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Temporal and spatial variation in the distribution of epineustonic competent larvae of *Concholepas concholepas* along the central coast of Chile

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ABSTRACT: The abundance of competent epineustonic larvae of the gastropod *Concholepas concholepas* (Gastropoda: Muricidae) in nearshore waters at 2 sites along the central coast of Chile was examined through monthly plankton tows from July 1999 to June 2000. Larvae were found in plankton collections from July 1999 to February 2000 with maximum abundance in September and October. Settlement in artificial collectors deployed onshore on the lower intertidal zone showed the same unimodal pattern with a settlement peak during October and November. Variation in larval distribution among sampling dates was related to the occurrence of north-south winds. We found that *C. concholepas* larvae were more abundant closer to shore after moderate southerly wind periods than on calm days, probably because of the shoreward advection of the upper sea surface layer. While sampling during a strong coastal upwelling event (produced by strong southwesterly winds), *C. concholepas* larvae were only found in the upwelled waters between the front and the coast. This unusual pattern contrasts with what would be expected for typical epineustonic larvae, suggesting the existence of a mechanism of transport or retention by which *C. concholepas* larvae stay near coastal settling areas, thus avoiding offshore dispersion.

KEY WORDS: *Concholepas concholepas* · Larval distribution · Settlement · Upwelling · Wind speed

INTRODUCTION

For many coastal benthic invertebrates, dispersive planktonic larvae represent a critical phase in their life cycle (Thorson 1950). Settlement, defined here as the transition between the planktonic larval phase and life in the benthos, is followed by recruitment, i.e. the incorporation of new individuals into benthic populations. Settlement is determined by the interaction of larval characteristics (i.e. developmental mode, larval duration) with oceanographic and geographic factors (i.e. coastal circulation and coast-line configuration) (Archambault & Bourget 1999). In contrast to terrestrial plants, for which seed dispersal patterns are generally inversely proportional to the distance from the parental sources (Nathan & Muller-Landau 2000), it is thought that marine benthic invertebrate larvae are transported extensively by ocean circulation away from the parental population, thereby decoupling local reproduction from recruitment (Strathmann 1990, Caley et al. 1996). When released, planktonic larvae of intertidal and subtidal species are first driven by coastal currents and then possibly transported by the general oceanic circulation, sometimes over long distances (Mileikovsky 1968, Scheltema 1971, 1986). During this period, ranging from a few days to several months, losses due to predation or competition for food are common (Sale 1990). The onshore migration of competent larvae back to the adult habitat is a critical period because regional or local oceanographic events, as well as coastline configuration, may determine the number of settlers and therefore the success of the benthic population (Archambault & Bourget 1999, Incze

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et al. 2000, Shanks et al. 2000). Coastal oceanic frontal features, generated, for example, by internal waves or upwelling dynamics, can play an important role in the horizontal advection of larvae into coastal sites (Kingsford 1990, Pineda 1991, 1999, Shanks 1995, Shanks et al. 2000). At the local scale, small physical and biotic environmental heterogeneity will determine settlement patterns (Eckman 1983, Bourget et al. 1994, Miron et al. 1996, Guichard & Bourget 1998, Incze et al. 2000, Jeffery & Underwood 2000, Navarrete & Wieters 2000). These characteristics, in which local populations receive propagules from distant sites, has led to the assumption that populations of benthic marine species with planktonic larval phase are open (Gaines & Roughgarden 1985, Roughgarden et al. 1985, 1988, Possingham & Roughgarden 1990, Caley et al. 1996). An important consequence of such an open population structure is that settlement rates are highly variable and usually unpredictable in space and time. Therefore, quantifying patterns of spatial and temporal variation in settlement as well as identifying the processes responsible for such variation has become a central issue in marine ecology.

Because of its high economic value and the important ecological role it plays in intertidal and subtidal communities, the muricid gastropod Concholepas concholepas (Bruguière 1789), locally known as 'loco', has been intensively studied in the past 2 decades along the coast of Chile (Castilla & Durán 1985, Moreno et al. 1986, Durán & Castilla 1989, Power et al. 1996, Castilla 1999, 2000). Consumed by humans since prehispanic times (Jerardino et al. 1992), this species has suffered from increasing exploitation since the mid-1970s. At the beginning of the 1980s, it became the largest gastropod fishery in the world (FAO 1982, Castilla & Jerez 1986). However, at the same time, signs of it being strongly overexploited were detected (Castilla 1995, Castilla & Fernández 1998).

The known geographic distribution of Concholepas concholepas extends from central Peru to Cape Horn including the Juan Fernández Archipelago (Beu 1970, Stuardo 1979). Adult individuals live on rocky bottoms in the intertidal and subtidal zones down to approximately 30 m in depth. This species is one of the top predators in these systems, consuming a variety of sessile filter feeders such as barnacles, mussels and tunicates (Castilla et al. 1979, Guisado & Castilla 1983, Moreno et al. 1986). In central Chile, C. concholepas females lay egg capsules on low intertidal and shallow subtidal rocky surfaces during the fall months (Manríquez & Castilla 2001). After approximately 1 mo of intracapsular development, small veliger larvae (ca. 260 µm) are released and spend the next 3 mo in the water column (Gallardo 1979, DiSalvo 1988). There is evidence suggesting that C. concholepas veligers stay near the bottom during at least the first week of development, thereby probably decreasing dispersion (Moreno et al. 1993). Once the larvae become competent, they dwell at the sea surface feeding on plankton until they metamorphose on rocky intertidal and shallow subtidal bottoms. Settlement of the epineustonic competent lipped veligers has been well documented in the low intertidal zone, where newly settled individuals are generally found associated with small barnacles and mussels (Castilla et al. 1979, Gallardo 1979, Guisado & Castilla 1983, Rivas & Castilla 1987, Stotz et al. 1991). Although settlement has not been quantified in the subtidal zone, newly settled C. concholepas have been found at depths of up to 30 m (Arias 1991, Stotz et al. 1991, Moreno et al. 1993).

Although the developmental sequence of Concholepas concholepas larvae is well known, little has been done to understand their spatial distribution, especially in water masses near the coast. During the past decade, 2 studies have investigated the relationships between local wind forcing, large-scale oceanographic phenomena such as El Niño Southern Oscillation (ENSO), and C. concholepas settlement (Moreno et al. 1993, 1998). Evidence from these studies suggests that settlement of C. concholepas could be related to the dynamics of local surface winds over the ocean. The authors hypothesize that alternate sequences of southerly and northerly winds that generate successive upwelling and relaxation events, respectively, may be the principal mechanism by which competent larvae of C. concholepas are advected towards the shore. This onshore transport mechanism may be disrupted by events such as El Niño and La Niña, apparently explaining the species recruitment failure observed during El Niño phenomena (Moreno et al. 1998).

In this study, we primarily attempt to investigate the physical aspects that are most likely to affect the spatial distribution of competent larvae of Concholepas concholepas in waters adjacent to the shore (<5 km), and which might be related to the subsequent patterns of local recruitment. Specifically our objectives were to investigate in nearshore environments: (1) the annual variation in the abundance of larvae and newly settled individuals; (2) the spatial variation of larval abundance among sampling dates (monthly) in relation to hydrographic factors, such as wind stress and water column temperature; and (3) the pattern of distribution and abundance of larvae during a strong upwelling event.

MATERIALS AND METHODS

Study sites and sampling design. From July 1999 through June 2000, surface zooplankton samples were