacle larvae perform DVM, but the amplitude decreased with increasing wave height – which may be either a plastic response to environmental cues or merely turbulent mixing impeding the ability of larvae to perform vertical migration.

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### 1. Introduction

In most marine benthic species the pelagic larval stage is capable of much greater dispersal than juveniles and adults, making the fate of larvae a key determinant of marine population connectivity (Cowen et al. 2000; Pineda et al. 2007; Scheltema 1971), metapopulation dynamics (Castorani et al. 2015; Shurin 2000), distribution patterns (Burrows et al. 1999; Crisp et al. 1981) and species coexistence and community

structure (Aiken and Navarrete 2014; Gaines and Roughgarden 1985; Menge 2000; Wieters et al. 2008). The combined forcing of various physical and biological factors, as well as their behavior in the water column, can influence the development and survival of the planktonic stages of these benthic species (Barnes 1956). With the exception of some fish, most planktonic larvae are not strong enough swimmers to overcome the velocity of horizontal currents typically encountered in the coastal ocean, but most of them are able to determine their vertical position in the water column, either by swimming fast enough and/or through buoyancy control mechanisms, with great consequences for transport and exposure to different biotic and abiotic sources of mortality (Drake et al. 2015; Metaxas and Saunders 2009; Miller and Morgan

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2013; Queiroga et al. 2007; Shanks and Brink 2005; Young 1995). Consequently, characteristic vertical distribution and regular vertical migration are important attributes exhibited by nearly all groups of invertebrate holo- and mero-zooplankton (Brinton 1967; Carriker 1951; dos Santos et al. 2007; Escribano et al. 2009; Lampert 1989; Queiroga and Blanton 2004).

A common migration pattern is diel vertical migration (DVM) between surface and deeper waters. This behavior apparently enables zooplankters to avoid visual predators and reduce their metabolic rates by migrating into darker, colder bottom waters during the day, and to feed in the higher phytoplankton concentrations typical of near-surface waters during the night (Forward and Rittschof 2000; Thorson 1964; Zaret and Suffern 1976). But reverse patterns of DVM are also common (e.g. Poulin et al. 2002). Besides ecological and physiological consequences for individual larvae, their ability to control depth allows them to alter the velocity fields they experience, since the magnitude and direction of the ocean currents commonly vary through the water column, especially in near-shore waters (e.g. Bonicelli et al. 2014; Cudaback et al. 2005; Lentz and Fewings 2012; Pineda 1999). This is particularly important in the case of larvae of coastal organisms because it can alter dispersal trajectories and determine the likelihood of competent larvae to return to shore (Cowen et al. 2006; Guizien et al. 2006; Metaxas and Saunders 2009; Morgan and Anastasia 2008; Morgan et al. 2009a; North et al. 2008; Shanks and Shearman 2009).

Although connecting larval behavior with specific patterns of dispersal and onshore settlement remains a major challenge for observational studies (Dudas et al. 2009; Levin 2006; Metaxas and Saunders 2009; Pineda et al. 2010), coupled hydrodynamic-dispersal models illustrate the generally large effect of DVM behavior as compared to passive Lagrangian behavior (Aiken et al. 2011; Guizien et al. 2006; Marta-Almeida et al. 2006; Ospina-Alvarez et al. 2012). Observational studies of near-shore larval distribution in upwelling ecosystems indicate that diel variation in the vertical position of competent, i.e. ready-to-settle, larvae can largely determine whether they remain near-shore or are swept offshore (dos Santos et al. 2007; Marta-Almeida et al. 2006; Morgan et al. 2009a, 2009b; Poulin et al. 2002; Shanks and Brink 2005; Shanks and Shearman 2009). Proximity to shore, where adult habitat is found, is necessary for successful settlement of competent larvae and, therefore, mechanisms that allow these late larval stages to remain close to shore could be under strong selection (Poulin et al. 2002; Shanks 1986). If DVM plays a role in near-shore retention of competent larvae under some predictable set of hydrographic conditions, one would expect a large number of species to exhibit this behavior. Indeed, a great number of benthic marine species do exhibit DVM, but not all of the species examined display this behavior (dos Santos et al. 2007; Marta-Almeida et al. 2006; Tapia et al. 2010). Since DVM and other behaviors that affect vertical distribution patterns may be adaptations for foraging, accelerating development, avoiding predators, and/or altering transport trajectories, these behaviors are likely to vary among species and through ontogeny within a species (Hays 1995). Moreover, there is evidence that DVM is not a fixed, characteristic attribute of a given species and larval stage, but a highly plastic behavior that is modulated by multiple environmental factors (e.g. Carriker 1951; Benneth et al. 2002; Escribano et al. 2009; Miller and Morgan 2013; Morgan et al. 2012; Morgan et al. 2014; Queiroga and Blanton 2004; Rawlinson et al. 2004). For example, for some zooplankton species vertical migration through the water column is constrained by salinity gradients and current velocities (Carriker 1951), oxygen concentration (Criales et al. 2007; Escribano et al. 2009), temperature gradients (Brinton 1967; Gerritsen 1982), the presence of predators (Loose and Dawidowicz 1994), or turbulence (Fuchs and DiBacco 2011; Lagadeuc et al. 1997; Weidberg et al. 2015). Therefore, key parameters for understanding larval dispersal and connectivity, as well as successful onshore settlement, include: the average depth at which the larvae of different species are found in the water column; whether they undergo diurnal, ontogenetic, or other regular changes in their

vertical distribution; and how robust their vertical movements might be in the face of environmental variability.

Here, patterns of vertical and cross-shore distribution are described for the most common barnacle and mussel species found in the rocky intertidal zone of the central coast of Chile. As adults, these intertidal species engage in direct and indirect interactions that have been amply documented (Castilla 1999; Kefi et al. 2015; Navarrete et al. 2010), but knowledge of their larval ecology is still limited. Larval stages of barnacle and mussel species on other shores of the world have been the subject of many field and laboratory studies since the late 1950's (e.g. Barnes 1956; Bayne 1964; Crisp 1955; Hoffman et al. 2012; Pineda 1999; Shanks and Shearman 2009), most of them directed towards understanding the settlement process, but some also to document larval distribution in the water column. Results from these studies indicate that vertical distributions of barnacle and mussel larvae, and whether or not they perform DVM, are both species- and stage-specific (e.g. Garland et al. 2002; Govindarajan et al. 2015; MacTavish et al. 2016; Porri et al. 2006; Poulin et al. 2002; Tapia and Pineda 2007). Still, the understanding of how variability in near-shore conditions may affect the behavior, vertical distribution, and transport of these larvae in near-shore waters is incomplete. Since previous studies suggest that larvae of these species are found in greater numbers near the shore (e.g. Hoffman et al. 2012; Navarrete et al. 2015; Shanks and Shearman 2009; Vargas et al. 2006), the main objective of this study is to characterize vertical distribution and diel vertical migration in competent larval stages of mussel and barnacle larvae within the inner-shelf. Circulation in the inner-shelf can be extremely complex, since it is affected by topography and multiple sources of local physical forcing (e.g. tides, sea breezes, river plumes, surface and internal waves) that produce high-frequency and vertically-structured flows (e.g. Bonicelli et al. 2014; Lentz and Fewings 2012; Pfaff et al. 2015; Sobarzo et al. 2010; Vargas et al. 2006, 2004; Woodson et al. 2007). Therefore, an attempt was made to relate larval vertical distribution and DVM to predominant physical conditions during the surveys. To this end, stratified samples at 10 stations within the first 3 km from shore were conducted at El Quisco, Chile, on multiple occasions, day and night, and measured prevalent physical conditions.

## 2. Materials and methods

### 2.1. Study area

All surveys were conducted in El Quisco, Chile (33°23'38"S 71°41'55"W), a stretch of the coast characterized by a narrow continental shelf (10–20 km), moderate influence of upwelling winds (Narváez et al. 2004; Nielsen and Navarrete 2004), comparatively high chlorophyll concentrations in near-shore waters (Wieters et al. 2003), and little to no influence of freshwater plumes (Narváez et al. 2004).

### 2.2. Data collection

#### 2.2.1. Near-shore surveys

Paired day/night zooplankton surveys were conducted in front of El Quisco Bay (Fig. 1) on 4 different spring and summer dates (Table 1) aboard the research boats *Megalodon* and *Ilán*, of the Estación Costera de Investigaciones Marinas (ECIM) at Las Cruces, Chile. Two transects perpendicular to the coast, with a total of 10 stations, were sampled during the day and night. Daytime/nighttime surveys were completed/started at least an hour before/after sunset. Rough seas sometimes altered this design, especially the night surveys (Table 1), so not all 10 stations were sampled on all sample dates. At each station, vertical zooplankton tows were conducted in 10-meter depth bins using a 0.5 m diameter closing net with 65 µm mesh. It is important to acknowledge that small changes in vertical position will probably be missed with the coarse binning, but comparatively moderate (few meters) to large (10's meters) changes should be well captured. Zooplankton samples

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