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Avoiding offshore transport of competent larvae during upwelling events: The case of the gastropod *Concholepas concholepas* in Central Chile

Abstract—The coast of central Chile is characterized by the occurrence of coastal upwelling during the austral spring and summer seasons, which probably has important consequences for the cross-shelf transport of larval stages of many species. Three cruises were conducted off the locality of El Quisco during upwelling-favorable wind periods to determine the surface distribution of epineustonic competent larvae of the gastropod *Concholepas concholepas* during such events. Contrary to the predictions of a traditional model, where neustonic-type larvae are transported offshore under such conditions, competent larvae of this species were exclusively found in the area between the shore and the upwelling front. Two additional cruises were conducted during calm periods to determine diel variation in the vertical distribution of *C. concholepas* competent larvae. The absence of competent larvae at the surface during early night hours suggests a reverse vertical migration. Thus, the retention of *C. concholepas* competent larvae in the upwelled waters could be the result of the interaction between their reverse diel vertical migration and the typical two-layer upwelling dynamics.

Over the past two decades, oceanographers and marine ecologists have dedicated intensive efforts to determining the links among physical oceanography, larval distribution, and their dispersal and subsequent recruitment to adult habitats. Most of these studies have demonstrated the relationship between the supply of competent larvae and temporal and spatial variability in settlement of invertebrate species (e.g., Roughgarden et al. 1988; Young 1997). Results from these studies have led to the belief that larval advection mechanisms are key factors explaining the dynamics of nearshore benthic populations of invertebrates with pelagic larval stages (Roughgarden et al. 1988; Botsford et al. 1994). In this context, and perhaps with the exception of some late larval stages of fish and crustaceans (Luckenbach and Orth 1992; Stobutzki and Bellwood 1997), it is generally considered that larval horizontal swimming capability is of minor impor-

tance regarding larval transport (Shanks 1995) and that net transport is essentially driven by the interaction of physical oceanic processes and the vertical distribution of larvae in the water column (Roughgarden et al. 1988; Shanks 1995). Several cross-shelf larval transport processes have been identified on different coasts of the world, including wind drifting, onshore propagating tidal waves and bores, and upwelling fronts moving onshore during relaxation. Along eastern ocean boundary conditions, like those found on the Pacific coasts of South and North America and the Atlantic coast of Africa, coastal upwelling forced by equatorward winds is a dominant oceanographic feature (Strub et al. 1998). Thus, it is expected that upwelling conditions will exert a strong influence on the cross-shelf transport of larval stages of many species on these coasts. Indeed, simulation and field studies have shown the importance of Ekman-driven circulation on larval transport and their subsequent settlement (Roughgarden et al. 1988; Shanks 1995; Brubaker and Hooff 2000). The position of larvae in the water column determines the net transport they undergo. Neustonic larvae are first advected offshore by Ekman transport, concentrated by the upwelling front, and then driven back toward the coast during the relaxation phase of the event, causing a settlement pulse (Wing et al. 1995; Shanks et al. 2000).

Many holoplanktonic species undergo daily vertical migrations (Thorson 1964; Mileikovsky 1973; Forward 1988), a pattern also shown by pelagic larval stages of some fish and invertebrate species (e.g., fish, Forward et al. 1996a,b and crustacean, Shanks 1986). The most common diel vertical migration type (DVM) corresponds to a deeper distribution of larvae during daytime and surfacing at night (Richards et al. 1996). However, in some cases, planktonic organisms follow a reverse pattern with nocturnal descent (Ohman et al. 1983 and references therein). Besides DVM, other characteristics such as larval buoyancy and sinking or swimming behavior can interact with water mass movements

in shallow stratified seas, thus affecting their horizontal transport. Such interactions have been demonstrated through simulations (Botsford et al. 1994; Hill 1998) and field studies. The later have mostly been concerned with tidal currents in estuarine systems (e.g., Forward et al. 1996a) but also with open coast wind-driven systems (Shanks 1986; Blanton et al. 1995).

Like other eastern boundary current systems, central Chile is characterized by the occurrence of coastal upwelling, with maximum upwelling-favorable winds (south and southwest) during the austral spring and summer months. Winds are intermittent, with periods of 3–10 d, producing alternating upwelling and relaxation conditions (Strub et al. 1998). In central Chile, upwelling is mostly confined to a narrow extension from the coast, compared with those found in many other midlatitudes (Strub et al. 1998).

The gastropod *Concholepas concholepas* (Bruguière 1789), locally known as “loco,” is the most studied marine invertebrate species in Chile (Castilla 1988). Because of its economic value and ecological importance as a top predator, numerous studies have been conducted to describe the life-cycle ecology and to understand the population dynamics of this species. Adults live on rocky bottoms in the intertidal and subtidal zones down to ~40 m in depth. In central Chile, female *C. concholepas* lay egg capsules on low intertidal and shallow subtidal rocky surfaces during austral fall months (Manríquez and Castilla 2001). After ~1 month of intracapsular development, small planktotrophic veliger larvae (~260 μm) are released and spend the next 3 months in the water column (DiSalvo 1988). Once the larvae become competent, they dwell at the sea surface until they settle on rocky intertidal and shallow subtidal habitats down to 30 m deep (Stotz et al. 1991; Moreno et al. 1993; Martínez and Navarrete 2002). Studies elsewhere have shown that epineustonic competent *C. concholepas* larvae are rare components of the coastal surface plankton of Chile (Moreno et al. 1993; Poulin et al. 2002).

Although the developmental sequence of *C. concholepas* larvae is well known, little is known about the distribution and transport processes of the different larval stages, particularly about the pelagic-benthic transition. Recent studies have documented the existence of a positive relationship between *C. concholepas* settlement and upwelling intensity index in southern Chile (Moreno et al. 1998) and the possible influence of upwelling events on the distribution of competent larvae in nearshore waters (Poulin et al. 2002). Moreover, a recent study showed the absence of competent larvae in coastal surface waters during night tows, which contrasted with their abundance during daylight hours and suggested that this larval stage could undergo vertical migration (Poulin et al. 2002). In this study we investigate the spatial distribution of *C. concholepas* competent larvae during upwelling events, characterize diel changes in the abundance of competent larvae in the water column, and propose a transport model that would allow competent larvae to remain nearshore during upwelling events.

Study site and sampling grid—Surface zooplankton samples were collected off El Quisco (33°23′48.9″S, 71°41′40.5″W) in the central coast of Chile. Plankton sam-

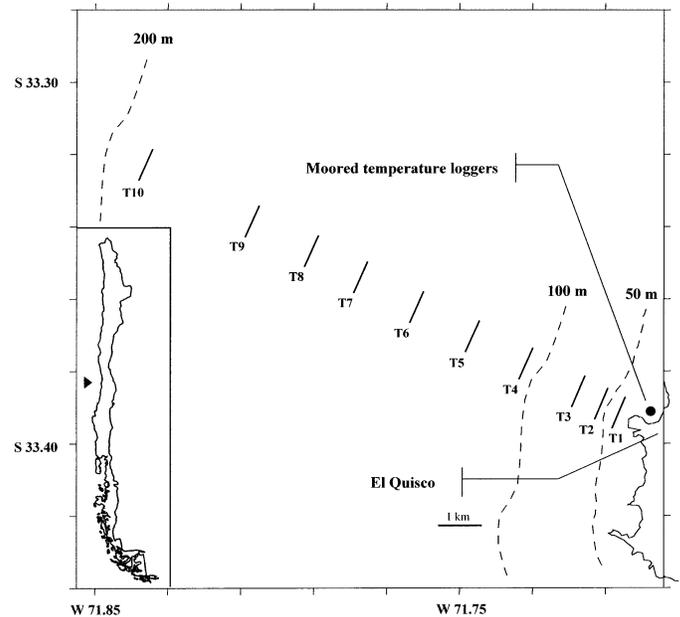


Fig. 1. Grid sampling design off El Quisco. Transects are 1 km in length. The distance of transects from the shore is 0.5 km for T1, 1 for T2, 2 for T3, 4 for T4, 6 for T5, 8 for T6, 10 for T7, 12 for T8, 14 for T9, and 18 for T10. Broken lines represent the 50, 100, and 200 m isobaths. The dark circle indicates the location of moored temperature loggers.

ples were preserved in a 5% buffered formaldehyde seawater solution and larvae were then identified and counted in the laboratory under a dissecting scope. The field sampling scheme used throughout this study consisted of 1 km long transects parallel to the coastline and ranged from 0.5 to 18 km from the shoreline (Fig. 1).

Three surveys were conducted during strong equatorward wind periods: 5 November 1999 when transects T2, T3, T4, T5, T6, T7, and T8 were visited (see Fig. 1), 25 September 2000 (transects T2, T3, T4, T5, T6, T7, T8, T9, and T10), and 6 October 2000 (transects T2, T3, T4, T5, T6, T7, T8, and T9). Samples were collected by use of a floating neustonic net (700 μm mesh size), specially designed to collect premetamorphic larvae of *C. concholepas* in the top few centimeters of the water column (DiSalvo 1988; Poulin et al. 2002). Because the rectangular mouth of this net (0.8 \times 0.4 m) is not totally submerged and because competent *C. concholepas* larvae are suspended in the first centimeters of the water column, larval abundance were simply expressed as number of larvae per kilometer towed. For each transect, towed distance was directly measured from a flow meter attached to the net.

Two extra cruises were conducted to determine diel variation in the vertical distribution of *C. concholepas* competent larvae. These cruises took place during calm periods to minimize the possible effect of physical mixing of the water column on larval behavior, and consisted of samples every 1.5–2 h along transects T1 and T3 (Fig. 1) during the day-night transition (from 1300 to 2200 h) on 23 October 2000 and transects T2 and T3 during the night-day transition (from 0100 to 1000 h) on 11 November 2000. To look for

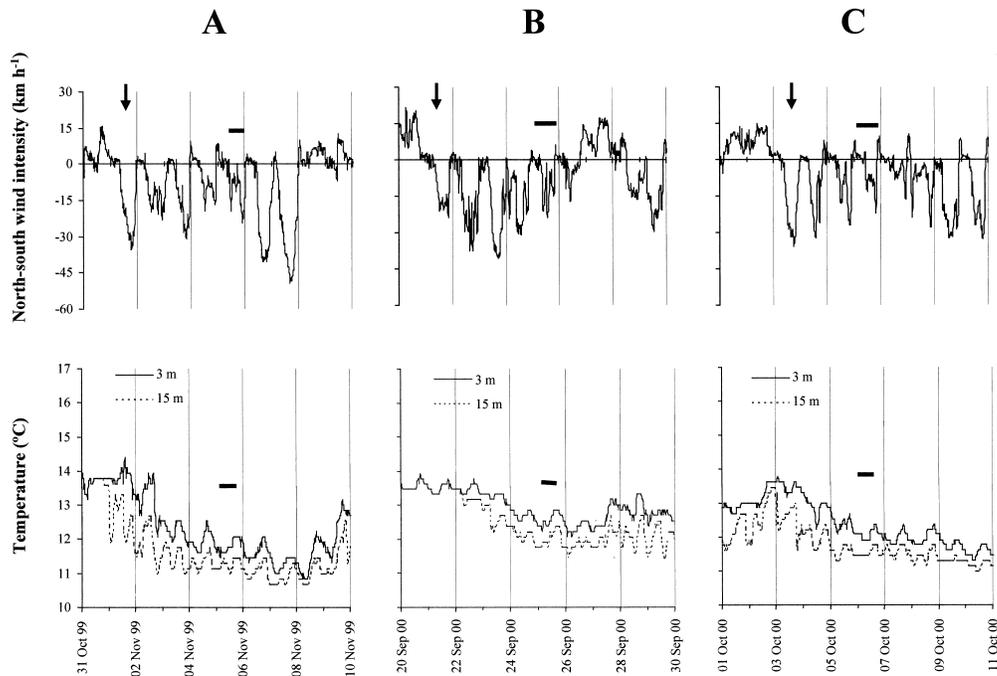


Fig. 2. North-south wind speed (top panels) and 3 and 12 m depth temperature (bottom panels) registered during the three upwelling-favorable wind episodes corresponding to (A) 11 November 1999, (B) 25 September 2000, and (C) 6 October 2000 cruises. Arrows indicate the beginning of equatorward wind periods. Sampling hours are highlighted by dark lines.

the presence of competent larvae in subsurface waters, two nonclosing conical nets (0.7 m diameter and 350 μ m mesh size) were towed at 5 and 15 m depth along with the neustonic net described above.

Hydrography—Wind speed and direction data were recorded as vector averages every 10 min by a Campbell meteorological station located onshore at the Estación Costera de Investigaciones Marinas of Las Cruces, 15 km south of El Quisco. Sea water temperature was measured at 30-min intervals, at 3 and 12 m deep with temperature loggers (Stow Away Tidbits, 0.2°C precision) moored at \sim 150 m from the shoreline off El Quisco (Fig. 1). During all surveys, surface to 25-m deep profiles of water column variables (temperature, dissolved oxygen, and salinity) were conducted at the beginning and at the end of each transect by use of a conductivity-temperature-depth meter with an incorporated oxygen meter (Seabird-19). Advanced very high resolution radiometer (AVHRR) satellite images of the study area (32.5–34° S and 74–71° W) were inspected to observe, over a larger scale, the daily variation in sea surface temperature (SST) corresponding to one of the upwelling-favorable wind episodes (1–7 November 1999).

Distribution of *Concholepas* competent larvae during upwelling events—Three cruises took place within periods characterized by the occurrence of strong upwelling favorable winds. Wind patterns showed the typical diurnal cycle observed in central Chile, with maximum intensity after midday and a relatively calm period in the morning. After 2 or 3 d after the intensification of equatorward winds, we

observed a descent of \sim 3°C in the temperature of the water column at El Quisco (Fig. 2).

The SST from satellite images for the period between 1 and 15 November 1999 showed the evolution of this particularly strong upwelling event. During the first 2 d of the 7-d-long southerly wind episode, cold water surged in front of the upwelling centers of Punta Curaumilla and Punta Topocalma, north and south of El Quisco, respectively (Fig. 3A). The following days were marked by a progressive expansion of the coastal area affected by colder waters. The cruise conducted on 5 November 2000 corresponded to the fifth day since the beginning of strong southerly wind conditions and by then colder water right in front of El Quisco was clearly visible in the AVHRR images. The superficial cold water tongue extended \sim 8 km offshore on this date, and the cruise transect extended beyond the visible thermal front (see transect line in Fig. 3B).

Profiles of water column temperature obtained during the three cruises showed that the system was characterized by the presence of colder water below 10–15 m, which reached the surface near the shore (Fig. 4). In all cases, it was possible to identify the presence of a thermal front separating offshore warmer surface water from inshore colder and more saline upwelled water, located at about 8, 6, and 10 km from shoreline during each of the respective cruises (Fig. 4). Although variable in abundance from cruise to cruise, *C. concholepas* competent larvae were found only in recently upwelled waters, between the thermal front created by the upwelling and the shore (Fig. 4). This pattern was particularly evident on the 25 September 2000 cruise, when sam-

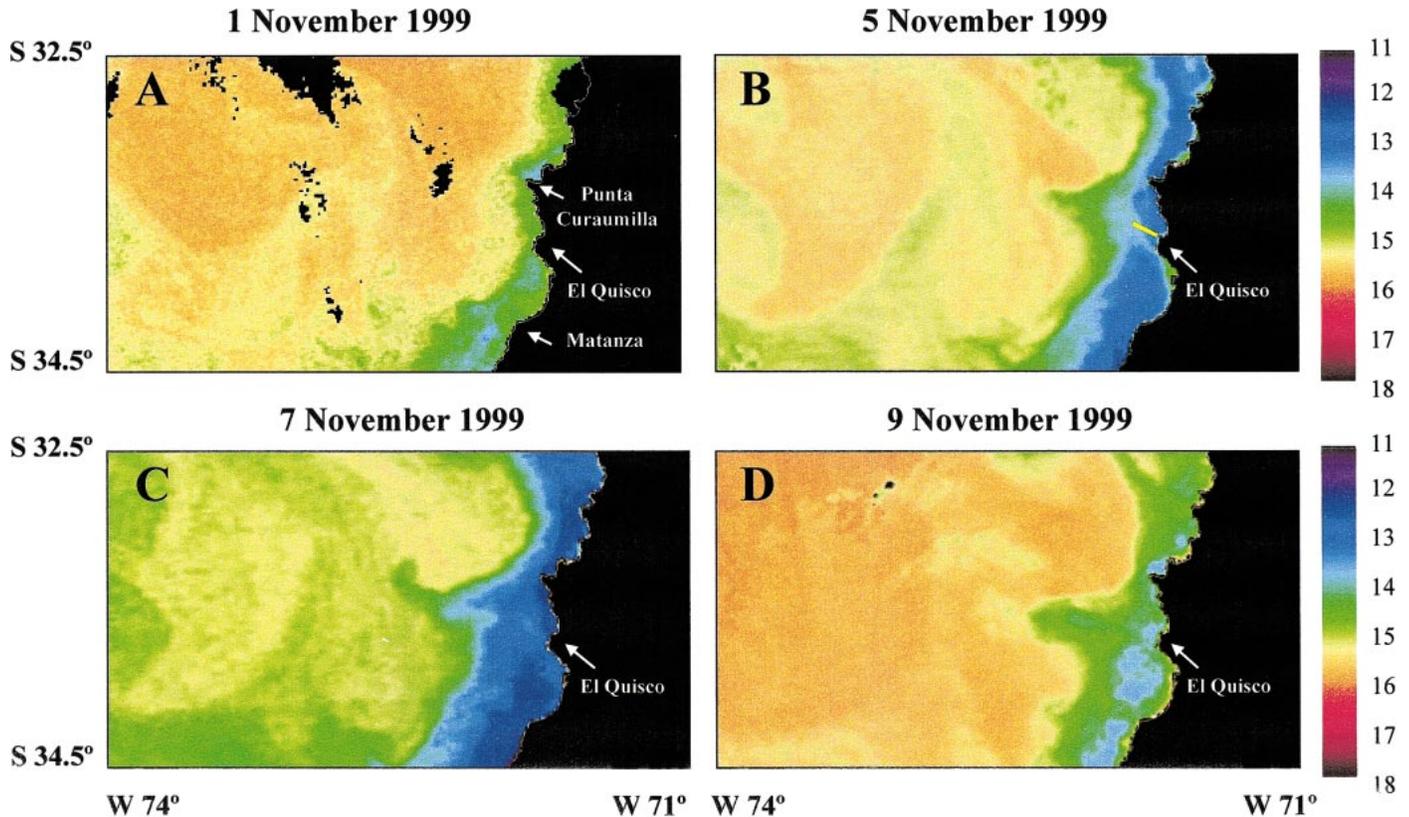


Fig. 3. AVHRR images of sea surface temperature showing the evolution of the November 1999 upwelling event: (A) beginning of the upwelling event showing upwelled cold water around upwelling centers, (B) day when the cruise took place (transects location correspond to the yellow line), (C) maximum extension of the cold upwelled water, and (D) relaxation phase.

pling extended up to 18 km offshore and no larvae were found beyond the front (Fig. 4B).

Day-night variation—The day-night transition cruises conducted in October and November 2000 showed important variation in the larval distribution at the surface during the course of the day. In the case of the day to night sampling conducted on 23 October 2000, peak larval abundance was found in late afternoon, ~1600 and 1700 h in transects T1 and T3, respectively (Fig. 5A). Although larval abundance varied during the course of the day, the presence of larvae during daylight hours contrasted with their absence in night samples. A similar pattern was observed during the night to day sampling conducted on 11 November 2000, when competent larvae were absent from the surface at night, between 0130 and 0300 h, but started to appear at the surface before sunrise (Fig. 5B). After sunrise, the abundance of larvae at the surface continuously increased during the course of the morning, reaching a maximum between 0800 and 1000 h, when the cruise was terminated.

Only two competent larvae were found in all the subsurface tows (5 and 15 m deep) that were simultaneously performed during the night-day transition surveys. Both larvae were found on the 11 November 2000 cruise at 15 m deep and around 0200 h in the morning along transect 2.

Discussion—Wind patterns, water column structure and satellite images confirmed the occurrence of wind-driven up-

welling of cold water within the spatial and temporal domain of our observations. These upwelling events are common in this region and have been studied from different perspectives (Johnson et al. 1980; Strub et al. 1998), but so far few studies had shown upwelling activity in waters so close to the shore. Surface temperature from satellite images showed that upwelling usually initiates around southern and western ends of capes, where the coastline is oriented in a predominantly north-south direction (see also Johnson et al. 1980; Strub et al. 1998).

During upwelling events, *C. concholepas* competent larvae were exclusively found in the recently upwelled cold waters, between the upwelling front and the shore. Larvae were not concentrated at the cold side of the front but were distributed rather homogeneously within the upwelled waters. This pattern is not in accordance with the general model proposed by other authors for epineustonic larvae of invertebrates and fish along the Pacific and Atlantic coasts of North America (Fig. 6A) (Wing et al. 1995; Brubaker and Hooff 2000; Shanks et al. 2000). Those studies have shown that epineustonic larvae are usually advected offshore by the displaced surface mixed layer and are therefore found in the warm side of the upwelling front. Considering the poor horizontal swimming capability of *C. concholepas* larvae, it is unlikely that they would be able to cross the upwelling front, swimming against the Ekman surface current along the surface. Therefore, it is possible that vertical positioning (e.g.,

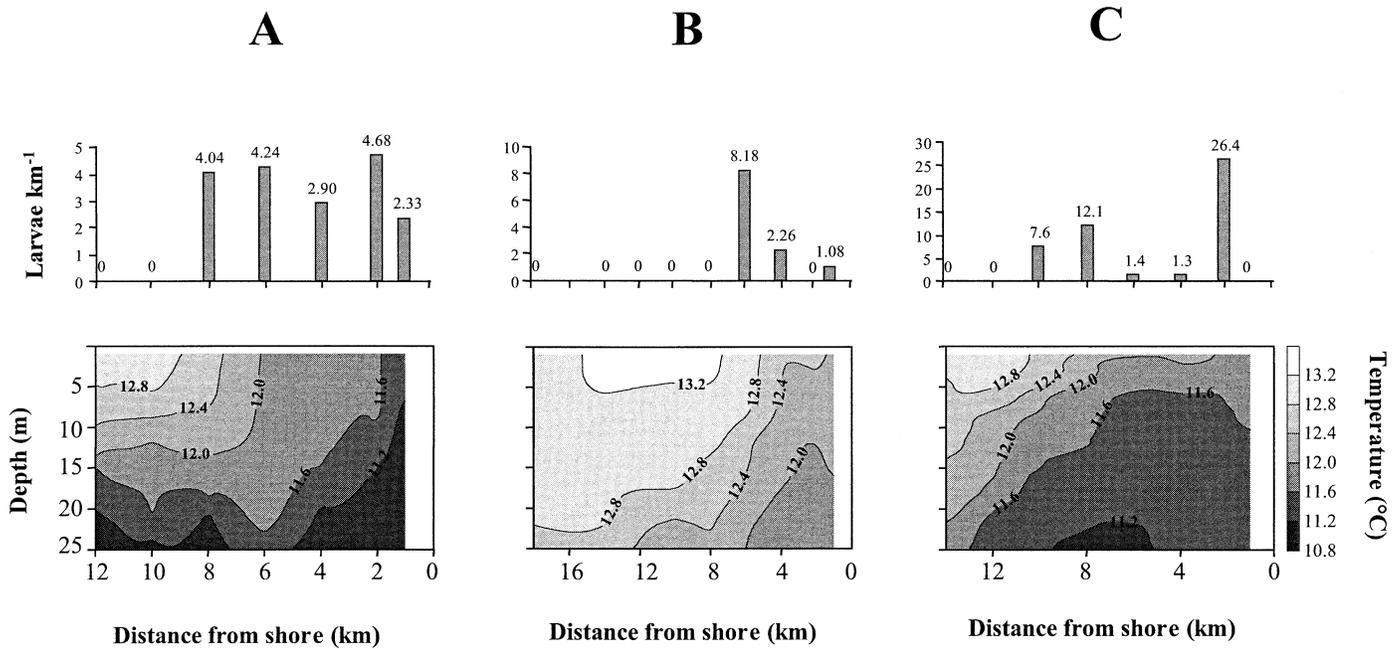


Fig. 4. Water column section showing the distribution of isotherms (bottom panels) and corresponding spatial distribution of competent larvae found at the sea surface (top panels) on (A) 11 November 1999, (B) 25 September 2000, and (C) 6 October 2000.

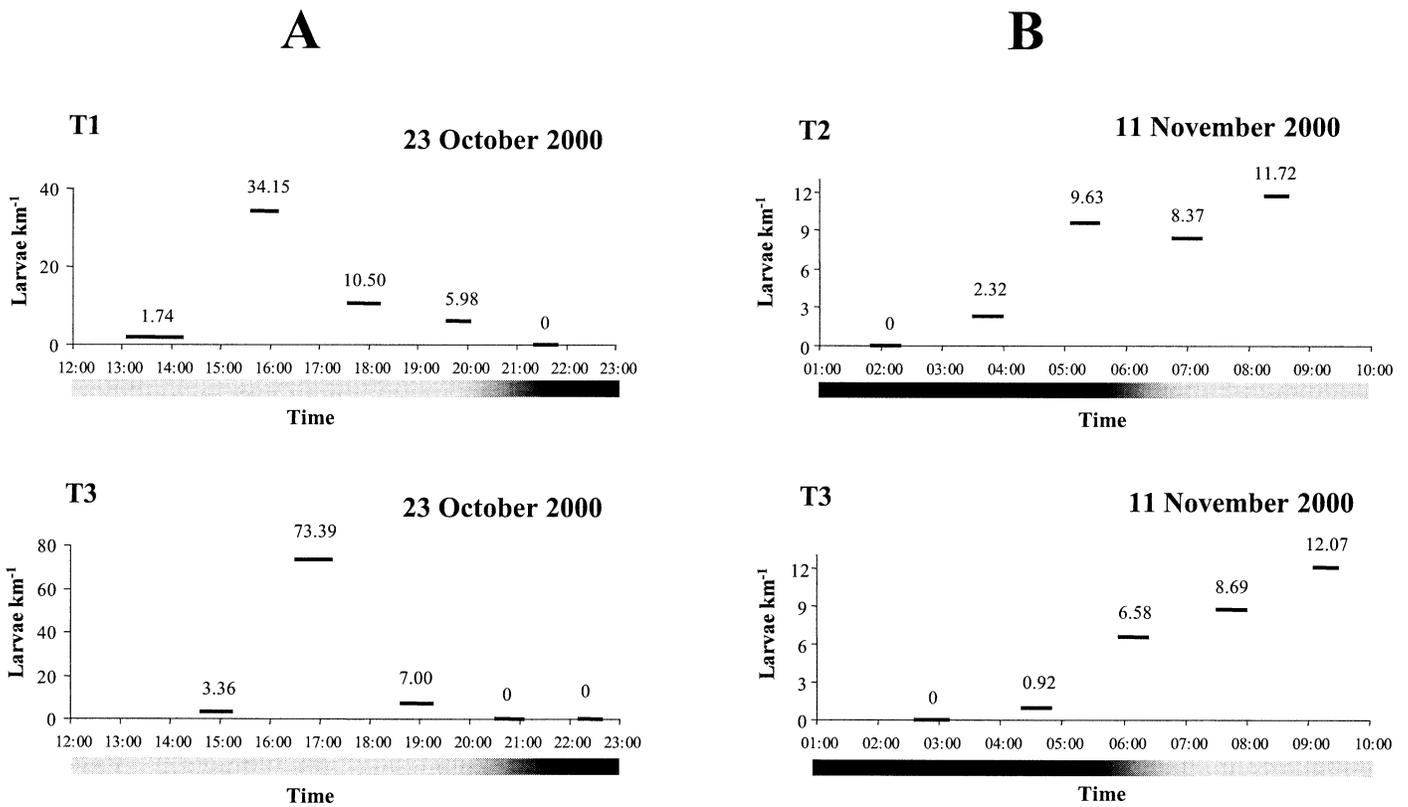


Fig. 5. Temporal variation in the distribution of competent larvae along the surface during (A) day-night and (B) night-day cruises.

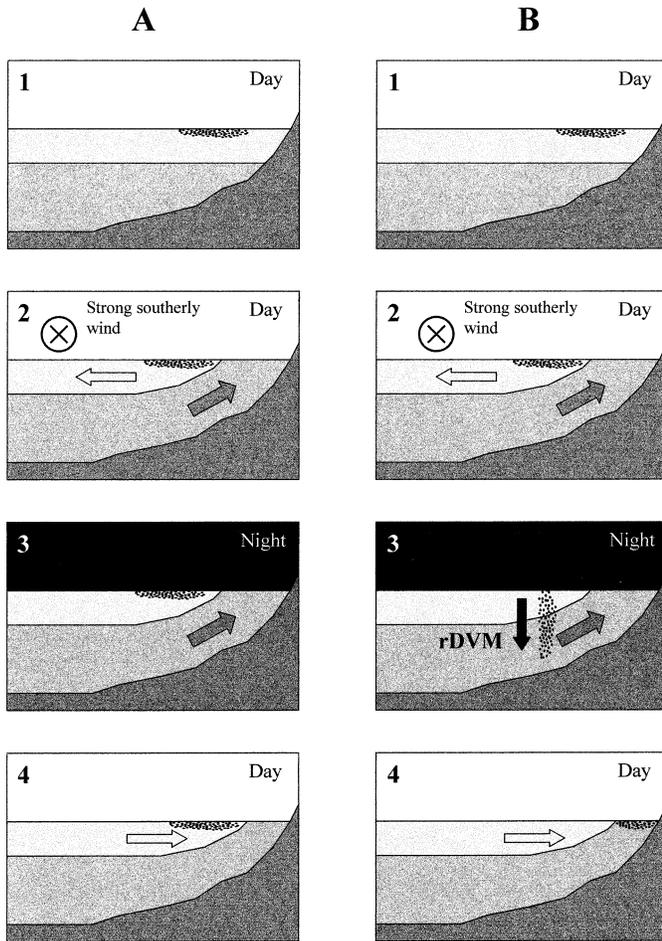


Fig. 6. (A) General model for neustonic larval transport during upwelling: neustonic larvae located at the surface (panel 1) are first advected offshore by Ekman transport, concentrated by the upwelling front (panels 2 and 3), and then driven back towards the coast during the relaxation phase (panel 4). (B) Two-layer model that integrates reverse vertical migration of *C. concholepas* competent larvae, which explains their observed distribution off El Quisco during upwelling.

vertical migration) in the water column could allow larvae to avoid offshore advection during upwelling events.

Although only two competent larvae were collected in the subsurface tows, the absence of larvae along the surface in early night tows suggests that competent larvae of *C. concholepas* can undergo reverse DVM. These results agree well with those of a previous study that covered a larger spatial extent in the same region (Poulin et al. 2002). In that study, the absence of competent larvae on the surface during night cruises contrasted with their presence in the same area during daylight hours. Alongshore horizontal transport beyond the sampling area, as an alternative explanation for the disappearance of larvae from the surface, is unlikely given the stability of the water column through the course of the repetitive tows.

On the 23 October 2000 cruise, the disappearance of larvae from the surface coincided with sunset, which suggests that larval sinking behavior may be a response to variation

in light intensity. A change in daylight is a well-known stimulus for DVM in many marine invertebrate and fish larvae (e.g., Forward 1988; Richards et al. 1996). However, other factors such as chemical cues from predators (Forward and Rittschof 2000) or endogenous rhythms (Forward et al. 1996b) cannot be ruled out. In contrast, the appearance of larvae at the surface was observed a few hours before sunrise (see Fig. 5), which suggests that light might not be the factor triggering the upward migration of *C. concholepas* larvae. The mechanisms by which competent larvae remain at the surface during the day, migrate to deeper waters around sunset, and ascend again before daylight are not yet well understood. However, laboratory and field observations suggest some of the mechanisms that could aid larvae complete DVM. Competent larvae of *C. concholepas* have been reported to use surface water tension to float at the surface and also adhere to floating objects (DiSalvo 1988; authors' pers. obs.). This behavior, as well as the existence of a byssal thread (DiSalvo 1988), could explain their location at the surface during daytime, probably even in the face of moderate to strong wind mixing. Larval distribution under different sea conditions should be further investigated. Recent studies have shown that the development of large chromatophores on larval structures provides an efficient protection against ultraviolet radiation in epineustonic invertebrate larvae (Miner et al. 2000). In addition to their dark and thick larval shell, chromatophores are well developed in the foot of *C. concholepas* competent larvae (DiSalvo 1988), which might help protect competent larvae from harmful UV radiation. The disappearance of competent *C. concholepas* larvae from the surface at sunset may be the result of active downward swimming or rapid sinking by the retraction of the foot and the velum. Free-falling behavior has been observed in *C. concholepas* competent larvae (DiSalvo 1988), echinoderms (Pennington and Emler 1986), fish (Forward et al. 1996b), and bivalve larvae (Manuel et al. 2000). Given the large and thick larval shell, *C. concholepas* larvae most likely drop at sunset by simply retracting the velum and foot. Active swimming and a bubble capture mechanism (DiSalvo 1988) would permit competent *C. concholepas* larvae to reach surface again in the morning.

Reverse DVM can represent a way of circumventing the potentially high mortality rates on settling grounds if predatory invertebrates and especially fishes predominate on suitable benthic habitat during daylight hours (Ohman et al. 1983; Morgan 1995). In shallow waters, reverse DVM in *C. concholepas* competent larvae may thus reduce predation at settlement, which might be particularly important considering that this species exhibits bottom-searching behavior (DiSalvo 1988). Because of the high frequency of upwelling events affecting the central coast of Chile during the months when competent larvae are found in the water, it is expected that the DVM would have important consequences on cross-shelf transport of *C. concholepas* competent larvae. We propose a two-layer model to explain the surface *C. concholepas* larval distribution observed during upwelling events, which in Fig. 6 is contrasted with the transport model described elsewhere for epineustonic larvae. When upwelling-favorable winds begin to intensify, larvae would be first advected offshore as a consequence of Ekman transport of the

surface layer. At night, active or passive downward migration would allow larvae to cross the thermal front (located no deeper than 20–25 m, *see Fig. 4*) and enter into the cold water being upwelled shoreward. The following day, and depending on their initial position, larvae would reach the surface again, on either side of the front. During the course of the upwelling event, the repetitive occurrence of the 24-h migration cycle would lead to a progressive incorporation of larvae in the upwelled water and the retention of larvae between the upwelling front and the shore. The rate at which larvae cross from the warm waters into the cold upwelled waters will vary depending on the surface and bottom current velocities. Considering a general case, when surface offshore current velocity is faster than onshore flow of the bottom layer (e.g., Lentz 1994; Strub et al. 1998), the net displacement of larvae will also be offshore but at a slower rate than that of the front because of the time that larvae spent at the bottom layer during night hours. Thus, larvae would be progressively incorporated into the upwelled zone, but the effectiveness of the mechanism will depend on the offshore surface current velocity, the time spent in each layer, and their initial position. In the case of a faster onshore flow of the bottom layer (e.g., Ramp and Abbott 1998), larvae will undergo a net onshore transport, would be retained between the upwelling front and the coast and would be concentrated near the shore. Thus, the proposed two-layer model and reverse DVM should therefore result in the presence of larvae between the front and the shore under most upwelling conditions, which corresponds well with the observed surface distribution of *C. concholepas* competent larvae on the fourth and fifth days of each of the three upwelling events studied here.

In summary, the interaction between the reverse DVM and upwelling circulation may serve *C. concholepas* larvae to avoid loss of competent larvae by large-scale offshore advection, restricting their distribution to a coastal zone delimited by the upwelling front. Under particular circumstances (see above), this basic mechanism could produce net larval transport onshore, but this effect is expected to be localized and it should vary geographically along with changes in bottom topography (Ramp and Abbot 1998). In most cases, when a two-layer model dominates local upwelling circulation, larvae undergoing DVM (normal or reverse) would be retained in upwelled waters.

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Ultrasonic in situ measurements of density, adiabatic compressibility, and stability frequency

Abstract—An in situ density profile has been measured with an ultrasonic density probe in the mining lake Merseburg-Ost 1b. From the acquired measurements of sound speed and acoustic impedance, the important physical properties of in situ density and adiabatic compressibility could be calculated. It was also shown that these two properties sufficed to determine the stability frequency, which hence becomes a directly observable physical magnitude. Measurements of all magnitudes are presented. Currently the accuracy only suffices to provide new insight in the density structure of natural water bodies in cases of unusual composition of dissolved substances. However, as all required data are acquired in situ and density is measured directly, i.e., without need of empirical

formulations (“equations of state”), the ultrasonic approach has the potential to become a reliable reference for density measurements in limnic waters, when chemical conditions are complex or spatial or temporal variation of dissolved substances becomes relevant for the stability of the water column.

Owing to the variable composition of the dissolved substances, density measurements in inland waters are still hard to acquire at the required accuracy (Schimmele and Herzprung 2000). The oceanographic approach of calibrating temperature and electrical conductivity (via salinity) against