

Available online at www.sciencedirect.com



Continental Shelf Research 24 (2004) 1573-1585

CONTINENTAL SHELF RESEARCH

www.elsevier.com/locate/csr

# High-frequency observations of wind-forced onshore transport at a coastal site in Baja California

Fabián J. Tapia<sup>a,\*</sup>, Jesús Pineda<sup>a</sup>, Francisco J. Ocampo-Torres<sup>b</sup>, Heidi L. Fuchs<sup>a</sup>, P. Edward Parnell<sup>c</sup>, Paulina Montero<sup>d</sup>, Sergio Ramos<sup>b</sup>

<sup>a</sup> Biology Department MS-34, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

<sup>b</sup> Departamento de Oceanografía Física, Centro de Investigación Científica y de Educación Superior de Ensenada, Km 107 Carretera Tijuana-Ensenada, Ensenada, BC 22860, Mexico

<sup>c</sup> Scripps Institution of Oceanography, Integrative Oceanography Division, 9500 Gilman Drive 0227, La Jolla, CA 92093-0227, USA <sup>d</sup> Centro de Ciencias y Ecología Aplicada, Universidad del Mar, Carmen 446 - Cerro Placeres, Valparaíso, Chile

Received 26 August 2003; received in revised form 27 February 2004; accepted 26 March 2004

Available online 20 July 2004

#### Abstract

We investigated the effect of the daily sea breeze on the surface flow at Bahia Salsipuedes, Baja California, Mexico. Drifter-tracking experiments were conducted over a 2-week period in July, 1999. Surface drifters were deployed daily and their trajectories tracked from a small boat for 3–7 h. Wind speed and direction, as well as the vertical distribution of temperature and current velocities were measured throughout the observation period. Our results indicate that strong winds associated with the daily sea breeze at the study area can produce onshore surface currents with velocities of up to  $10 \text{ cm s}^{-1}$  (net transport of up to 2 km in a diurnal cycle). There was a hyperbolic relationship between onshore wind stress and net onshore transport of the drifters. A decrease in stratification and more consistent pattern of onshore transport were associated with sustained winds >  $6 \text{ m s}^{-1}$  towards the end of the study. Progressive vector diagrams computed from near-surface currents failed to predict the trajectory of drifters, especially on days where wind forcing was more consistent in terms of direction and magnitude. We discuss the implications of these results regarding the collection of settlement data and their interpretation in terms of larval supply to coastal populations. © 2004 Elsevier Ltd. All rights reserved.

Keywords: Sea breeze; Onshore transport; Drifters; Neuston; Baja California

## 1. Introduction

The dynamics of coastal populations is highly dependent on the mechanisms and processes affecting the spatial distribution and the fate of larvae prior to settlement. Research efforts during the past decades have been focused on the physical processes that are likely to affect the distribution of larvae relative to adult populations (e.g. Johnson, 1939; Scheltema, 1968; Butman, 1987; Pineda, 1994b; Epifanio and Garvine, 2001), and on the importance of substrate availability (e.g. Bertness et al., 1992; Pineda, 1994a). Such a

\*Corresponding author. E-mail address: ftapia@whoi.edu (F.J. Tapia).

<sup>0278-4343/\$ -</sup> see front matter © 2004 Elsevier Ltd. All rights reserved. doi:10.1016/j.csr.2004.03.013

'supply side' approach (see Underwood and Fairweather, 1989) has yielded valuable insights on the relevance of physical processes as predictors of the local and regional dynamics of adult populations. In order to characterize the variability of larval supply to coastal populations, however, it is necessary to assess patterns of larval distribution at spatial and temporal scales that are relevant to a species' life cycle and ecology. Plankton patchiness and logistic constraints preclude the use of such sampling strategy in most cases, thus forcing the use of proxies for larval supply that are more feasible to monitor over extended periods of time (e.g. settlement—see Pineda, 2000).

Settlement has been the proxy of choice in a number of studies focused on the supply of larvae to adult populations of coastal invertebrates, such as crabs (Wing et al., 1995b; Reyns and Sponaugle, 1999), sea urchins (Ebert et al., 1994; Wing et al., 1995a), and barnacles (Gaines et al., 1985; Pineda, 1994a). Artificial and/or natural surfaces are provided for the larvae to settle on, and monitored at intervals of days to weeks. Settlement time series data are then analyzed in conjunction with environmental data series to identify temporal correlations between larval supply and physical variability (e.g. Farrel et al., 1991; Wing et al., 1995a; Pineda and López, 2002). A number of published studies have documented correlations between larval settlement and physical processes occurring at a range of temporal scales: from intraseasonal changes in wind forcing (Bertness et al., 1996), upwelling intensity (Wing et al., 1995a), and the stratification of the water column (Pineda and López, 2002), to interannual changes in river discharge (Gaines and Bertness, 1992). The importance of higher-frequency physical variability for settlement, however, has not been extensively studied and cannot be resolved at the sampling frequencies typically used in settlement surveys. Therefore, inferences made so far about larval transport are probably biased towards lowerfrequency mechanisms if based only on settlement data (Pineda, 2000).

Few high-frequency mechanisms with a potential effect on the onshore transport of larvae have been documented so far. Internal tidal bores, a seasonal and somewhat predictable phenomenon that occurs in coastal environments at scales of hours to days, are an example of high-frequency forcing likely to affect the onshore transport of both planktonic and neustonic larvae (Pineda, 1994b, 1999).

The diurnal sea breeze, which is also seasonal and locally predictable in its occurrence, represents another highly episodic phenomenon that could potentially affect larval settlement (Kaplan et al., 2003; but see Epifanio and Garvine, 2001, p. 54). The sea breeze is characterized by a daily regime of variability, generated by oscillations in the landsea temperature gradient, which in some regions can explain fluctuations of up to  $7 \,\mathrm{m \, s^{-1}}$  in onshore wind speed (Simpson, 1994). Such daily surges in onshore winds may affect the cross-shore distribution of material suspended in the upper centimeters of the water column (i.e. neuston), including the larvae of a number of coastal invertebrates. Thus, by modulating the onshore flow of surface waters, the sea breeze could have an effect on the timing and variability of recruitment in coastal populations with neustonic larvae.

In this contribution we investigate the effect of the sea breeze on cross-shore surface currents by means of drifter-tracking experiments, which were conducted over a period of 2 weeks at Bahia Salsipuedes in northern Baja California. Our results demonstrate the potential for the diurnal sea breeze to substantially affect onshore transport of neustonic material. We discuss the implications of these results regarding the collection of settlement data and their interpretation in terms of larval supply to coastal populations.

# 2. Materials and methods

The experiments were conducted on 13–22 July, 1999 (Table 1), at Bahia Salsipuedes (31° 56' N, 116° 46' W) in northern Baja California (Fig. 1). Every morning at about 7:30–9:30 AM (PDT), we deployed a set of 5–6 drifters, which were circular pieces of soft and flexible, Scootguard<sup>TM</sup> non-slip surface (30 cm in diameter, 1 mm thickness) with six small lead "split-shot" lead weights (2.5 g each) attached to the edges (Fig. 2). When deployed, the drifters remained at the air–sea interface, with less

Date	Drifter deployments				Wind speed		Wind direction		PVD-drifter discrepancy		
	Number drifters	Time start	Time end	Number observ.	Mean $(m s^{-1})$	S.D. $(m s^{-1})$	Mean (deg)	S.D. (deg)	PO dist (km)	LD dist (km)	(PO/LD)
13-Jul-99	5	10:40	13:15	9	2.45	0.42	125.4	49.2	1.04	1.03	1.01
15-Jul-99	5	10:00	14:50	12	2.11	0.50	100.9	31.5	1.04	1.60	0.65
16-Jul-99	6	8:15	15:30	18	2.80	1.03	104.3	66.4	2.36	1.68	1.40
19-Jul-99	5	8:50	15:00	19	3.88	2.26	96.5	74.8	0.94	2.08	0.45
20-Jul-99	5	7:15	12:15	17	3.13	3.00	92.6	79.1	0.97	2.00	0.49
21-Jul-99	5	7:30	11:50	14	3.01	2.01	109.0	69.4	1.40	1.77	0.79
22-Jul-99 <sup>a</sup>	5	7:45	13:40	21	3.18	3.05	102.1	71.4	—	1.63	

 Table 1

 Details on the time (PDT), number of observations, and wind conditions during the drifter deployments at Bahia Salsipuedes, Baja California

The magnitude and variability of wind forcing is presented in relation to an index of discrepancy between observed drifter displacements and those predicted from Progressive Vector Diagrams (PVDs). PO dist: Distance between the end points of the actual drifter path and a PVD; LD dist: Linear distance between the initial and final positions recorded for drifters on each day.

<sup>a</sup>No current meter data available on this day.



Fig. 1. Geographic location of Bahia Salsipuedes. The star indicates the study site.

than 2 each drifter was recorded about every 20 min using boat's proximity to the surf zone. The location of depending on the weather conditions and on the and tracked from onset of the sea breeze wind forcing (Fig. 2). Drifters were deployed at the location every day 12:00 each day), increase differential GPS 50% of their surface in onshore a small motor boat for 3–7h, (31° 56.31' N; at winds that occurred at 8:00approximately events (i.e. area exposed to direct 116° 46.72′ W), the a sudden same

between the design (Fig. column, rather than their own response to wind interface. by pieces forcing. Our assumption was based on the drifter motion We assumed that the drifters were tracking the of the uppermost layers of kelp that collected 2), drifter paths and on Ħ were the situ, found at the air-sea and those statistical and of the similarity deployed followed water



Fig. 2. Side view picture (A), and top and side view schematics (B and C) of the drifters used in this study. The arrows (and black circles in B and C) indicate the position of the six small lead weights attached to the drifter's edge. The edge areas (dark shading in B and C) correspond to the fraction of the drifter's surface that remained underwater. The central area (light shade in B and C) corresponds to the portion that was exposed to the wind during a deployment.

concurrently with the drifters (Solow, WHOI, pers. comm.).

Throughout the observation period we monitored the thermal structure of the water column using a string of Onset StowAway XTI loggers (response time <15 s), programmed with a sampling interval of 40 s and located at 2, 5, 8, and 11 meters above the bottom (mab), plus one logger at the surface. We also monitored the vertical structure of nearshore currents with a bottommounted, upward looking 1200 kHz Doppler current meter (RD Instruments, San Diego, CA), which measured at intervals of 40 s (100 pings per ensemble) and in bins of 0.4 m within a depth range of 0.95–14.55 mab. Both the temperature mooring and the current meter were located at a depth of 16 m (31° 56.28' N; 116° 45.68' W). Average wind velocity and direction were recorded over 5 min intervals using a CMB3280 Aanderaa

Coastal Monitoring Buoy, anchored at a nearby location  $(31^{\circ} 55.28' \text{ N}; 116^{\circ} 45.39' \text{ W}, \text{ ca. 2 km}$  south of the current meter mooring). Prior to the analysis, wind directions were rotated and aligned to the average shoreline orientation  $(355^{\circ})$ , and then decomposed into alongshore and cross-shore components.

We studied the effect of wind forcing on the water column using two different approaches. First, on a time-domain approach, we studied the effect of wind forcing on stratification by computing wind stress at the surface as

$$\tau_0| = \rho u^{*2},\tag{1}$$

where  $\rho$  is air density and  $u^*$  is the friction velocity, which was computed from wind speed data as in Large et al. (1995, Eq. 8). We calculated stratification as the square of the Brunt–Väisälä frequency ( $N^2$ ) for each one of the four pairs of temperature series (i.e. 2–5 mab, 5–8 mab, 8–11 mab, and 11 mab -surface) as

$$N^2 = -\frac{g}{\rho_0} \frac{\partial \rho}{\partial z},\tag{2}$$

where g is gravity (9.8 m s<sup>-2</sup>),  $\rho_0$  is the mean density of the water column, and z is depth. We then obtained depth-averaged values for  $N^2$  by vertically averaging the four series mentioned above. The temperature and wind time series were low-pass filtered prior to the computations (cutoff frequency of  $6 \text{ cycles } h^{-1}$ ), and a constant salinity value of 34 psu was assumed. Second, on a frequency-domain approach. we performed spectral analyses on the time series for wind temperature  $(\sim 5,000)$ observations) and  $(\sim 42,000 \text{ observations})$  collected at the study site between 7-23 July and 4-23 July, respectively. Raw data were linearly detrended prior to the computation of an average Welch periodogram. The wind and temperature series were divided into non-overlapping segments of  $2^{10}$  (3.6d) and  $2^{13}$ points (3.8 d), respectively.

To understand the contribution of wind to onshore transport, we analyzed the effect of wind stress on the motion and trajectory of the drifters. We computed net onshore displacements for each drifter/day, and then performed a nonlinear regression of net onshore displacement versus the onshore wind stress integrated over the duration of each deployment. We also analyzed changes in the correlation between drifter trajectories and wind direction as a function of wind speed for each deployment. For *n* average drifter positions recorded during a deployment, we computed n-1velocity vectors. Velocity vectors were decomposed into cross-shore and alongshore components of the drifter trajectories, which were linearly regressed against the respective components of wind forcing. We chose a 10 min lag between wind measurements and the drifter observations to which they were paired (i.e. midpoint between drifter observations). We tested whether drifter trajectories can be predicted from currentmeter data by comparing the observed trajectories with progressive vector diagrams (PVDs) from our measurements of horizontal velocities near the surface. The predicted (x, y) positions were computed as

$$x(t_n) = \Delta t \sum_{i=1}^n u(t_i), y(t_n) = \Delta t \sum_{i=1}^n v(t_i),$$
 (3)

where u(t) and v(t) are the east and north current speeds measured by the current meter at time t, and  $\Delta t$  is the sampling interval (Emery and Thomson, 1998, p. 165). Due to large errors introduced by tidal fluctuations in water depth, surface wave action, and side lobbing, data collected from the surface bins by the Doppler current meter had to be discarded. Thus, our uppermost bin with reliable data was located at 13 mab, on average 2 m below the surface.

Finally, we observed settlement of invertebrate larvae on the drifters. Although these observations were not quantitative, we use the taxonomic composition of the settlers and the time scales over which settlement was observed to conjecture on the potential effects of sea breeze events on the distribution and onshore transport of neustonic larvae.

#### 3. Results

We completed 7 days of drifter observations during which a total of 36 drifters were deployed and tracked for an average of 5 h (Table 1). Wind speeds measured during the study were highly variable, with most of the variability explained by changes in the cross-shore component (Figs. 3a and 4a). Onshore winds dominated during the second half of the study, with daily oscillations of up to  $8 \text{ m s}^{-1}$  which extended for about 8 h (Fig. 3a). The dominance of a diurnal frequency in the variability of cross-shore winds was confirmed by the computed power spectra (Fig. 4a). Coincident with these daily surges in onshore winds, we observed short-term increases in the temperature of surface waters (Fig. 3b). Towards the end of the observation period, these rapid increases in temperature could be detected throughout the water column (Fig. 3b), which is consistent with the observed decrease in the depth-averaged stratification (Fig. 3c). A diurnal frequency dominated the variability of temperature between the surface and



Fig. 3. Wind speed (A), water temperature (B) and mean stratification of the water column (C) during the drifter deployments at Bahia Salsipuedes in July 1999. Tidal heights predicted for the port of Ensenada, Baja California, are also shown in C (gray line).

11 mab (Fig. 4b–c), and could be detected at depth to 2 mab (Fig. 4f). A second peak in the power spectra was found at the semi-diurnal frequency (i.e. about 2 cycles day<sup>-1</sup>, Fig. 4c–f), which dominated the variability of temperature near the bottom, but nonetheless could be detected up to 11 mab (Fig. 4c–f). Large fluctuations in stratification observed at the beginning of our study (Fig. 3c) appeared to be driven by the semi-diurnal internal tides rather than wind forcing.

Persistent wind forcing towards the end of the study caused a net onshore transport of the drifters (Fig. 5a), which increased as a function of wind stress integrated over the duration of the deployments (Fig. 5b). Drifters were transported onshore at speeds of up to  $10 \text{ cm s}^{-1}$ . The intensity

of wind forcing during the experiments determined the degree of correlation between drifter paths and wind direction (Fig. 6). A better alignment of drifter paths and wind on the cross-shore direction is consistent with the higher wind speeds recorded along this axis (Fig. 3a). The response of surface waters (and therefore drifter paths) to the temporal variability in wind forcing can be clearly seen in Fig. 7, in which the wind vectors have been superimposed on the drifter trajectories for July 20 and July 22.

The temporal variability in the horizontal velocities of near-surface currents (Fig. 8b) was consistent with the timing and intensity of wind forcing (Fig. 8a). Near-surface currents showed a tendency to be decoupled from currents measured



Fig. 4. Power spectra computed for the wind (A) and temperature time series (B–F) recorded at Bahia Salsipuedes in July 1999. Bars on the right-hand side of each panel correspond to 95% confidence intervals. The dashed lines indicate diurnal variability; mab: meters above the bottom.

deeper in the water column (Fig. 8b). PVDs computed from horizontal velocities measured at 13 mab (Fig. 9) showed a poor performance as predictors of drifter trajectories. The observed trajectories seemed to be the result of an interaction between wind and tidal forcing, which explained most of the variability in the PVDs (Fig. 9). The discrepancy between predicted and observed drifter displacement varied as a function of the magnitude and variability of wind forcing during the deployments. The largest discrepancies were observed on days with strong and persistent winds, whereas smaller values tended to occur on days with more variable wind forcing, both in terms of speed and direction (Table 1). A closer inspection of Fig. 9 and the wind data series (Fig. 3a) suggests that not only the magnitude and variability of wind forcing, but also its timing relative to the tidal cycle (Fig. 3c) ultimately determined drifter trajectories.

We incidentally observed settlement of neustonic zooplankton on the drifters. The most abundant taxa corresponded to flatworms (0.5–  $52.8 \text{ indiv h}^{-1}$ ), brachyuran and anomuran megalopae (0.4–3.0 indiv h $^{-1}$ ), isopods (0.2–2.0 indiv h $^{-1}$ ), amphipods (0.2–1.7 indiv h $^{-1}$ ), and lepadid barnacle larvae (0.4–1.0 indiv h $^{-1}$ ). The highest settlement rates for these taxa were observed during the last four days of the study (19–22 July), which exhibited the strongest onshore winds (Fig. 3a).

#### 4. Discussion

Our results indicate that neustonic material has the potential to be transported onshore by the daily sea breeze at Bahia Salsipuedes (Fig. 5). A causal relationship is supported by the observed drifter trajectories (Figs. 5 and 6) and their response to short-term fluctuations in wind direction (Fig. 7), as well as by the discrepancies between actual drifter trajectories and those predicted by progressive vector diagrams (PVDs) computed from the horizontal velocities of nearsurface currents (Fig. 9). These results are relevant because currents in the coastal ocean are generally more energetic on the alongshore axis (Winant,



Fig. 5. (A) Average paths followed by drifters on different days; the numbers are the July date corresponding to each trajectory, whereas the arrow indicates the point of deployment. (B) Net onshore displacement of drifters as a function of onshore wind stress integrated over the duration of each deployment. The large open circle in (A) indicates the position of the Doppler current meter and temperature moorings.



Fig. 6. (A) Changes in the correlation between average drifter and wind direction as a function of the average wind speed during each deployment. Linear regression analyses were performed separately for alongshore (closed symbols) and cross-shore (open symbols) components of wind and drifter direction, and for each day with drifter deployments (July 13, 15, 16, 19, 20, 21, 22). (B and C) Example of how the values indicated with squares (in A) were obtained for July 21; *W* is average wind speed for the deployment.

1980), with few mechanisms acting on the crossshore dimension with sufficient energy to generate onshore transport at the temporal and spatial scales observed here (e.g. internal tidal bores—see Pineda, 1994b).

The surface drifters used in this study are an effective means to investigate the short-term

response of the surface layer (i.e. first few centimeters) to local wind forcing. Water movement at this biologically relevant layer—where a suite of particles including neustonic plankton can be accumulated (see LeFevre, 1986)—is left unresolved by most instruments, including acoustic current meters and other drifter designs that



Fig. 7. Example of drifter trajectories in relation to the temporal variability of wind forcing on July 20 and July 22, 1999. Open circles correspond to drifter positions, whereas the thin lines are a vectorial representation of the average wind speed and direction measured during the interval prior to each drifter observation. Closed circles indicate the point of drifter deployment.

can go deeper into the water column and/or be directly affected by wind forcing. One disadvantage of our approach, however, is the need to visually and continuously track the drifters from a boat. Currently available technology should make it feasible to address such problem by attaching a small positioning/tracking device to each surface drifter, so that their position can be recorded without compromising their ability to track the surface layer.

The discrepancies we observed between actual drifter paths and those predicted by PVDs should be taken into account before any conclusions about larval transport are drawn from Eulerian current data. Our data suggest that the observed discrepancies between the PVDs and drifter trajectories may be due to an interaction between the magnitude and variability of wind forcing and tidal currents. However, one source of error that could explain part of the discrepancy is the varying distance between our top bin with reliable current meter data (13 mab) and the surface of the water column. Given that our main objective was to study the effect of the daily sea breeze on the onshore transport of surface currents, the experi-

ments were conducted at roughly the same time of the day. This means that on some days the observations took place at high tide (July 13, 15), at low tide (July 20, 21), or during the transition from low to high (July 16, 19). Unfortunately, a pressure sensor was not available and therefore we lack accurate data on the sea level at our study site during drifter deployments. Tidal predictions for Ensenada (ca. 20 km south of Bahia Salsipuedes), indicate sea-level fluctuations of up to 2.4 m during the course of the deployments, which would have increased the distance from the top ADCP bin to the surface from 2 to 4.4 m. Such a change could certainly increase the discrepancy between the trajectories predicted from a PVD and those actually followed by the drifters, especially on a highly stratified water column (Figs. 8 and 9).

Our observations were focused on drifter paths and on the physical variables associated with the water column's response to wind forcing, and did not include an assessment of the spatial distribution and/or settlement of neustonic larvae in the area. Therefore, a connection between this transport mechanism and the recruitment of coastal species with neustonic larvae is yet to be demonstrated. If there is a connection, however, and larvae of coastal invertebrates are in fact transported onshore by the sea breeze, it would be possible to predict the spatial-temporal distribution of larval settlement in some populations based on local wind patterns and shore orientation. An assessment of the effect of sea breeze events on the spatial distribution and timing of settlement is thus warranted.

A follow up of our study should include a survey of neustonic meroplankton in the area with concurrent drifter deployments and settlement observations. Given the diurnal frequency of sea breeze events, any attempt to link such events to local settlement patterns will have to consider observations taken at shorter intervals than it is customary (i.e. at least semi-diurnally). Lack of temporal resolution could result in a misinterpretation of the mechanisms that determine the timing and intensity of settlement in populations with neustonic larvae.

Wind-driven onshore transport of neustonic invertebrates has been suggested as a cause of



Fig. 8. Example of the effect of wind forcing (A) on the circulation (B) and thermal structure (C) of the water column in Bahia Salsipuedes on July 19, 1999. The shaded area in A corresponds to the duration of the drifter deployment. The stickplots in B show the variability in direction and magnitude (see scale bar at lower left corner) of horizontal currents at the same depths at which temperature was recorded. The vectors indicate the direction currents are flowing towards (up is north).

the spatial patterns observed in barnacle settlement (Kendall et al., 1982; Bertness et al., 1996), and in the spatial distribution of neustonic isopods (Locke and Corey, 1989), post-larval crabs (Shanks, 1986; Eggleston et al., 1998) and lobster megalopae (Hudon and Fradette, 1993). If such wind events are persistent and consistent enough over demographically relevant time scales, they



Fig. 9. Comparison of observed versus predicted trajectories of drifters at Bahia Salsipuedes, Baja California, in July 1999. Open circles indicate the observed drifter trajectories. Predicted trajectories (closed circles) correspond to a PVD, computed from horizontal current velocity data collected at 13 mab. The gray line is a PVD computed using only those frequencies of the current data that correspond to the barotropic tide. The insets show average wind speed and direction  $(0^\circ = N)$  over the duration of each deployment. The scale bar at the lower left corner of each panel corresponds to a distance of 1 km.

could have an impact on the connectivity and/or demographic isolation among adjacent coastal populations. At sea level, the sea breeze is highly asymmetrical, with a marked predominance of onshore over offshore winds (Fig. 3a). Hence, the sea breeze can have a cumulative effect (i.e. over more than one diurnal cycle) on the cross-shore distribution of neustonic larvae. A persistent sea breeze-mediated onshore transport could allow neustonic larvae to either remain close to the shoreline throughout their development, or to repeatedly reach it, hence increasing their probability of being close to adult habitats when competent to settle. Thus, the sea breeze could constitute an effective transport and/or retention mechanism in areas with a configuration of shoreline and wind forcing such as that observed at Bahia Salsipuedes.

The effect of wind forcing on larval retention and demographic isolation could be intensified if larval behavior is invoked, such as the reverse vertical migration hypothesized by Poulin et al. (2002) for neustonic larvae of the subtidal gastropod Concholepas concholepas. Even under conditions of strong upwelling (i.e. strong offshore Ekman transport), the larvae of C. concholepas are consistently found between the shoreline and the upwelling front. Such observation, along with data on the temporal variability of larval distribution, suggests that a reverse vertical migration behavior might be allowing these larvae to stay close to subtidal habitats (see Fig. 6 in Poulin et al., 2002). The interaction between physical processes like the sea breeze and behavioral mechanisms such as vertical migrations could increase the local retention of neustonic larvae and the demographic isolation of adjacent populations.

Finally, these results might also be relevant for understanding the onshore transport of pollutants, often discharged a few kilometers from shore near coastal cities (e.g. Boehm et al., 2002). Such discharges are likely to contain buoyant particles than can reach surface waters. Our observations suggest that such particles could be rapidly transported onshore by the sea breeze.

## Acknowledgements

Supported by US NSF grant to JP and Mexican CONACYT grant DAJ J002/750/00 C-834/00 to FJO-T. FT was supported by the Chilean MID-EPLAN, and PM by WHOI and CIPO-IAI. M. Hendershott (SIO) first suggested to one of us (JP) the use of low profile, flexible floating objects for measuring surface circulation. We thank J. Leichter (SIO), M. López (CICESE), and two anonymous reviewers for their comments on an earlier version of this manuscript, and S. Ortegon and A. Bravo for their assistance in the field. This is WHOI contribution number 11,098.

## References

- Bertness, M.D., Gaines, S.D., Stephens, E.G., Yund, P.O., 1992. Components of recruitment in populations of the acorn barnacle *Semibalanus balanoides* (Linnaeus). Journal of Experimental Marine Biology and Ecology 156, 199–215.
- Bertness, M.D., Gaines, S.D., Wahle, R.A., 1996. Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. Marine Ecology Progress Series 137, 103–110.
- Boehm, A.B., Sanders, B.F., Winant, C.D., 2002. Cross-shelf transport at Huntington Beach. Implications for the fate of sewage discharged through an offshore ocean outfall. Environmental Science and Technology 36, 1899–1906.
- Butman, C.A., 1987. Larval settlement of soft-sediment invertebrates: The spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. Oceanography and Marine Biology Annual Review 25, 113–165.
- Ebert, T.A., Schroeter, S.C., Dixon, J.D., Kalvass, P., 1994. Settlement patterns of red and purple sea urchins (*Strongy-locentrotus franciscanus* and *S. purpuratus*) in California, USA. Marine Ecology Progress Series, 111, 41–52.
- Eggleston, D.B., Armstrong, D.A., Elis, W.E., Patton, W.S., 1998. Estuarine fronts as conduits for larval transport: Hydrodynamics and spatial distribution of Dungeness crab postlarvae. Marine Ecology Progress Series 164, 73–82.
- Emery, W.J., Thomson, R.E., 1998. Data Analysis Methods in Physical Oceanography. Pergamon Press, New York.
- Epifanio, C.E., Garvine, R.W., 2001. Larval transport on the Atlantic continental shelf of North America: A review. Estuarine Coastal and Shelf Science 52, 51–77.
- Farrel, T.M., Bracher, D., Roughgarden, J., 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. Limnology and Oceanography 36, 279– 288.
- Gaines, S., Brown, S., Roughgarden, J., 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. Oecologia 67, 267–272.
- Gaines, S.D., Bertness, M.D., 1992. Dispersal of juveniles and variable recruitment in sessile marine species. Nature 360, 579–580.
- Hudon, C., Fradette, P., 1993. Wind-induced advection of larval decapods into Baie de Plaisance (Îles de la Madeleine, Québec). Canadian Journal of Fisheries and Aquatic Sciences 50, 1422–1434.
- Johnson, M.W., 1939. The correlation of water movements and dispersal of pelagic larval stages of certain littoral animals, especially the sand crab *Emerita*. Journal of Marine Research 2, 236–245.

- Kaplan, D.M., Largier, J.L., Navarrete, S., Guiñez, R., Castilla, J.C., 2003. Large diurnal temperature fluctuations in the nearshore water column. Estuarine Coastal and Shelf Science 57, 385–398.
- Kendall, M.A., Bowman, R.S., Williamson, P., Lewis, J.R., 1982. Settlement patterns, density and stability in the barnacle *Balanus balanoides*. Netherlands Journal of Sea Research 16, 119–126.
- Large, W.G., Morzel, J., Crawford, G.B., 1995. Accounting for surface wave distortion of the marine wind profile in lowlevel ocean storms wind measurements. Journal of Physical Oceanography 25, 2959–2971.
- LeFevre, J., 1986. Aspects of the biology of frontal systems. Advances in Marine Biology 23, 163–299.
- Locke, A., Corey, S., 1989. Amphipods, isopods and surface currents: A case for passive dispersal in the Bay of Fundy, Canada. Journal of Plankton Research 11, 419–430.
- Pineda, J., 1994a. Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. Marine Ecology Progress Series 107, 125–138.
- Pineda, J., 1994b. Internal tidal bores in the nearshore: Warmwater fronts, seaward gravity currents and the onshore transport of neustonic larvae. Journal of Marine Research 52, 427–458.
- Pineda, J., 1999. Circulation and larval distribution in internal tidal bore warm fronts. Limnology and Oceanography 44, 1400–1414.
- Pineda, J., 2000. Linking larval settlement to larval transport: assumptions, potentials, and pitfalls. In: Färber-Lorda, J. (Ed.), Oceanography of the Eastern Pacific, Vol. 1. CICESE, Ensenada, pp. 84–105.
- Pineda, J., López, M., 2002. Temperature, stratification and barnacle larval settlement in two Californian sites. Continental Shelf Research 22, 1183–1198.
- Poulin, E., Palma, A.T., Leiva, G., Narvaez, D., Pacheco, R., Navarrete, S.A., Castilla, J.C., 2002. Avoiding offshore transport of competent larvae during upwelling events: The case of the gastropod *Concholepas concholepas* in Central Chile. Limnology and Oceanography 47, 1248–1255.
- Reyns, N., Sponaugle, S., 1999. Patterns and processes of brachyuran crab settlement to Caribbean coral reefs. Marine Ecology Progress Series 185, 155–170.
- Scheltema, R.S., 1968. Dispersal of larvae by Equatorial ocean currents and its importance to the zoogeography of shoalwater tropical species. Nature 217, 1159–1162.
- 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. Marine Biology 92, 189–199.
- Simpson, J.E., 1994. Sea Breeze and Local Winds. Cambridge University Press, Cambridge.
- Underwood, A.J., Fairweather, P.G., 1989. Supply side ecology and benthic marine ecology. Trends in Ecology and Evolution 4, 16–20.
- Winant, C.D., 1980. Coastal circulation and wind-induced currents. Annual Review of Fluid Mechanics 12, 271–301.

- Wing, S.E., Largier, J.L., Botsford, L.W., Quinn, J.F., 1995a. Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnology and Oceanography 40, 316–329.
- Wing, S.R., Botsford, L.W., Largier, J.L., Morgan, L.E., 1995b. Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Marine Ecology Progress Series 128, 199–211.