

Current reversals as determinants of intertidal recruitment on the central Oregon coast

Sarah E. Dudas, Brian A. Grantham, Anthony R. Kirincich, Bruce A. Menge, Jane Lubchenco, and John A. Barth

Dudas, S. E., Grantham, B. A., Kirincich, A. R., Menge, B. A., Lubchenco, J., and Barth, J. A. 2009. Current reversals as determinants of intertidal recruitment on the central Oregon coast. – *ICES Journal of Marine Science*, 66: 396–407.

The influence of current reversals on intertidal invertebrate recruitment was investigated using two seasons of nearshore physical and intertidal biological observations along the central Oregon coast, an intermittent upwelling system. In 1998, upwelling periods were punctuated by infrequent wind reversals and widespread increases in nearshore temperature, whereas 1999 was characterized by frequent, shorter wind reversals. In 1998, barnacle recruitment was best at the site experiencing more frequent reversals of the predominantly equatorward currents, higher poleward velocities, and coincident temperature increases. In 1999, barnacle recruitment peaked at the site with greater poleward current velocities, and maximum mussel recruitment at the site with consistent deep (10 m) onshore currents. Barnacle recruitment generally increased with onshore surface currents and temperature; mussel recruitment showed variable, weaker correlations. The data indicate that substantial decreases or complete reversals of upwelling-driven alongshore currents may be important for barnacle recruitment, but topographically driven differences in the response of currents to wind changes may generate local recruitment differences. This suggests that even relatively straight coastlines may have enhanced recruitment zones attributable to the variable local oceanography. Further, the interannual differences observed in current reversals and recruitment patterns highlight the potential importance of upwelling variation for onshore communities.

Keywords: barnacle, current reversal, invertebrate, larvae, mussel, recruitment, transport, upwelling.

Received 1 September 2007; accepted 5 October 2008; advance access publication 2 December 2008.

S. E. Dudas, B. A. Grantham, B. A. Menge, and J. Lubchenco: Department of Zoology, Oregon State University, 3029 Cordley Hall, Corvallis, OR 97331, USA. Present address of B. A. Grantham: Ontario Ministry of Natural Resources, Aquatic Research and Development Section, 2140 East Bank Drive, DNA Building, c/o Trent University, Peterborough, Ontario, Canada K9J 7B8. A. R. Kirincich and J. A. Barth: College of Oceanic and Atmospheric Sciences, Oregon State University, 104 COAS Administration Building, Corvallis, OR 97331, USA. Present address of A. R. Kirincich: Woods Hole Oceanographic Institution, 266 Woods Hole Road, Woods Hole, MA 02543, USA. Correspondence to S. E. Dudas: tel: +1 541 9083908; fax: +1 541 7373360; e-mail: dudass@science.oregonstate.edu.

Introduction

During coastal upwelling in eastern boundary currents, equatorward winds interact with the Coriolis force to cause offshore movement of surface water and its replacement with cool, nutrient-rich water from depth (Huyer, 1983). The regular renewal of nutrients in upwelling zones drives highly productive ecosystems that support many of the world's fisheries, making such regions important both ecologically and economically. In addition to nutrient pulses, the flow dynamics involved with upwelling in coastal areas are important to ecosystem dynamics. Persistent equatorward winds, and their corresponding currents, can result in the formation of upwelling fronts, where cold, dense, nutrient-rich, upwelled water meets warmer, less-dense oceanic water. Invertebrate larvae spawned from the intertidal can be carried offshore by surface currents and accumulate in these fronts (Roughgarden *et al.*, 1991; Grantham, 1997). Variations in upwelling circulation include periods when upwelling-favourable winds relax or reverse, generating downwelling currents with poleward and onshore flows (Huyer, 1983; Send *et al.*, 1987; Dale *et al.*, 2008), which may bring larvae back to

shore. Studies in upwelling systems around the world have shown links between invertebrate larval recruitment and correlates of upwelling, such as windstress and sea surface temperature (Farrell *et al.*, 1991; Roughgarden *et al.*, 1991; Wing *et al.*, 1995a, b; Shkedy and Roughgarden, 1997; Jonsson *et al.*, 2004; Ma and Grassle, 2004; Lagos *et al.*, 2005; Queiroga *et al.*, 2006). For example, crab settlement has been correlated with temperature increases associated with upwelling relaxation (Wing *et al.*, 1995a, b). Similarly, pulses in barnacle recruitment have been associated with temperature increases and decreases in offshore wind (Farrell *et al.*, 1991; Noda, 2004). Few studies have investigated mussel recruitment and upwelling events, but clam-settlement pulses have been correlated with downwelling (Weissberger and Grassle, 2003). A California study found a correlation between barnacle, but not mussel, recruitment and temperature (Broitman *et al.*, 2005).

The overall perspective that has grown out of these and similar studies will be termed the “current reversal” hypothesis. That is, for many species, recruitment to intertidal habitats depends on the shoreward transport of larvae during upwelling relaxation

© 2008 International Council for the Exploration of the Sea. Published by Oxford Journals. All rights reserved.
For Permissions, please email: journals.permissions@oxfordjournals.org.

and downwelling. We do not subscribe to the notion that this process explains all recruitment. There are alternative mechanisms of larval transport (e.g. internal waves, Shanks, 1986; internal tidal bores, Pineda, 1994; topographically generated fronts, McCulloch and Shanks, 2003; and residual tidal currents, Thiebaut *et al.*, 1998), and recruitment can occur without association with relaxation or downwelling, as we have observed along the coast of Oregon (BAM, unpublished data). Further, factors such as larval developmental stage or behaviour can be important (Dobrestov and Miron, 2001; Shanks and Brink, 2005). Nonetheless, the examples summarized above strongly suggest that relaxation and downwelling events can have an important influence on recruitment for many ecologically important species. Linking recruitment and oceanographic transport mechanisms requires detailed biological and oceanographic data and is challenging.

Scale mismatches are a major difficulty in understanding recruitment mechanisms. Although there have been many studies on the relationship between upwelling and recruitment, most have compared recruitment with large-scale measures, such as an upwelling index or regional winds, or with data taken well offshore (Wing *et al.*, 1998b), or in sheltered, lower wave-exposure areas and/or conditions (Farrell *et al.*, 1991; Wing *et al.*, 2003). These studies often provide valuable insight (Roughgarden *et al.*, 1991), but they do not provide the resolution necessary to understand the cause of among-site (scales of kilometre to tens of kilometre) variation. Therefore, the physical mechanisms that ultimately transport larvae onshore and produce spatial variation in recruitment at local scales (km) remain poorly understood; this inner shelf remains a “black box”. The difficulties in measuring oceanographic variables over the inner shelf, particularly in high wave-exposure environments, doubtless underlie the previous reliance on large-scale oceanographic patterns. Here, our focus was on relating physical processes on the inner shelf, within 1 km of shore, to patterns of recruitment of key sessile invertebrate species on rocky shores.

Oceanographic background

The oceanographic dynamics of the Oregon coast are strongly influenced by the California Current system (Huyer, 1983; Barth, 2003). During winter, currents are typically poleward, but from mid-April through September, equatorward upwelling-favourable winds are interspersed with relaxations or reversals (i.e. downwelling-favourable winds) approximately every 3–10 d (Hickey, 1979; Huyer, 1983). Relaxations and downwelling winds frequently result in poleward flows along the coast (Kosro, 1987, 2005).

Our study area encompasses 75 km of the central Oregon coast differing in shelf width (i.e. distance to the 200-m isobath), from 32 km near Cape Foulweather to >61 km near Heceta Bank (Figure 1). Currents in the region can be linked directly to wind-forcing and the response to winds in generally <12 h, often within <6 h over the inner shelf (ARK and co-workers, unpublished data), although this can vary spatially, with wind-forcing having better correlations with currents at the northern end of the study region (Kosro, 2005). During upwelling, currents in the area are steered along isobaths (Figure 1), so the coastal jet is close to shore in the north, but follows the 100 m isobath offshore around Stonewall and Heceta Banks in the south (Castelao and Barth, 2005). An area of weak mean flow develops inshore of the jet at the south end of Heceta Bank (Oke *et al.*, 2002; Kosro, 2005). During relaxations, the flow reverses inshore of 50–

100 m, whereas the offshore flow continues equatorward (Send *et al.*, 1987), resulting in the formation of a cyclonic circulation over Heceta Bank (Oke *et al.*, 2002; Kosro, 2005). Nearshore phytoplankton and detritus concentrations are higher there than at the more northern sites (Menge *et al.*, 1997a), possibly reflecting the retentive nature of this feature. This is associated with between-community differences in these regions (Menge *et al.*, 1994, 1997b; Menge, 2000). Long-term datasets of invertebrate recruitment along the Oregon coast show persistent annual differences in barnacle and mussel recruitment among sites (Connolly *et al.*, 2001; Menge *et al.*, 2004). These differences may be attributable to oceanographic conditions that vary along the Oregon coast and influence larval availability and onshore delivery. Larval availability will be influenced not only by oceanography but also by spawning timing and larval production.

Species background

Barnacles and mussels were chosen as the focal organisms in this study, because these two taxa are dominant space occupiers on exposed rocky shores in Oregon and other places worldwide

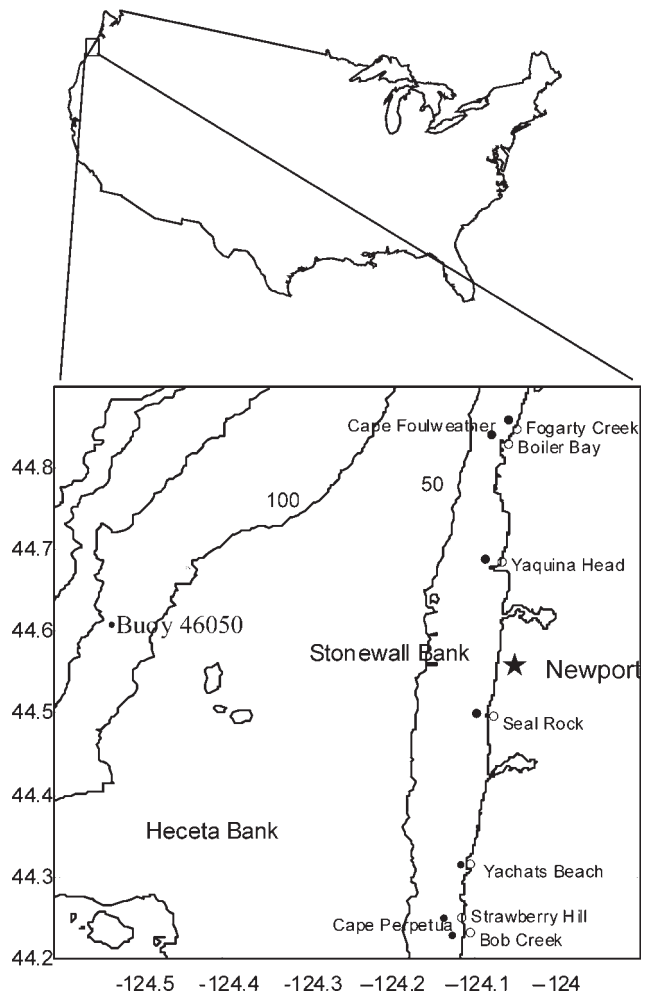


Figure 1. Location of moorings (filled circles) and intertidal sampling sites (open circles) on the Oregon coast. The first contour line is at 50 m; others are at 100-m intervals. During upwelling conditions, alongshore currents flow equatorward and across-shore currents offshore.

(Menge and Branch, 2001), and they are very important ecologically, serving as food, substratum and shelter for other intertidal organisms. Intertidal barnacle species in the region include *Balanus glandula*, *Balanus nubilus*, *Chthamalus dalli*, *Pollicipes polymerus*, and *Semibalanus cariosus*. Mussels include *Mytilus trosulus* and *Mytilus californianus*. These taxa range from Alaska to California (Lamb and Hanby, 2005). Generally, barnacles and mussels in the region reproduce during spring and summer (Leslie, 2004; Petes, 2007) and have planktonic larvae that can spend weeks (Pyefinch, 1948; Grantham *et al.*, 2003) in the water column before settlement. Specific spawning times and/or larval production magnitude can be influenced by a number of factors, including temperature, food availability, and intertidal height (Hines, 1978). Mussel larvae in our study area appear to have variable horizontal distributions (Rilov *et al.*, 2008) and may be depth-stratified, with competent larvae being found in midwater. Although relatively little is known about the barnacle larval distribution in Oregon, in central California, *B. glandula*, *P. polymerus*, and *Chthamalus* spp. cyprids tend to be found near the surface (Grosberg, 1982).

The goal of our study was to investigate the influence of current reversals by examining the relationship between nearshore (<1 km from shore) oceanographic processes and intertidal barnacle and mussel recruitment at both regional (tens of kilometre) and local (km) scales. Our approach was to measure recruitment and nearshore oceanographic conditions simultaneously over the inner shelf at multiple sites along the central coast of Oregon. The primary objectives were to determine: (i) the relationship between current reversals and barnacle and mussel recruitment; (ii) the coherence of recruitment among sites; and (iii) the influence of between-year differences in upwelling characteristics on recruitment. We hypothesized that if upwelling relaxations and/or downwelling events influence intertidal recruitment, then current reversals (and associated increases in temperature and wind direction changes) should coincide with barnacle and mussel recruitment events.

Methods

Study area

Four sites were studied in 1998 and five in 1999 (Figure 1). Sites were chosen to represent the range of variation in intertidal community structure observed along the central coast of Oregon and to span the differences in shelf width that affect upwelling dynamics in this region. Two of the intertidal sites, Boiler Bay and Strawberry Hill, have been subjected to intensive research for the past two decades (Menge, 2000; Menge *et al.*, 2004). The low intertidal sessile community at Boiler Bay is dominated by macroalgae, and the abundance of both barnacles and mussels is low, whereas at Strawberry Hill the opposite is true. Strawberry Hill also has higher densities of limpets and invertebrate predators and, correspondingly, higher rates of grazing and predation, as well as more rapid barnacle and mussel growth (Menge *et al.*, 1997b, 2008; Menge, 2000; Freidenburg *et al.*, 2007). These differences in community structure are hypothesized to result from variation in oceanographic conditions between the northern and southern ends of the study area.

Moorings and recruitment

At each site, moorings were deployed 600–1000 m offshore in water 15 m deep. Moorings were equipped with Onset

Stowaway® XTI temperature loggers (sampling every 2 min) and Oregon Environmental Instruments vector-averaging current meters (VACMs; sampled for 1 min every 4 min). Temperature loggers were located 3, 8, and 13 m deep. In 1998, VACMs were deployed at 4 and 13 m on each of four moorings. To provide greater spatial coverage in 1999, a single VACM was located at 10 m on each of five moorings. Therefore, the currents in 1999 may more closely resemble the “deep” currents of 1998. Current-meter data were corrected for magnetic declination, then rotated to the first principal axis of the depth-averaged currents. For the 1998 current-meter data, the first principal axis was taken as the averaged currents from 4 and 13 m, and for 1999, as the 10 m currents only. Hourly averaged current data were used to reduce any potential bias attributable to surface waves below the instrumental uncertainty. Current data were filtered, using a 40-h half-power low-pass filter, to isolate the subtidal components before computing daily averages. Hourly wind data were obtained from the National Data Buoy Center’s Stonewall Banks buoy, 20 nautical miles west of Newport, OR (Buoy 46050: 44°38′28″N 124°29′59″W). Local winds are an appropriate indicator of current variability in the region over a broad range of time-scales (2–10 d weather-event scales to inter-annual changes; Huyer *et al.*, 1978). Mesoscale eddies in the offshore deep region have a small influence on currents over the inner shelf compared with the local wind-driven currents, so were excluded from the analysis. Upwelling episodes were indicated by equatorward winds and currents, and downwelling episodes by poleward winds and currents.

Concurrent measurements of recruitment were made at intertidal sites directly inshore of the moorings. Recruitment of the barnacles *B. glandula*, *C. dalli*, and *P. polymerus* was measured at each intertidal site using five Plexiglas plates covered with 3 M Safety-Walk® anti-slip tape, which provides a textured surface for settlement (Farrell *et al.*, 1991; Menge *et al.*, 1999). Mussel recruitment rates were measured using five S.O.S. (Tuffy™) scrub pads that provide a plastic matrix for mussels to set in (Menge *et al.*, 1994). Plates and tuffys were changed on periods ranging from 3 to 14 d, then returned to the laboratory where barnacle cyprids and metamorphs and settled mussels were identified and counted. It is important to note that because of the variable deployment period of the recruitment collectors, post-settlement processes (e.g. mortality through predation, desiccation, or thermal stress, and/or increased recruitment attributable to facilitation by congeners) may have influenced our observed recruitment. Moreover, because of the longer deployment intervals, we were not able to establish the specific day of recruitment pulses, and/or there may have been more than one recruitment pulse per deployment. More recent, high-sampling-frequency studies have been conducted to resolve this issue and will be the subject of later manuscripts.

Statistical analysis

For each biological deployment interval, average daily barnacle and mussel recruitment and physical oceanographic conditions (e.g. current velocity, direction, water temperature) were determined. Average physical oceanographic conditions were selected for analysis instead of the variance in oceanographic conditions, because preliminary analyses indicated that averages were better able to capture upwelling and downwelling signals. To calculate average currents, the magnitude of the currents in across-shore and alongshore directions were determined, then averaged over

the corresponding biological deployment intervals. The data were not normally distributed, so Spearman's rank correlations were used to determine the association between recruitment during the 3–14-d intervals, and the average physical oceanographic conditions during the same time. Owing to the variable deployment periods, we were not able to conduct lagged correlations. Because the biological sample deployment periods (i.e. recruitment collectors) were relatively long compared with the physical measurements, no autocorrelation within the time-series used for correlation analysis was apparent (i.e. Box-Ljung Q statistics were <0.05). Statistical analyses were conducted using SYSTAT (version 10), Statistica (version 7.0), and Matlab (version 7.0.4.365).

Results

Current reversals and recruitment

In both years of the study, predominantly upwelling-favourable winds were punctuated by reversals to downwelling-favourable

winds, each resulting in coast-wide increases in nearshore water temperature (Figures 2 and 3). In 1998, alongshore wind reversals beginning around days 191 and 209 (July 11 and 29) were accompanied by reversals in alongshore surface and bottom currents, and increased barnacle recruitment at the southern sites Strawberry Hill and Bob Creek (Figure 2). In contrast, at Fogarty Creek (northern site), current reversals and barnacle recruitment only took place during the second wind reversal. At Boiler Bay (northern site) barnacle recruitment took place during both wind reversals, but this was only accompanied by alongshore and across-shore current reversals during the second event. During the first wind reversal, only across-shore currents reversed. Examination of all sites showed slower maximum poleward velocities at the northern sites (i.e. 12 and 25 cm s^{-1} for Fogarty Creek and Boiler Bay, respectively) compared with the sites some 80 km to the south (i.e. 32 cm s^{-1} for both Strawberry Hill and Bob Creek) during reversal events.

In 1999, upwelling-favourable winds were punctuated by shorter, more frequent periods of downwelling-favourable winds

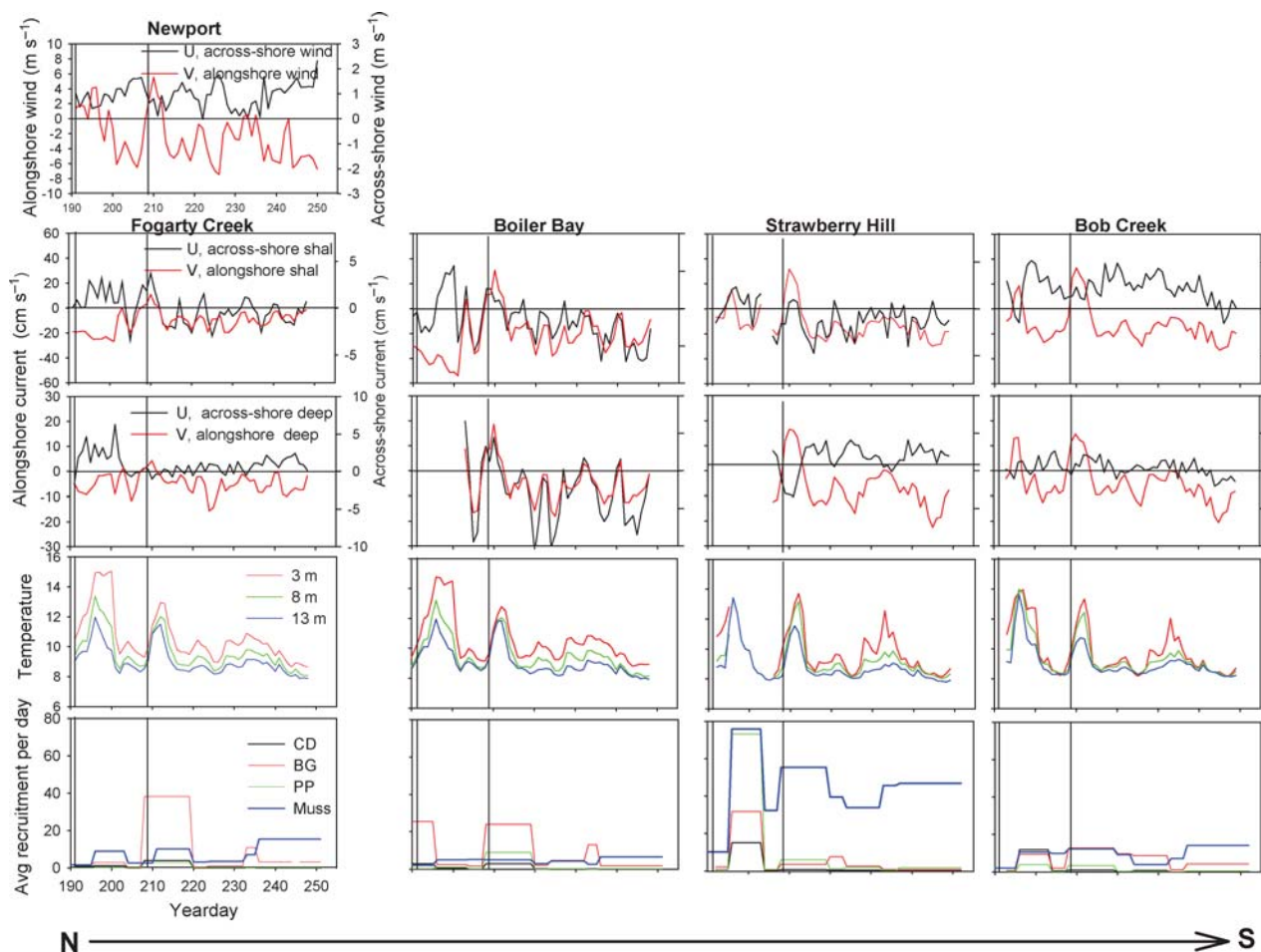


Figure 2. Physical and biological measurements, 1998. The upper panel is Newport wind velocities (m s^{-1}). Panels under each site depict: (top) shallow (4 m) across-shore (U) and alongshore (V) current velocities (cm s^{-1}); (upper middle panel) deep (13 m) alongshore and across-shore current velocities (cm s^{-1}); (lower middle panel) temperature ($^{\circ}\text{C}$) at 3 m (red), 8 m (green), and 13 m (blue) depth; (bottom) average daily barnacle recruitment per 100 cm^2 for the barnacles *B. glandula* (red), *C. dalli* (black), and *P. polymerus* (green), and the mussels *Mytilus* spp. (blue). Note that recruitment time-series were not continuous measurements, but are shown as such to clarify temporal trends between different species and taxa. For winds and currents, positive values represent onshore (U) or poleward (V) directions, and negative values represent offshore (U) or equatorward (V) directions. Vertical lines denote days 191 and 209, when wind reversals began. Full oceanographic datasets are shown for detail. For correlation analysis, the physical data were averaged over the biological deployment intervals.

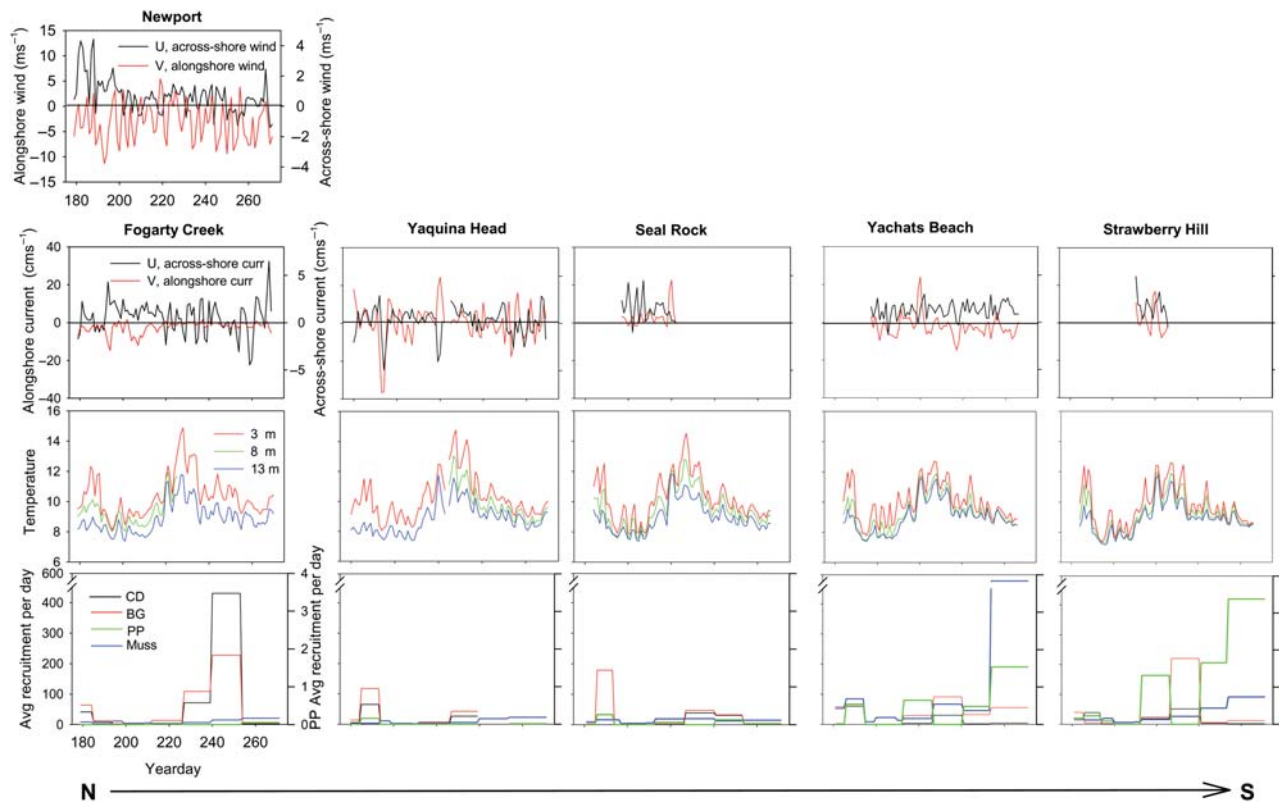


Figure 3. Biological and physical measurements, 1999. Panels are similar to Figure 2, but with current panels from each site representing velocities at a single (10 m) depth.

than in 1998 (Figure 3). Recruitment pulses at Fogarty Creek and Yachats Beach (60 km to the south) coincided with weak equatorward currents (e.g. day 240). At Yaquina Head (20 km from Fogarty Creek), there was recruitment when the current reversed to downwelling-favourable (poleward) currents.

Upwelling characteristics

In 1999, upwelling conditions were markedly different from 1998. Upwelling-favourable winds in 1999 were slightly stronger (by 1 m s^{-1}) and frequently changed direction, but the total

number of days with downwelling winds (i.e. poleward) was approximately twice that of 1998 (Table 1).

In 1998, periods of equatorward alongshore currents (consistent with upwelling) and their duration were relatively consistent among sites. The number of periods with equatorward (upwelling) currents at each station ranged from 4 to 6, and their duration ranged from 11.7 to 14.8 d (Table 1). The number of periods of poleward (downwelling) currents ranged from 3 to 5, and their duration from 1 to 2.7 d. The upwelling (i.e. equatorward) current velocities varied among sites, Boiler Bay (northern site)

Table 1. Upwelling characteristics for 1998 and 1999 including the number of events, the average alongshore depth-averaged velocity for upwelling (equatorward) and downwelling (poleward) currents (cm s^{-1}), and average duration at Fogarty Creek (FC), Boiler Bay (BB), Strawberry Hill (SH), Bob Creek (BC), Yaquina Head (YH), and Yachats Beach (YB), and Newport (NP) winds (m s^{-1}).

Parameter	Site	Upwelling			Downwelling		
		Number of events	Average velocity	Average duration	Number of events	Average velocity	Average duration
Currents 1998	FC	6	-5.5	12.3	5	1.4	1.0
	BB	5	-16.6	11.7	4	5.2	2.2
	SH	5	-13.2	11.8	4	8.2	2.0
	BC	4	-11.8	14.8	3	9.6	2.7
Currents 1999	FC	13	-2.4	3.8	13	0.8	1.1
	YH	17	-5.6	1.8	16	4.9	2.6
	YB	10	-4.0	3.8	10	3.1	2.7
NP wind 1998		10	-3.2	5.4	9	1.9	1.8
NP wind 1999		20	-4.3	3.0	19	1.8	1.2

Sites are listed north to south. Onshore, poleward currents are positive, and offshore, equatorward currents are negative. The period ranges from year days 182 to 251.

having the highest, and Fogarty Creek (northern site) the lowest. Downwelling current velocities tended to increase southwards by site from Fogarty Creek to Bob Creek.

In 1999, the number of periods with equatorward currents ranged from 10 to 13, and their duration from 1.8 to 3.8 d, and periods of poleward currents ranged from 10 to 13 and their duration from 1.1 to 2.7 d (Table 1). Of the three sites with sufficient current data for the whole 1999 season (from north to south, Fogarty Creek, Yaquina Head, and Yachats Beach), Yaquina Head had the highest upwelling and downwelling velocities.

Fogarty Creek is the only site for which we have sufficient current data for annual comparisons. At Fogarty Creek, depth-averaged alongshore current velocities were weaker and alternated more frequently between upwelling (equatorward) and downwelling (poleward) in 1999 than in 1998. Further, in 1999, periods of equatorward currents were shorter, durations of poleward currents similar, and the total number of poleward current days almost three times greater than in 1998. In terms of larval transport, this translates to a net equatorward transport (assuming passive dispersal and homogenous vertical distribution) of 151 km in 1998 compared with 12 km in 1999.

Timing and magnitude of recruitment pulses

Barnacle and mussel recruitment levels were generally positively correlated among all sites for 1998 and 1999, although the significance of the correlations varied between sites and species (Table 2). Sites closer in proximity had higher correlations in 42 of 80 cases.

In 1998, barnacle recruitment events at all sites coincided with warming events and were generally during alongshore current reversals or when the equatorward velocity decreased (Figure 2). In 1999, the long deployment periods of onshore recruitment relative to the rapid switches between upwelling and downwelling make it more difficult to determine whether there is a clear relationship between physical parameters and recruitment (Figure 3). However, 1999 barnacle recruitment pulses did appear to coincide with conditions similar to those of 1998, e.g. warmer temperature.

In 1998, mussel recruitment often coincided with current reversals and warming events, at least at Fogarty Creek (northern-most site) and Strawberry Hill (75 km to the south). Pulses were less pronounced, however, particularly at Boiler Bay (northern site), where mussel recruitment levels were lowest. In 1999, mussel recruitment did not appear to coincide with warming events or current reversals.

In 1998, Strawberry Hill (southern site) had the highest daily average barnacle and mussel recruitment during the study (mean ± s.e. barnacles, 19 ± 4; mussels, 43 ± 7). In 1999, maximum recruitment varied between the sites, with Yachats Beach (southern site) having the highest mussel recruitment (101 ± 62) and Fogarty Creek (northern site) having the highest levels of barnacle recruitment (110 ± 76). In both cases, this was due to an exceptionally high recruitment pulse later in the season. At Fogarty Creek, barnacle recruitment in 1999 was 11 times that of 1998. Similarly at Strawberry Hill, barnacle recruitment in 1999 was three times that of 1998. Mussel recruitment was variable between years, Fogarty Creek only showing a slight increase (i.e. only two more mussels per day) in 1999, and Strawberry Hill showing a decrease (by 10 mussel d⁻¹).

Table 2. Among-site Spearman's rank-order correlation coefficients for barnacle and mussel recruitment.

1998				1999				
Site	FC	BB	SH	Site	FC	YH	SR	YB
CD								
BB	0.95			YH	0.76			
SH	0.73	0.74		SR	0.87	0.77		
BC	0.53	0.41	0.81	YB	0.66	0.90	0.84	
				SH	0.65	0.88	0.76	0.93
BG								
BB	0.62			YH	0.57			
SH	0.33	0.19		SR	0.71	0.89		
BC	0.36	0.24	0.74	YB	0.76	0.83	0.97	
				SH	0.81	0.69	0.68	0.79
PP								
BB	0.86			YH	-0.22			
SH	0.67	0.85		SR	0.28	0.88		
BC	0.73	0.77	0.87	YB	0.66	0.55	0.88	
				SH	0.42	0.61	0.81	0.87
Total barnacles								
BB	0.55			YH	0.57			
SH	0.52	0.31		SR	0.71	0.91		
BC	0.52	0.21	0.91	YB	0.76	0.83	0.95	
				SH	0.67	0.86	0.81	0.88
Mussels (<i>Mytilus</i> spp.)								
Site	FC	BB	SH	Site	FC	YH	SR	YB
BB	0.83			YH	0.93			
SH	0.93	0.76		SR	0.53	0.50		
BC	0.68	0.88	0.59	YB	0.67	0.78	0.75	
				SH	0.85	0.87	0.77	0.80

Categories were *C. dalli* (CD), *B. glandula* (BG), *P. polymerus* (PP), total barnacles, and mussels (*Mytilus* spp.) for 1998 (left) and 1999 (right) at Fogarty Creek (FC), Boiler Bay (BB), Strawberry Hill (SH), Bob Creek (BC), Yaquina Head (YH), Seal Rock (SR), and Yachats Beach (YB). Sites are listed north to south top to bottom and left to right. Significant correlations ($p < 0.05$) are emboldened. Sample size ranges from $n = 8$ to 10.

Physical and biological correlations

In 1998, recruitment of *C. dalli* was generally positively correlated with onshore surface currents, poleward winds, and increased temperature at the two northern sites, Fogarty Creek and Boiler Bay (Table 3). At Boiler Bay, *B. glandula* and total barnacle recruitment were positively correlated with poleward winds and deep poleward currents. At Boiler Bay, mussel recruitment was negatively correlated with poleward winds, whereas coast-wide mussel recruitment was positively correlated with poleward winds. Coast-wide recruitment of *B. glandula* was positively correlated with shoreward shallow currents, deep poleward currents, and increased temperature. *Chthamalus dalli* recruitment showed similar patterns to the total barnacle recruitment, which also increased with poleward winds (Table 3). Therefore, at least at the northern Cape Foulweather sites, barnacle recruitment tended to increase with conditions indicative of downwelling, poleward and onshore currents, poleward winds, and warmer temperatures. Associations between recruitment and physical conditions at the southern sites Strawberry Hill and Bob Creek tended to be

Table 3. Spearman's rank-order correlation coefficients for the recruitment of the barnacle species *C. dalli* (CD), *B. glandula* (BG), *P. polymerus* (PP), all species combined (Totbarn), and mussels, with 4 m (shal) and 13 m (deep) across-shore (U) and alongshore (V) currents (cm s^{-1} , positive is onshore or poleward, negative is offshore or equatorward), 3, 8, and 13 m temperatures ($^{\circ}\text{C}$) and Newport winds (m s^{-1}), followed by correlations for coastwide averages in 1998 at four sites, Fogarty Creek (FC), Boiler Bay (BB), Strawberry Hill (SH), and Bob Creek (BC), and 1999 with current measurements taken at 10 m, and sites, FC, Yaquina Head (YH), Seal Rock (SR), Yachats Beach (YB), and SH.

1998										1999							
Site/species	U shal	V shal	U deep	V deep	3 m temp.	8 m temp.	13 m temp.	U wind	V wind	Site/species	U Curr.	V Curr.	3 m temp.	8 m temp.	13 m temp.	U wind	V wind
FC/CD ²	0.73	-0.05	0.30	0.46	0.81	0.81	0.81	-0.15	0.73	FC/CD ¹	-0.90	0.75	0.73	0.71	0.72	0.32	-0.33
FC/BG ¹	0.50	0.54	0.19	0.50	0.29	0.29	0.29	-0.10	0.52	FC/BG ²	-0.85	0.75	0.83	0.77	0.80	0.28	-0.13
FC/PP ²	0.50	0.06	0.34	0.42	0.46	0.46	0.46	0.39	0.27	FC/PP ³	0.09	0.32	0.16	0.66	0.39	-0.43	0.05
FC/Totbarn	0.62	0.43	0.24	0.60	0.45	0.45	0.45	-0.14	0.60	FC/Totbarn	-0.88	0.73	0.8	0.714	0.75	0.35	-0.25
FC/Mussels	-0.19	0.10	0.31	0.07	0.00	0.07	0.07	-0.05	-0.48	FC/Mussels	-0.13	0.43	-0.12	-0.49	0.12	-0.27	0.15
BB/CD ³	0.62	-0.01	0.16	0.90	0.83	0.90	0.85	-0.27	0.78	YH/CD ²	0.32	-0.12	0.78	-0.50	0.68	0.51	-0.51
BB/BG ¹	0.38	-0.05	-0.21	0.79	0.64	0.68	0.46	-0.54	0.86	YH/BG ¹	0.48	-0.02	0.86	0.50	0.67	0.48	-0.50
BB/PP ²	0.39	-0.18	0.16	0.47	0.11	0.31	0.32	0.52	0.05	YH/PP ³	0.33	-0.44	0.16	-0.87	0.23	0.08	-0.66
BB/Totbarn	0.45	0.12	-0.21	0.79	0.64	0.68	0.46	-0.54	0.86	YH/Totbarn	0.48	-0.02	0.86	0.50	0.67	0.48	-0.50
BB/Mussels	-0.36	0.10	-0.14	-0.07	-0.64	-0.43	-0.26	0.62	-0.74	YH/Mussels	-0.20	-0.23	0.18	-	0.45	-0.20	-0.27
SH/CD ³	0.31	0.65	-0.06	0.32	0.25	0.23	0.66	0.17	0.30	SR/CD ²	n/a	n/a	0.52	0.69	0.64	-0.12	-0.46
SH/BG ²	0.45	0.52	-0.26	0.66	0.36	0.57	0.69	-0.36	0.36	SR/BG ¹	-	-	0.55	0.67	0.65	0.14	-0.35
SH/PP ¹	-0.07	0.02	0.37	0.14	-0.29	0.00	0.24	0.43	-0.24	SR/PP ³	-	-	0.33	0.41	0.37	-0.25	-0.42
SH/Totbarn	0.21	0.43	0.09	0.37	0.11	0.36	0.57	0.05	0.14	SR/Totbarn	-	-	0.55	0.67	0.65	0.14	-0.35
SH/Mussels	0.19	0.48	-0.43	0.43	0.31	0.43	0.26	-0.14	0.54	SR/Mussels	-	-	0.80	0.80	0.80	-0.40	-0.20
BC/CD ²	0.42	0.30	0.64	0.24	0.30	0.46	0.46	0.35	0.04	YB/CD ²	0.63	-0.11	0.70	0.85	0.85	0.11	-0.04
BC/BG ¹	0.69	0.10	0.19	-0.07	-0.19	0.12	0.12	0.17	-0.19	YB/BG ¹	0.64	-0.07	0.68	0.82	0.82	0.14	-0.04
BC/PP ³	0.26	0.32	-0.16	0.24	0.34	0.60	0.60	0.05	0.28	YB/PP ³	0.79	0.32	0.20	0.37	0.37	-0.32	-0.04
BC/Totbarn	0.71	0.05	0.26	-0.01	-0.05	0.26	0.26	0.21	-0.19	YB/Totbarn	0.64	-0.07	0.68	0.82	0.82	0.14	-0.04
BC/Mussels	-0.38	-0.21	0.10	-0.02	-0.12	-0.02	0.02	0.38	-0.38	YB/Mussels	0.25	-0.58	0.18	0.29	0.46	-0.25	-0.61
										SH/CD ²	n/a	n/a	0.78	0.80	0.66	0.58	0.02
										SH/BG ¹	-	-	0.73	0.85	0.82	0.40	0.18
										SH/PP ³	-	-	0.22	0.32	0.39	-0.12	-0.14
										SH/Totbarn	-	-	0.8	0.85	0.75	0.55	0.1
										SH/Mussels	-	-	0.20	0.30	0.47	0.00	-0.17
Coast-wide average										Coast-wide average							
CD ³	0.67	-0.05	0.29	0.79	0.64	0.76	0.76	0.12	0.36	CD ²	-0.78	-0.22	0.65	0.70	0.72	0.33	-0.33
BG ¹	0.91	0.41	-0.29	0.95	0.83	0.91	0.91	-0.33	0.81	BG ¹	-0.77	-0.22	0.73	0.72	0.70	0.47	-0.37
PP ²	0.55	-0.33	0.21	0.36	0.12	0.26	0.26	0.38	-0.10	PP ³	-0.32	-0.05	0.05	0.32	0.41	-0.17	-0.24
Totbarn	0.93	0.24	-0.14	0.98	0.91	0.95	0.95	-0.36	0.79	Totbarn	-0.78	-0.21	0.65	0.70	0.72	0.33	-0.33
Mussels	0.38	-0.26	0.12	0.24	0.10	0.12	0.12	0.26	0.71	Mussels	-0.75	-0.32	0.32	0.45	0.67	0.0	-0.48

Superscripts denote the abundance rank of the barnacle species, 1 denoting the most abundant. Significant correlations ($p < 0.05$) are emboldened, and n/a indicates insufficient data. Sample size ranges from $n = 6$ to 10.

similar, but correlations were not significant. In no case was recruitment of *P. polymerus* significantly correlated with any physical variable.

In 1999, similar patterns were observed (Table 3). At Fogarty Creek (northern site) recruitment of *B. glandula*, *C. dalli*, and total barnacles were negatively correlated with deep (10 m) onshore currents, but positively correlated with alongshore poleward currents and warmer temperatures. At the other four sites, correlations were primarily positive with temperature (including *B. glandula*, *C. dalli*, and total barnacles). Mussel recruitment increased with higher temperature at Seal Rock, the only site where mussel recruitment was associated with a physical process. At Yachats Beach (southern site), *P. polymerus* recruitment increased with shoreward deep currents, the only case in which this barnacle showed an association with a physical process. Seal Rock and Strawberry Hill moorings had limited current-meter deployments, which were insufficient for statistical analysis.

Coast-wide patterns were generally similar for *B. glandula*, *C. dalli*, and total barnacles, with negative correlations with deep onshore flows and warmer temperatures (Table 3). Coast-wide mussel recruitment was negatively correlated with deep onshore currents, and positively correlated with deep temperature. Note that the negative correlations with deep onshore flows implies that surface-dwelling larvae were swept offshore during upwelling, consistent with the patterns observed in 1998, where positive correlations were observed between recruitment and onshore near-surface currents.

Differences in upwelling characteristics between years may have influenced the correlation analyses for each year. The frequent alternation between upwelling and downwelling events in 1999 made the analyses more difficult, because physical processes that were varying on the order of days were being correlated with biological deployments ranging from several days to weeks. In 1998, when reversals were more sustained, the recruitment-collector deployments were similar in duration to reversal-event scales. Moreover, the relative magnitude of across-shore currents was much weaker than that of alongshore currents, making them more difficult to measure accurately (i.e. a lower signal-to-noise ratio), and their results can be influenced strongly by a slight variation in the axis of rotation. Despite these mismatches and the low biological sampling frequency, however, we observed evidence for strong associations between shoreward shallow currents, warmer temperatures, and poleward currents, all indications of downwelling.

Discussion

Recruitment, physical processes, and the current-reversal hypothesis

Recent modelling studies indicate that current reversals, like those observed here, are driven by alongshore pressure gradients set up by an interaction between upwelling winds and coastal topography (Gan and Allen, 2002; Oke *et al.*, 2002). When upwelling-favourable (i.e. equatorward) winds are reduced to near zero, these pressure gradients drive poleward and onshore flows near the coast. Reversal of these poleward winds causes poleward, onshore flow, resulting in downwelling conditions. Our results reveal alongshore current reversals almost simultaneously across the study area in response to extended wind reversals (Figures 1 and 2; Kirincich, 2005), supporting the hypothesis that large-scale rather than local processes drive upwelling and downwelling events. Across-shore currents were weaker and more variable among sites, but generally

reversed at similar times. For example, in 1998 during the second wind reversal, all sites experienced both across-shore and alongshore current reversals (Figure 2).

Empirical studies by Send *et al.* (1987) show that during relaxations, the direction of alongshore flow is usually well-defined, but that across-shore flow often fluctuates from onshore to offshore, and in some cases there may not even be onshore flow. These results are consistent with our observations, including the absence of current reversals at our northern sites during some relaxations. Further, although current reversals would be expected when upwelling winds drop to near zero (Gan and Allen, 2002; Oke *et al.*, 2002), our results suggest that periods with average poleward winds may be necessary to produce the current reversals that move larvae onshore before recruitment. Because of logistical constraints on the frequency of our recruitment measurements, however, we are unable to pinpoint the precise timing of recruitment events. This limited the correlation analysis, because physical conditions had to be averaged over the length of the recruitment deployments. Also, we could not calculate the cumulative wind-stress necessary to produce a recruitment event or the distance larvae may have had to travel during such an event. However, data from Wing *et al.* (1995b) show that a relaxation in equatorward windstress 3–5-d long produces poleward currents of 15–20 cm s⁻¹ (Send *et al.*, 1987; Breaker and Bratkovich, 1993). Our results were similar, with maximum alongshore velocities of 32 cm s⁻¹, suggesting poleward transports of up to 28 km d⁻¹.

Our barnacle recruitment results were consistent with others that show correlations between changes in windstress or sea surface temperature, and regional recruitment of barnacles, crabs, and sea urchins (Farrell *et al.*, 1991; Roughgarden *et al.*, 1991; Wing *et al.*, 1995a, b; Shkedy and Roughgarden, 1997; Almeida and Queiroga, 2003), but they go further in demonstrating the link between wind reversals, nearshore current reversals, and recruitment at local scales. Previous studies have suggested a relationship between current reversals and recruitment events (Wing *et al.*, 1995a, b, 1998a; Morgan *et al.*, 2000), but none has measured nearshore currents and recruitment concurrently and directly. Our results are evidently the first to demonstrate a link between local-scale currents and recruitment and provide support for the current-reversal hypothesis.

Our study contrasts with prior studies in other ways. First, earlier studies were done largely in California, a region that experiences upwelling relaxation events (i.e. equatorward windstress close to zero) more often than actual wind reversals. In Oregon, the winds are usually either equatorward or poleward, and are rarely near zero (ARK and JAB, unpublished data). Therefore, in Oregon, onshore transport is more likely during current reversals rather than relaxations, as in California. The California studies were also largely carried out in regions with complex coastal topography (Wing *et al.*, 1995b, 1998a, b; Morgan *et al.*, 2000), whereas this study was done in Oregon, in a region with relatively simple, linear coastal topography. For example, prominent capes and points, such as Cape Blanco, Point Reyes, Cape Mendocino, and Point Arena, exhibit similar oceanographic dynamics, with the coastal jet separating near the headland (Kosro and Huyer, 1986), forming potentially retentive upwelling shadows (Graham and Largier, 1997; Wing *et al.*, 1998b; Morgan *et al.*, 2000) or eddies (Washburn *et al.*, 1993) in the lee of the capes. The central Oregon coastline, in contrast, has few large shoreline features that might be expected to influence oceanographic conditions similarly. However, like many coastal regions, Oregon's

coast has complex bathymetry and varies in shelf characteristics (width and topography). These variations in shelf topography are thought to influence oceanography along the coast (Kosro, 1987; Castelao and Barth, 2005). Windforcing along the Oregon coast is spatially uniform, but coastal circulation is variable (ARK and JAB, unpublished data). North of Newport, across-shore circulation is consistent with standard conceptual two-dimensional across-shore circulation (i.e. offshore surface flow and onshore bottom flow during upwelling; Oke *et al.*, 2002). South of Newport, where alongshore topography is more variable (e.g. wider shelf and offshore bank), circulation is three-dimensional (i.e. it varies across-shore with depth, and along-shore), and circular flow is often observed (Oke *et al.*, 2002; Castelao and Barth, 2005; Kosro, 2005). During upwelling-favourable winds, alongshore flow is higher in the north (e.g. Fogarty Creek, Boiler Bay) than at southern sites (e.g. Yachats Beach, Strawberry Hill, Bob Creek), where nutrients and phytoplankton abundance are greater (Leslie *et al.*, 2005; Barth *et al.*, 2007; Menge *et al.*, 2008). Correspondingly, levels of chlorophyll *a* over the inner shelf at Strawberry Hill show consistently higher levels than at Boiler Bay (Menge *et al.*, 1997b; Leslie *et al.*, 2005). With higher productivity, we might expect the southern sites to have better recruitment (i.e. more food becoming available), but this is not always the case, suggesting that site-specific topography may be influential. The importance of local topography has been highlighted in a recent Oregon study in which a topographically generated front at the mouth of a bay appeared to influence the distribution and shoreward transport of larvae (McCulloch and Shanks, 2003). Most of our sites are on relatively straight coastline, but perhaps recruitment at Boiler Bay (a northern site) could be influenced by a similar mechanism.

Although there was between-site variation in the strength and significance of the recruitment and physical variable correlations, when all the data were averaged, coast-wide correlation patterns were similar (significant positive correlations between recruitment and surface onshore flow and warmer temperature; e.g. correlations between total barnacle recruitment and onshore surface flow and 3 m temperatures were 0.93 and 0.91, respectively, in 1998). Barnacle and mussel recruitment were relatively coherent among sites. For example, comparing the northernmost with successively more southerly sites, recruitment of *C. dalli* at Fogarty Creek in 1998 was positively correlated with *C. dalli* recruitment at Boiler Bay ($r = 0.95$), Strawberry Hill ($r = 0.73$), and Bob Creek ($r = 0.53$). For mussels, correlations were 0.83, 0.93, and 0.68 for the same comparisons. These patterns further support our belief that regional processes influence recruitment.

The correlations between mussel recruitment and onshore flows and temperature increases were much weaker and more variable than for barnacle recruitment (Table 3, Figures 2 and 3). Although relatively little is known about the vertical distribution in the water column of barnacles and mussels in the Pacific Northwest, early research suggests that barnacle depth distribution may be species-specific. In central California, *B. glandula* cyprids tend to be found near the surface (Grosberg, 1982), along with *P. polymerus* and *Chthamalus* spp., although distributions can change within oceanographic features (i.e. in southern California upwelling fronts; Pineda, 1999). Other species such as *Balanus crenatus* and *Semibalanus* spp. cyprids are found deeper in the water column (Grosberg, 1982; Miron *et al.*, 1995). Mussel larvae often show depth stratification by size, with larger larvae deeper (Dobrestov and Miron, 2001). Results from a recent

study on the central Oregon coast in 2005 (Rilov *et al.*, 2008) support this notion, showing greater mussel settlement deeper (i.e. 5 m) on moorings 350–500 m from shore. If competent mussel larvae are deeper in the water column, they may be transported onshore during upwelling conditions, when bottom layers in a stratified water column are generally moving onshore, rather than during downwelling, when these layers are generally moving offshore. The negative correlations between alongshore winds and mussel recruitment observed at several sites in 1998 and 1999 are consistent with this interpretation. In other words, mussel recruitment was often better when upwelling winds were stronger. However, if competent mussel larvae are also near the surface, they may be transported onshore during downwelling. If barnacle cyprids are always at the surface, they are more likely to be transported onshore during downwelling and show stronger correlations with downwelling, compared with mussels, as we have observed here.

Other transport mechanisms may operate in concert with, or separately from, current reversals. These include internal waves (Shanks, 1986) and internal tidal bores (Pineda, 1994). Internal waves can be formed by the interaction of tidal currents and bottom topography (Shanks, 1995). Conditions necessary for the production of tidally generated internal waves (tides, sharp bottom relief, and some water column stratification) are present in waters next to nearly all landmasses. As internal waves progress towards the shore, they change shape when wave amplitude becomes non-negligible with respect to water depth. At this point, the wave becomes asymmetrical with a steeper leading edge and a flatter trailing end, and it propagates as an internal tidal bore (Pineda, 1991). Studies have shown that larvae are more concentrated in the internal wave convergence areas and may be passively transported by them (Shanks, 1983, 1995). Contrasting studies have shown that tidal bores may serve as a larval transport mechanism (Pineda, 1991, 1994). The lengthy deployment interval of our biological collectors prevented us from examining the influence of these shorter term transport mechanisms on recruitment. However, within this study region, both the timing of recruitment and current reversals between sites were relatively coherent. This suggests that at least at these scales, current reversals influence onshore larval transport.

Insights from interannual comparisons

The differences in recruitment between 1998 and 1999 provide further evidence of the importance of relaxation or downwelling events for recruitment into the intertidal. In 1998, sustained upwelling current events lasted more than twice as long as in 1999 and were punctuated by just a few downwelling events. In 1999, upwelling and downwelling currents alternated more frequently (a few days), and upwelling events were shorter and weaker than 1998. Therefore, in 1999, when there was more downwelling overall, recruitment was greater. These results are consistent with other studies that have shown that the timing of upwelling intermittency and variability is critical to variation in interannual settlement (Wing *et al.*, 1998b).

The strength and the duration of upwelling events are affected by longer time-scale cycles such as ENSO (*El Niño*/Southern Oscillation), which influences the California Current. Crab and sea urchin recruitment has been positively correlated with environmental conditions associated with wind-driven upwelling, indicating that recruitment will be lower in *El Niño* years when the California Current is weaker (Wing *et al.*, 2003). Other studies

have found the opposite, barnacle recruitment peaking during the 1983 *El Niño* when upwelling was low (Roughgarden *et al.*, 1988), and similarly during the 1997/1998 *El Niño* (Connolly and Roughgarden, 1999). A crab recruitment study in northern California during the 1997/1998 *El Niño* and 1999 *La Niña* showed lower recruitment during the *La Niña* as a consequence of the extremely strong upwelling during that particular year, which likely restricted settlement by transporting larvae offshore (Lundquist *et al.*, 2000). It appears that the recruitment response to upwelling conditions may be dome-shaped rather than linear, maximum recruitment coinciding with a certain level of upwelling that increases productivity but does not permanently advect larvae offshore (Lundquist *et al.*, 2000). In Oregon during 1998, the signatures of the *El Niño* (e.g. warmer temperatures) were fading in June, but upwelling was above normal through September (Huyer and Fleischbein, 2002). By 1999, the ocean was anomalously cooler, indicating *La Niña* conditions. Barnacle recruitment in our study was lower in 1998, suggesting that barnacle recruitment might be lower during periods of more sustained upwelling. However, mussel recruitment changed little between years and sites, so upwelling dynamics may not be as important for their onshore recruitment as for barnacles.

Influence of larval availability

The number of larvae available to be transported onshore may influence correlations between recruitment and physical processes at each site. Both barnacles and mussels spawn throughout spring and summer, and because of their lengthy planktonic phase, larvae may originate far from their final settlement site. Low geographical variation in gene flow of *B. glandula* indicates that populations in our study area, and hundreds of kilometres to the north and south, are well mixed over evolutionary time-scales (Sotka and Palumbi, 2006). Therefore, larval availability and subsequent recruitment at a site may be influenced by spawning and reproduction hundreds of kilometres away. Over “ecological” time-scales, the temporal coherence in recruitment pulses between sites, for both mussels and barnacles, suggests that near-shore larval availability was relatively uniform throughout the study area. This is supported by larval trap data collected from the region during 1998 and 1999, which showed no consistent among-site differences in the abundance of mussel larvae, and barnacle larvae appear to follow a similar pattern (BAG, unpublished data; Rilov *et al.*, 2008). Larval availability therefore is likely to have a minimal influence on the strength of the recruitment–oceanography correlations between these sites.

Differences in recruitment among years could result from inter-annual variation in either larval availability or transport mechanism. At Fogarty Creek, barnacle recruitment was $11\times$ higher in 1999 than in 1998, but larval trap data from the region show that the abundance of barnacle larvae at Fogarty Creek was generally less in 1999 (G. Rilov, unpublished data). This suggests that transport may be more important than larval abundance in generating the better recruitment observed in 1999. At Strawberry Hill, where recruitment was $3\times$ higher in 1999, preliminary data suggest that the abundance of barnacle larvae was higher too (G. Rilov, unpublished data), and this could have contributed to the interannual differences. It is important to note, however, that greater abundances of larvae may not necessarily translate into higher onshore recruitment, if the larvae are not transported onshore.

Our results have a number of important implications for understanding larval transport and recruitment patterns that may be applicable to other upwelling areas such as the east coast of the USA (Ma and Grassle, 2004), South America (Lagos *et al.*, 2005), and Europe (Jonsson *et al.*, 2004; Queiroga *et al.*, 2006). First, the relationship between current reversals and barnacle recruitment events implies that recruitment will be better in regions with intermittent upwelling than in those with persistent upwelling (Send *et al.*, 1987). This is consistent with observations that recruitment is better in Oregon and Washington than in central California (Connolly *et al.*, 2001; Menge *et al.*, 2004), where upwelling is stronger and less intermittent (Huyer, 1983). Second, regional differences in the ocean’s response to changes in wind, such as those observed on the northern and southern ends of our study area, suggest the possibility that “hidden” zones of enhanced recruitment may exist along even relatively straight coastlines (i.e. on scales of tens of kilometres). The spatially variable recruitment of mussels along this coast (Menge *et al.*, 2004) is consistent with this idea. Third, at smaller scales, and as concluded in a similar study in South Africa (Porri *et al.*, 2006), variations in currents and recruitment generated by small-scale topographic features appear to be important in explaining local differences in marine communities. Fourth, the poleward flow during current reversals can reduce the alongshore transport of larvae, decreasing the scale of dispersal, and helping to maintain populations at their northern limits. All of these are critical factors in deciding on appropriate spatial scales for marine conservation efforts, such as marine reserves.

The insights from the interannual comparisons also have implications for climate change. Vecchi *et al.* (2006) have shown that wind patterns are changing in response to global warming and that future conditions in the equatorial Pacific may resemble *El Niño* years (i.e. when upwelling weakens). If this extends to the northern Pacific, we may begin to see changes in barnacle recruitment. Conversely, Bakun and Weeks (2004) suggested that upwelling may intensify in the face of global warming. If climate change increases upwelling intensity enough, it could reduce onshore recruitment by advecting larvae offshore, resulting in less onshore recruitment. Climate change may also affect recruitment, not only by influencing the intensity of upwelling, but also its frequency and duration.

Conclusions

Our results show that current reversals associated with the reversal of upwelling-favourable winds influence barnacle recruitment on the Oregon coast. To our knowledge, this is the first study to highlight the relationship between nearshore currents and barnacle recruitment. Although recruitment appears to be temporally coherent over regional scales (tens of kilometres), spatial variation in the magnitude of recruitment may be further influenced by local differences in currents. As management decisions typically address issues at such local scales, understanding how small-scale topography affects recruitment is critical. The next step in elucidating these patterns is to examine the local-scale variability between recruitment and oceanography, matching the biological recruitment time-scales more closely with those of the oceanographic processes. A complementary study to address this issue began in 2002, and data are currently being analysed to investigate further the connection between recruitment, current reversals, and local variability in both.

Acknowledgements

We thank Ron Barrell, captain of the RV “Sacajawea”, for logistic support, Greg Hudson, Jacque Pamplin and Melissa Foley for assistance with the mooring fieldwork, and Fred Jones and his ship operation staff for coordinating our boat trips, helping to load, and providing storage space. Dale Pillsbury and Jay Simpkins provided advice and assistance during the mooring design process and generously provided material to construct the first prototypes. We also thank three anonymous reviewers for their constructive comments that greatly improved the manuscript. The research was supported by the David and Lucile Packard Foundation, the Andrew W. Mellon Foundation (to BAM and JL), and an National Science Foundation (SGER) grant (OCE97-29 396) to BAM. This is contribution number 318 from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans, funded primarily by the Gordon and Betty Moore Foundation and David and Lucile Packard Foundation.

References

- Almeida, M. J., and Queiroga, H. 2003. Physical forcing of onshore transport of crab megalopae in the northern Portuguese upwelling system. *Estuarine, Coastal and Shelf Science*, 57: 1091–1102.
- Bakun, A., and Weeks, S. J. 2004. Greenhouse gas buildup, sardines, submarine eruptions and the possibility of abrupt degradation of intense marine upwelling ecosystems. *Ecology Letters*, 7: 1015–1023.
- Barth, J. A. 2003. Anomalous southward advection during 2002 in the northern California Current: evidence from Lagrangian surface drifters. *Geophysical Research Letters*, 30: 6-1–6-4.
- Barth, J. A., Menge, B. A., Lubchenco, J., Chan, F., Bane, J. M., Kirincich, A. R., McManus, M. A., et al. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California Current. *Proceedings of the National Academy of Sciences*, 104: 3719–3724.
- Breaker, L. C., and Bratkovich, A. 1993. Coastal-ocean processes and their influence on the oil spilled off San Francisco by the M/V Puerto Rican. *Marine Environmental Research*, 36: 153–184.
- Broitman, B. R., Blanchette, C. A., and Gaines, S. D. 2005. Recruitment of intertidal invertebrates and oceanographic variability at Santa Cruz Island, California, U.S.A. *Limnology and Oceanography*, 50: 1473–1479.
- Castelao, R. M., and Barth, J. A. 2005. Coastal ocean response to summer upwelling favourable winds in a region of alongshore bottom topography variations off Oregon. *Journal of Geophysical Research*, 110: C10S04.
- Connolly, S. R., Menge, B. A., and Roughgarden, J. 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology*, 82: 1799–1813.
- Connolly, S. R., and Roughgarden, J. 1999. Theory of marine communities: competition, predation and recruitment-dependent interaction strength. *Ecological Monographs*, 69: 277–296.
- Dale, A. C., Barth, J. A., Levine, M. D., and Austin, J. A. 2008. Observations of mixed layer restratification by onshore surface transport following wind reversal in a coastal upwelling region. *Journal of Geophysical Research*, 113: C01010. doi:10.1029/2007JC004128.
- Dobrestov, S. V., and Miron, G. 2001. Larval and post-larval vertical distribution of the mussel *Mytilus edulis* in the White Sea. *Marine Ecology Progress Series*, 218: 179–187.
- Farrell, T. M., Bracher, D., and Roughgarden, J. 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnology and Oceanography*, 36: 279–288.
- Freidenburg, T. L., Menge, B. A., Halpin, P. M., Webster, M., and Sutton-Grier, A. 2007. Cross-scale variation in top-down and bottom-up control of algal abundance. *Journal of Experimental Marine Biology and Ecology*, 347: 8–29.
- Gan, J., and Allen, J. S. 2002. A modeling study of shelf circulation off northern California in the region of the Coastal Ocean Dynamics Experiment: response to relaxation of upwelling winds. *Journal of Geophysical Research*, 107: 6-1–6-30.
- Graham, W. M., and Largier, J. L. 1997. Upwelling shadows as near-shore retention sites: the example of northern Monterey Bay. *Continental Shelf Research*, 17: 509–532.
- Grantham, B. A. 1997. Coastal upwelling, larval recruitment, and the dynamics of upper intertidal barnacle communities. PhD thesis, Stanford University.
- Grantham, B. A., Eckert, G. L., and Shanks, A. L. 2003. Dispersal potential of marine invertebrates in diverse habitats. *Ecological Applications*, 13: S108–S116.
- Grosberg, R. K. 1982. Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on vertical distribution of adults. *Ecology*, 63: 894–899.
- Hickey, B. M. 1979. The California Current system—hypotheses and facts. *Progress in Oceanography*, 8: 191–270.
- Hines, A. H. 1978. Reproduction in three species of intertidal barnacles from central California. *Biological Bulletin*, 154: 262–281.
- Huyer, A. 1983. Coastal upwelling in the California Current system. *Progress in Oceanography*, 12: 259–284.
- Huyer, A., and Fleischbein, J. 2002. The coastal ocean off Oregon and northern California during the 1997–8 *El Niño*. *Progress in Oceanography*, 54: 311–341.
- Huyer, A., Smith, R. L., and Sobey, E. J. 1978. Seasonal differences in low-frequency current fluctuations over the Oregon continental shelf. *Journal of Geophysical Research*, 83: 5077–5089.
- Jonsson, P. R., Berntsson, K. M., and Larsson, A. I. 2004. Linking larval supply to recruitment: flow-mediated control of initial adhesion of barnacle larvae. *Ecology*, 85: 2850–2859.
- Kirincich, A. R. 2005. Wind-driven inner-shelf circulation off central Oregon during summer. *Journal of Geophysical Research*, 110: C10S13. doi:10.1029/2004JC002611.
- Kosro, P. M. 1987. Structure of the coastal current field off northern California during the Coastal Ocean Dynamics Experiment. *Journal of Geophysical Research*, 92: 1637–1654.
- Kosro, P. M. 2005. On the spatial structure of coastal circulation off Newport, Oregon, during the spring and summer 2001 in a region of varying shelf width. *Journal of Geophysical Research*, 110: 16.
- Kosro, P. M., and Huyer, A. 1986. CTD and velocity surveys of seaward jets off northern California July 1981 and 1982. *Journal of Geophysical Research*, 91: 7680–7690.
- Lagos, N. A., Navarrete, S. A., Veliz, F., Masuero, A., and Castilla, J. C. 2005. Meso-scale spatial variation in settlement and recruitment of intertidal barnacles along the coast of central Chile. *Marine Ecology Progress Series*, 290: 165–178.
- Lamb, B., and Hanby, B. P. 2005. *Marine Life of the Pacific Northwest*. Harbour Publishing.
- Leslie, H. M. 2004. Advancing marine reserve science: from field experiments to marine conservation planning tools. PhD thesis, Oregon State University.
- Leslie, H. M., Breck, E. N., Chan, F., Lubchenco, J., and Menge, B. A. 2005. Barnacle reproductive hotspots linked to nearshore ocean conditions. *Proceedings of the National Academy of Science*, 102: 10534–10539.
- Lundquist, C. J., Botsford, L. W., Diehl, J. M., Lockwood, D. R., Morgan, L. E., and Pearson, E. L. 2000. Effects of *El Niño* and *La Niña* on local invertebrate settlement in northern California. *CalCOFI Reports*, 41: 167–176.
- Ma, H., and Grassle, J. P. 2004. Invertebrate larval availability during summer upwelling and downwelling on the inner continental shelf off New Jersey. *Journal of Marine Research*, 62: 837–865.

- McCulloch, A., and Shanks, A. L. 2003. Topographically generated fronts, very nearshore oceanography and the distribution and settlement of mussel larvae and barnacle cyprids. *Journal of Plankton Research*, 25: 1427–1439.
- Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology*, 250: 257–289.
- Menge, B. A., Berlow, E. L., Blanchette, C. A., Navarrete, S. A., and Yamada, S. B. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs*, 64: 249–286.
- Menge, B. A., Blanchette, C. A., Raimondi, P., Freidenburg, T. L., Gaines, S. D., Lubchenco, J., Lohse, D., *et al.* 2004. Species interaction strength: testing model predictions along an upwelling gradient. *Ecological Monographs*, 74: 663–684.
- Menge, B. A., and Branch, G. M. 2001. Rocky intertidal communities. *In* *Marine Community Ecology*, pp. 221–251. Ed. by M. D. Bertness, S. D. Gaines, and M. Hay. Sinauer Associates, Sunderland, MA.
- Menge, B. A., Chan, F., and Lubchenco, J. 2008. Response of a rocky intertidal ecosystem engineer and community dominant to climate change. *Ecology Letters*, 11: 151–162.
- Menge, B. A., Daley, B. A., Lubchenco, J., Sanford, E., Dahlhoff, E., Halpin, P. M., Hudson, G., *et al.* 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecological Monographs*, 69: 297–330.
- Menge, B. A., Daley, B. A., Wheeler, P. A., Dahlhoff, E., Sanford, E., and Strub, P. T. 1997b. Benthic–pelagic links and rocky intertidal communities: bottom-up effects on top-down control? *Proceedings of the National Academy of Science*, 94: 14530–14535.
- Menge, B. A., Daley, B. A., Wheeler, P. A., and Strub, P. T. 1997a. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. *Limnology and Oceanography*, 42: 57–66.
- Miron, G., Boudreau, B., and Bourget, E. 1995. Use of larval supply in benthic ecology: testing correlations between larval supply and larval settlement. *Marine Ecology Progress Series*, 124: 301–305.
- Morgan, L. E., Wing, S. R., Botsford, L. W., Lundquist, C. J., and Diehl, J. M. 2000. Spatial variability in red sea urchin (*Strongylocentrotus franciscanus*) recruitment in northern California. *Fisheries Oceanography*, 9: 83–98.
- Noda, T. 2004. Large-scale variability in recruitment of the barnacle *Semibalanus cariosus*: its cause and effects on the population density and predator. *Marine Ecology Progress Series*, 278: 241–252.
- Oke, P., Allen, J. S., Miller, R. N., and Egbert, G. D. 2002. A modeling study of the three-dimensional continental shelf circulation off Oregon. 2. Dynamical analysis. *Journal of Physical Oceanography*, 32: 1383–1403.
- Petes, L. E. 2007. Effects of environmental stress on intertidal mussel reproduction. PhD thesis, Oregon State University.
- Pineda, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science*, 252: 548–550.
- Pineda, J. 1994. Internal tidal bores in the nearshore: warm-water 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.
- Porri, F., McQuaid, C. D., and Radloff, S. 2006. Spatio-temporal variability of larval abundance and settlement of *Perna perna*: differential delivery of mussels. *Marine Ecology Progress Series*, 315: 141–150.
- Pyefinch, K. A. 1948. Methods of identification of the larvae of *Balanus balanoides* (L.), *B. crenatus* Bruguière and *Verruca stroemia* O.F. Müller. *Journal of the Marine Biological Association of the UK*, 28: 451–463.
- Queiroga, H., Almeida, M. J., Alpuim, T., Flores, A. A. V., Francisco, S., Gonzalez-Gordillo, I., Miranda, A. I., *et al.* 2006. Tide and wind control of megalopal supply to estuarine crab populations on the Portuguese west coast. *Marine Ecology Progress Series*, 307: 21–36.
- Rilov, G., Dudas, S. E., Menge, B. A., Grantham, B. A., Lubchenco, J., and Schiel, D. R. 2008. The surf zone: a semi-permeable barrier to onshore recruitment of invertebrate larvae? *Journal of Experimental Marine Biology and Ecology*, 361: 59–74.
- Roughgarden, J., Gaines, S., and Possingham, H. 1988. Recruitment dynamics in complex life cycles. *Science*, 241: 1460–1466.
- Roughgarden, J., Pennington, J. T., Stoner, D., Alexander, S., and Miller, K. 1991. Collisions of upwelling fronts with the intertidal zone: the cause of recruitment pulses in barnacle populations of central California. *Acta Oecologica*, 12: 35–51.
- Send, U., Beardsley, R. C., and Winant, C. D. 1987. Relaxation from upwelling in the Coastal Ocean Dynamics Experiment. *Journal of Geophysical Research*, 92: 1683–1698.
- Shanks, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic and invertebrates and fishes shoreward. *Marine Ecology Progress Series*, 13: 311–315.
- Shanks, A. L. 1986. Tidal periodicity in the daily settlement of intertidal barnacle larvae and an hypothesized mechanism for the cross-shelf transport of cyprids. *Biological Bulletin*, 170: 429–440.
- Shanks, A. L. 1995. Orientated swimming by megalopae of several eastern North Pacific crab species and its potential role in their onshore migration. *Journal of Experimental Marine Biology and Ecology*, 186: 1–16.
- Shanks, A. L., and Brink, L. 2005. Upwelling, downwelling, and cross-shelf transport of bivalve larvae: test of a hypothesis. *Marine Ecology Progress Series*, 302: 1–12.
- Shkedy, Y., and Roughgarden, J. 1997. Barnacle recruitment and populations dynamics predicted from coastal upwelling. *Oikos*, 80: 487–498.
- Sotka, E. E., and Palumbi, S. R. 2006. The use of genetic clines to estimate dispersal distances of marine larvae. *Ecology*, 87: 1094–1103.
- Thiebaut, E., Lagadeuc, Y., Olivier, F., Dauvin, J. C., and Retiere, C. 1998. Do hydrodynamic factors affect the recruitment of marine invertebrates in a macrotidal area? *Hydrobiologia*, 375/376: 165–176.
- Vecchi, G. A., Soden, B. J., Wittenberg, A. T., Held, I. M., Leetmaa, A., and Harrison, M. J. 2006. Weakening of tropical Pacific atmospheric circulation due to anthropogenic forcing. *Nature*, 441: 73–76.
- Washburn, L., Swenson, M. S., Largier, J. L., Kosro, P. M., and Ramp, S. R. 1993. Cross-shelf sediment transport by an anticyclonic eddy off northern California. *Science*, 261: 1560–1563.
- Weissberger, E. J., and Grassle, J. P. 2003. Settlement, first-year growth, and mortality of surfclams, *Spisula solidissima*. *Estuarine, Coastal and Shelf Science*, 56: 669–684.
- Wing, S. R., Botsford, L. W., Largier, J. L., and Morgan, L. E. 1995a. Spatial structure of relaxation events and crab settlement in the northern California upwelling system. *Marine Ecology Progress Series*, 128: 199–211.
- Wing, S. R., Botsford, L. W., Morgan, L. E., Diehl, J. M., and Lundquist, C. J. 2003. Inter-annual variability in larval supply to populations of three invertebrate taxa in the northern California Current. *Estuarine, Coastal and Shelf Science*, 57: 859–872.
- Wing, S. R., Botsford, L. W., Ralston, S. V., and Largier, J. L. 1998a. Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system. *Limnology and Oceanography*, 43: 1710–1721.
- Wing, S. R., Largier, J. L., and Botsford, L. W. 1998b. Coastal retention and longshore displacement of meroplankton near capes in eastern boundary currents: examples from the California Current. *Benguela Dynamics*, 19: 119–127.
- Wing, S. R., Largier, J. L., Botsford, L. W., and Quinn, J. F. 1995b. Settlement and transport of benthic invertebrates in an intermittent upwelling region. *Limnology and Oceanography*, 40: 316–329.

doi:10.1093/icesjms/fsn179