

NOTES

Limnol. Oceanogr., 00(0), 2002, 000–000
© 2002, by the American Society of Limnology and Oceanography, Inc.

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 importance 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 Hoeff 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 latter 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

¹ Present address: Departamento de Ecología Costera, Facultad de Ciencias, Universidad Católica de la Sma. Concepción. Paicavi 3000, Casilla 297, Concepción CP 4073978, Chile.

² Corresponding author (jcastill@bio.puc.cl).

Acknowledgments

We thank the enthusiastic field assistance of F. Veliz, A. Rosson, E. Hernández, and M. Andrade, skipper of the *Barracuda*, for their disposition and expertise. Comments by Alan Shanks and three reviewers helped improve this paper. This research was supported by Proyecto Italia-Chile (CICS-Eula Genova-PUCCH), an Andrew Mellon grant to J.C.C. and S.A.N., and FONDAP O. & B.M. grant to S.A.N. A.T.P. also acknowledges additional financial support from postdoctoral grant FONDECYT 3990032. The paper was completed during the tenure of FONDAP-FONDECYT grant 1501-0001 to the Center for Advanced Studies in Ecology and Biodiversity.

Notes

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 in press). 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. in press).

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. in press). 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. in press). 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 samples 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,

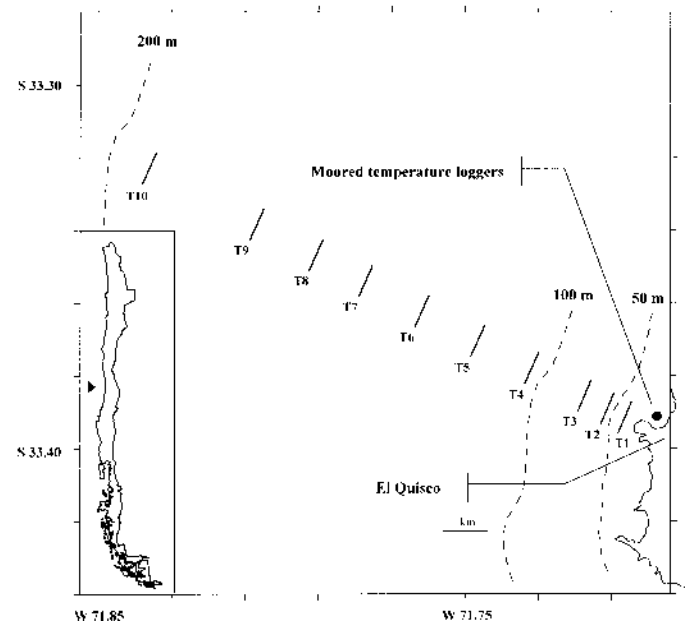


Fig. 1. Grid sampling design off El Quisco. Transects are 1 km in length. The distance of transects from the shore is 0.5 km for T1, 1 for T2, 2 for T3, 4 for T4, 6 for T5, 8 for T6, 10 for T7, 12 for T8, 14 for T9, and 18 for T10. Broken lines represent the 50, 100, and 200 m isobaths. The dark circle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

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. in press). 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 T2 (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 the presence of competent larvae in subsurface waters, two nonclosing conical nets (0.7 m diameter and 350 μm 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

Notes

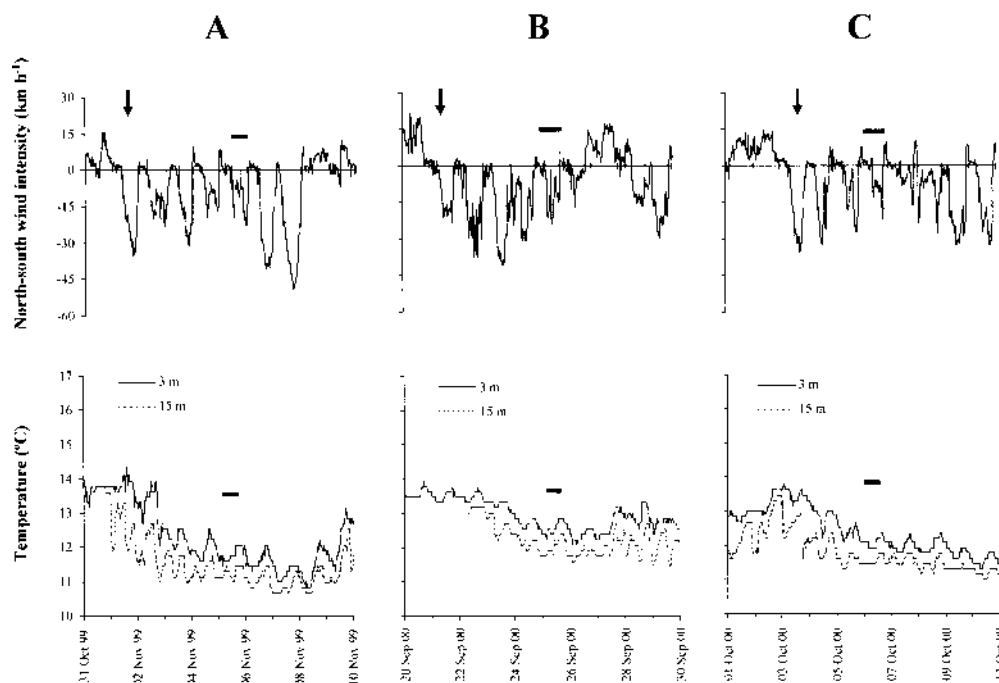


Fig. 2. North-south wind speed (top panels) and 3 and 12 m depth temperature (bottom panels) registered during the three upwelling-favorable wind episodes corresponding to (A) 11 November 1999, (B) 25 September 2000, and (C) 6 October 2000 cruises. Arrows indicate the beginning of equatorward wind periods.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

de Investigaciones Marinas of Las Cruces, 15 km south of El Quisco. Sea surface 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 ~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 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 ~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 ~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 sampling 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 1

Notes

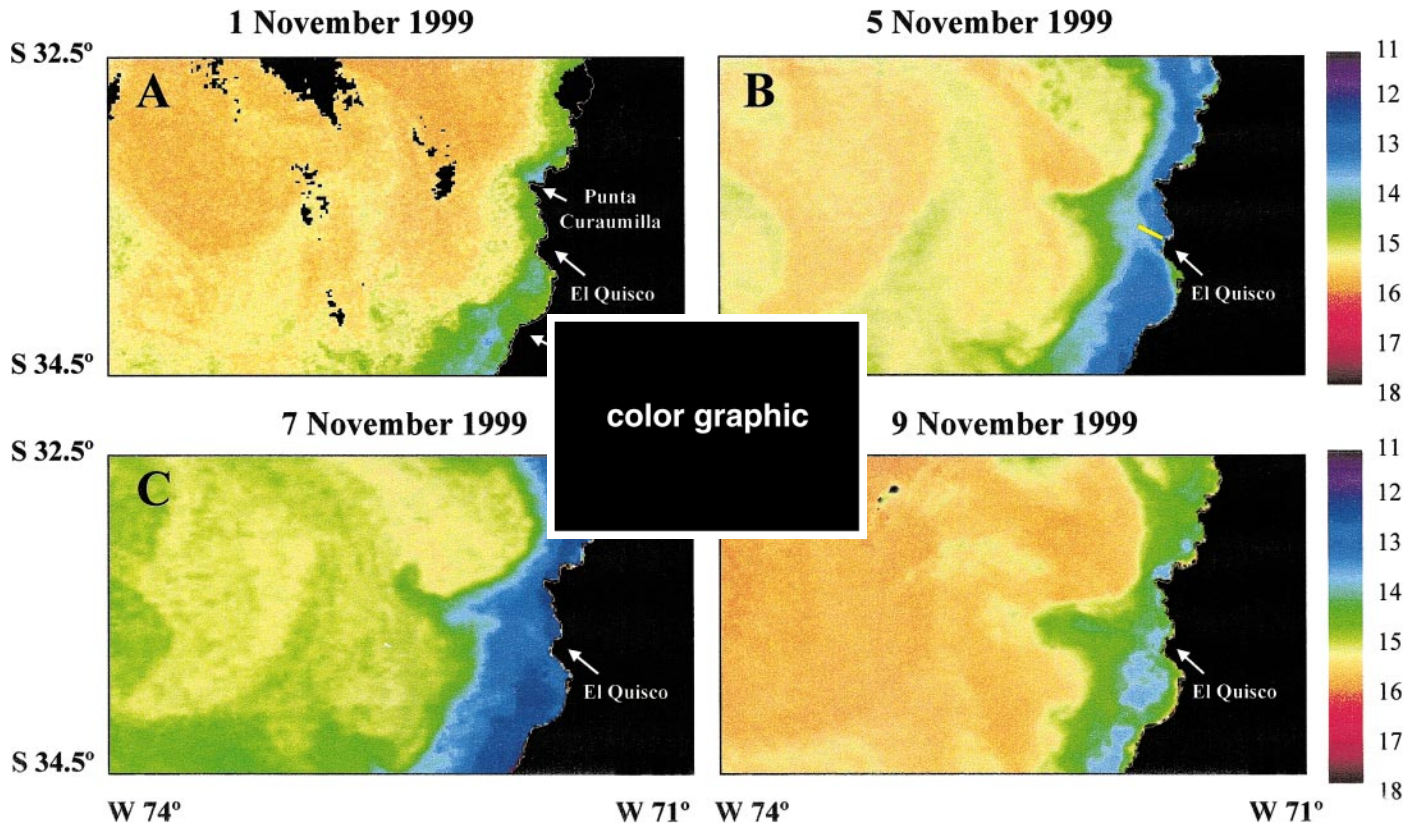


Fig. 3. AVHRR images of sea surface temperature showing the evolution of the November 1999 upwelling event: (A) beginning of the upwelling event showing upwelled cold water around upwelling centers, (B) day when the cruise took place (transects location correspond to the yellow line), (C) maximum extension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

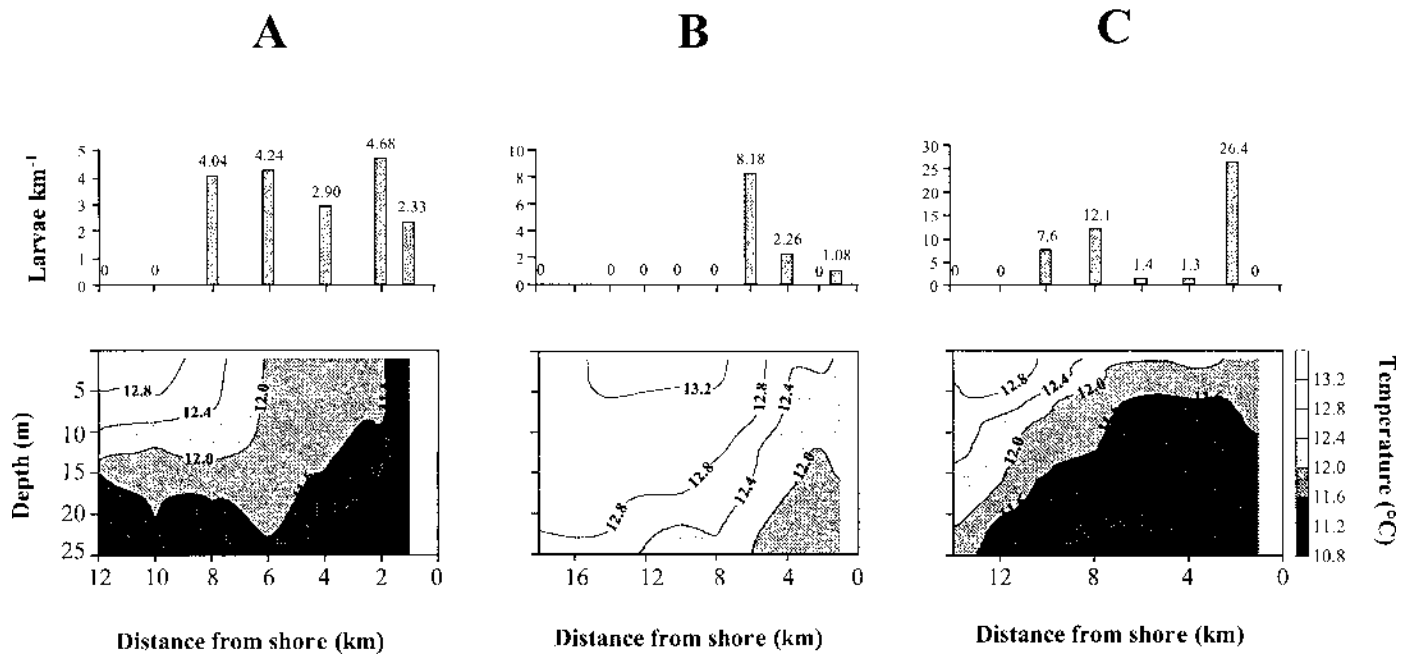


Fig. 4. Water column section showing the distribution of isotherms (bottom panels) and corresponding spatial distribution of competent larvae found at the sea surface (top panels) on (A) 11 November 1999, (B) 25 September 2000, and (C) 6 October 2000.

Notes

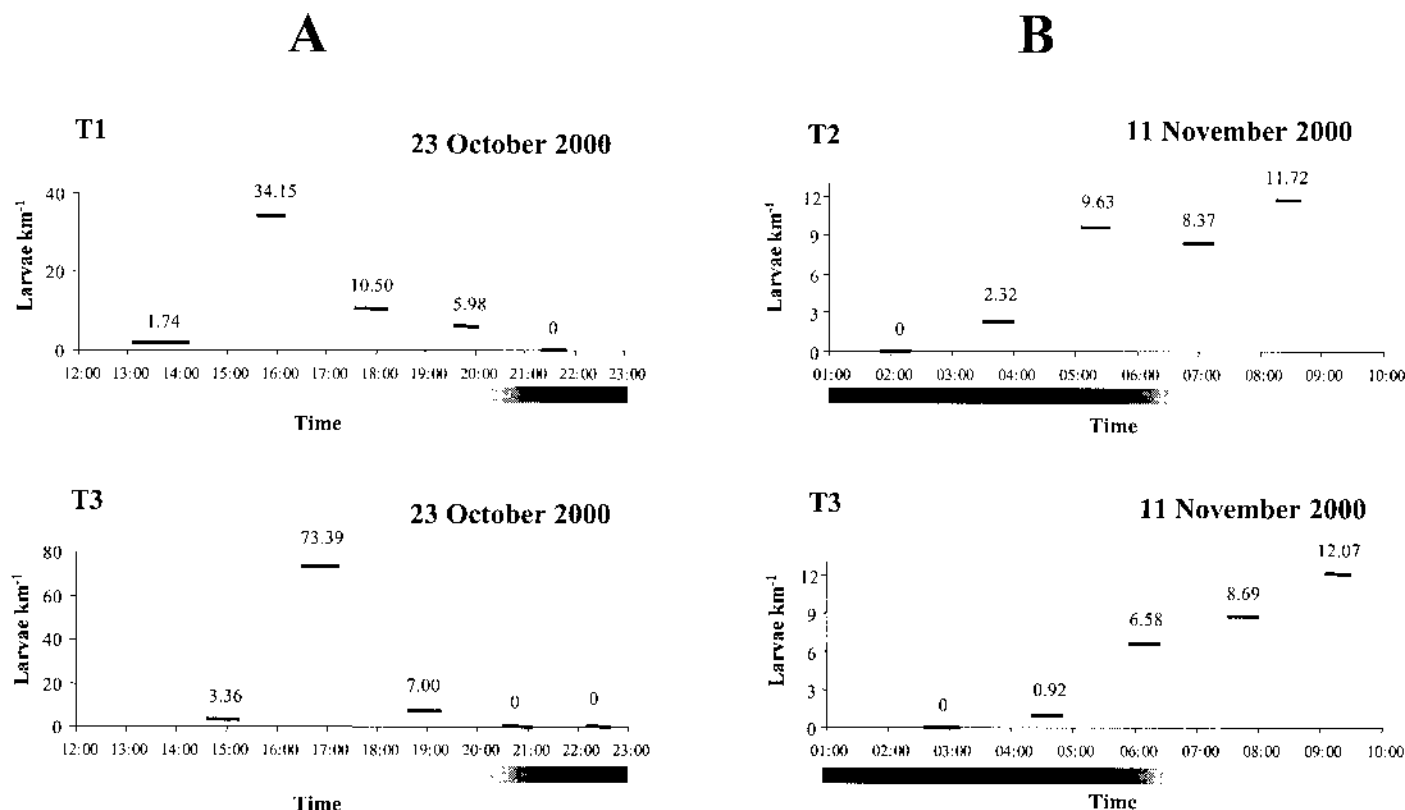


Fig. 5. Temporal variation in the distribution of competent larvae along the surface during (A) day-night and (B) night-day cruises.

and 2, 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 upwelling 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, when 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 lar-

vae 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., 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. in press). 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

Notes

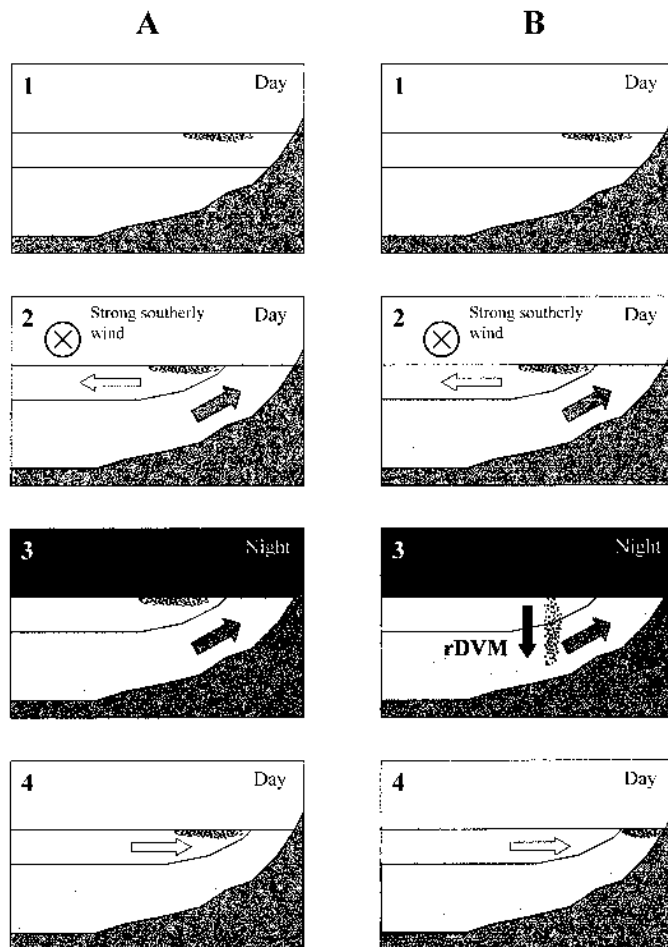


Fig. 6. (A) General model for neustonic larval transport during upwelling: neustonic larvae located at the surface (panel 1) are first advected offshore by Ekman transport, concentrated by the upwelling front (panels 2 and 3), and then driven back towards the coast during the relaxation phase (panel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

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 Emlet 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 off-

Notes

shore 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.

Elie Poulin, Alvaro T. Palma,¹ Germán Leiva,
Diego Narvaez, Rodrigo Pacheco, Sergio A. Navarrete, and
Juan C. Castilla²

Departamento de Ecología and Estación Costera de Investigaciones Marinas Las Cruces
Center for Advanced Studies in Ecology and Biodiversity
P. Universidad Católica de Chile
Alameda 340, Casilla 114-D
Santiago CP 6513677, Chile

References

- BLANTON, J. O., E. WENNER, F. WERNER, AND D. KNOTT. 1995. Effects of wind-generated coastal currents on the transport of blue crab megalopae on a shallow continental shelf. *B. Mar. Sci.* **57**: 739–752.
- BOTSFORD, L. W., C. L. MOLONEY, A. HASTINGS, J. L. LARGIER, T. M. POWELL, K. HIGGINS, AND J. F. QUINN. 1994. The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations. *Deep-Sea Res. II* **41**: 107–145.
- BRUBAKER, J., AND R. HOOFF. 2000. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. *Limnol. Oceanogr.* **45**: 230–236.
- CASTILLA, J. C. 1988. Una revisión bibliográfica (1980–1988) sobre *Concholepas concholepas* (Bruguière 1789) (Gastropoda: Muricidae): Problemas pesqueros y experiencias de repoblación. *Biol. Pesq. (Chile)* **17**: 9–19.
- DISALVO, L. H. 1988. Observations on the larval and post-metamorphic life of *Concholepas concholepas* (Bruguière, 1789) in laboratory culture. *Veliger* **30**: 358–368.
- FORWARD, R. B., JR. 1988. Diel vertical migration: Zooplankton photobiology and behavior. *Oceanogr. Mar. Biol. Annu. Rev.* **26**: 361–392.
- , J. S. BURKE, D. RITTSCHOF, AND J. M. WELSH. 1996a. Photoresponses of larval Atlantic menhaden (*Brevoortia tyrannus* Latrobe) in offshore and estuarine waters: Implications for transport. *J. Exp. Mar. Biol. Ecol.* **199**: 123–135.
- , AND D. RITTSCHOF. 2000. Alteration of photoresponses involved in diel vertical migration of a crab larva by fish mucus and degradation products of mucopolysaccharides. *J. Exp. Mar. Biol. Ecol.* **245**: 277–292.
- , R. A. TANKERSLEY, AND J. S. BURKE. 1996b. Endogenous swimming rhythms of larval Atlantic menhaden, *Brevoortia tyrannus* Latrobe: Implications for vertical migration. *J. Exp. Mar. Biol. Ecol.* **204**: 195–207.
- HILL, A. E. 1998. Diel vertical migration in stratified tidal flows: Implications for plankton dispersal. *J. Mar. Res.* **56**: 1069–1096.
- JOHNSON, D. R., T. FONSECA, AND H. SIEVERS. 1980. Upwelling in the Humboldt Coastal Current near Valparaíso, Chile. *J. Mar. Res.* **38**: 1–15.
- LENTZ, S. J. 1994. Current dynamics over the Northern California inner shelf. *J. Phys. Oceanogr.* **24**: 2461–2478.
- LUCKENBACH, M. W., AND R. J. ORTH. 1992. Swimming velocities and behavior of blue crab (*Callinectes sapidus*) megalopae in still and flowing water. *Estuaries* **15**: 186–192.
- MANRÍQUEZ, P. H., AND J. C. CASTILLA. 2001. Significance of marine protected areas in central Chile as seeding grounds for the gastropod *Concholepas concholepas*. *Mar. Ecol. Prog. Ser.* **215**: 201–211.
- MANUEL, J. L., C. M. PEARCE, D. A. MANNING, AND R. K. O'DOR. 2000. The response of sea scallop (*Placopecten magellanicus*) veligers to a weak thermocline in 9-m deep mesocosms. *Mar. Biol.* **137**: 169–175.
- MARTÍNEZ, P., AND S. A. NAVARRETE. In press. Temporal and spatial variation in settlement of the gastropod *Concholepas concholepas* in natural and artificial substrata. *J. Mar. Biol. Assoc. UK*.
- MILEIKOVSKY, S. A. 1973. Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. *Mar. Biol.* **23**: 11–17.
- MINER, B. G., S. G. MORGAN, AND J. R. HOFFMAN. 2000. Postlarval chromatophores as an adaptation to ultraviolet radiation. *J. Exp. Mar. Biol. Ecol.* **249**: 235–248.
- MORENO, C. A., G. ASENSIO, W. E. DUARTE, AND V. MARTÍN. 1998. Settlement of the muricid *Concholepas concholepas* and its relationship with El Niño and coastal upwellings in southern Chile. *Mar. Ecol. Prog. Ser.* **167**: 171–175.
- , ———, AND S. IBÁÑEZ. 1993. Patrones de asentamiento de *Concholepas concholepas* (Bruguière) (Mollusca: Muricidae) en la zona intermareal rocosa de Valdivia, Chile. *Rev. Chil. Hist. Nat.* **66**: 93–101.
- MORGAN, S. G. 1995. The timing of larval release, p. 157–192. In L. McEdward [ed.], *Ecology of marine invertebrates*. CRC Press.
- OHMAN, M. D., B. W. FROST, AND E. B. COHEN. 1983. Reverse diel vertical migration: An escape from invertebrate predators. *Science* **220**: 1404–1407.
- PENNINGTON, J. T., AND R. B. EMMET. 1986. Ontogenetic and diel vertical migration of a planktonic echinoid larvae, *Dendraster excentricus* (Eschscholtz): Occurrence, causes, and probable consequences. *J. Exp. Mar. Biol. Ecol.* **104**: 69–95.
- POULIN, E., A. T. PALMA, G. LEIVA, E. HERNÁNDEZ, P. MARTÍNEZ, S. A. NAVARRETE, AND J. C. CASTILLA. In press. Temporal and

Notes

74

- spatial variation in the distribution of epineustonic competent larvae of *Concholepas concholepas* (Gastropoda: Muricidae) in the central coast of Chile. Mar. Ecol. Prog. Ser.
- RAMP, S. R., AND C. L. ABBOTT. 1998. The vertical structure of currents over the Continental Shelf off Point Sur, CA, during Spring 1990. Deep-Sea Res. II **45**: 1443–1470.
- RICHARDS, S. A., H. P. POSSINGHAM, AND J. NOYE. 1996. Diel vertical migration: Modeling light-mediated mechanisms. J. Plankton Res. **18**: 2199–2222.
- ROUGHGARDEN, J., S. GAINES, AND H. POSSINGHAM. 1988. Recruitment dynamics in complex life cycles. Science **241**: 1460–1466.
- SHANKS, A. L. 1986. Vertical migration and cross-shelf dispersal of larval *Cancer* spp and *Randallia ornata* (Crustacea: Brachyura) off the coast of southern California. Mar. Biol. **92**: 189–199.
- . 1995. Mechanisms of cross-shelf dispersal of larval invertebrates and fish, p. 323–367. In L. McEdward [ed.], Ecology of Marine Invertebrates. CRC Press.
- , J. LARGIER, L. BRINK, J. BRUBAKER, AND R. HOFF. 2000. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnol. Oceanogr. **45**: 230–236.
- STOBUTZKI, I. C., AND D. R. BELLWOOD. 1997. Sustained swimming abilities of later pelagic stages of coral reef fishes. Mar. Ecol. Prog. Ser. **149**: 35–41.
- STOTZ, W. B., P. DE AMESTI, D. J. MARTINEZ, AND E. PEREZ. 1991. Lugares de asentamiento y desarrollo de juveniles tempranos de *Concholepas concholepas* (Bruguière, 1789) en ambientes inter y submareales de la IV Region, Coquimbo, Chile. Rev. Biol. Mar. Valparaiso **26**: 339–350.
- STRUB, P. T., J. M. MESIAS, V. MONTECINO, J. RUTLLAND, AND S. SALINAS. 1998. Coastal ocean circulation off Western South America, p. 273–313. In A. R. Robinson and K. H. Brink [eds.], The sea, vol. 11. John Wiley & Sons.
- THORSON, G. 1964. Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. Ophe-
lia **1**: 167–208.
- WING, S. R., L. W. BOTSFORD, J. L. LARGIER, AND L. E. MORGAN. 1995. Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Mar. Ecol. Prog. Ser. **128**: 199–211.
- YOUNG, C. M. 1997. Novelty of “supply-side ecology.” Science **235**: 415–416.

Received: 11 September 2001

Accepted: 19 February 2002

Amended: 2 April 2002

1. Author: This article has been lightly edited for grammar, style, and usage. Please compare against your original document and make changes on this galley. Please limit yourself to substantive changes that affect meaning. If no change is required in response to a question please write 'OK as set' in the margin. Copy editor

2. Please spell out SST.

3. Please update Martínez & Navarrete in press if possible.

4. Please update Poulin et al. in press if possible.