



Contents lists available at ScienceDirect

## Journal of Experimental Marine Biology and Ecology

journal homepage: [www.elsevier.com/locate/jembe](http://www.elsevier.com/locate/jembe)

# The surf zone: a semi-permeable barrier to onshore recruitment of invertebrate larvae?

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## ARTICLE INFO

## Article history:

Received 11 February 2008

Received in revised form 8 April 2008

Accepted 9 April 2008

Available online xxx

## Keywords:

Inner shelf

Larvae

Larval transport

Mussels

New Zealand

Oregon

Recruitment

Rocky shore

Settlement

Surf zone

## ABSTRACT

The supply of larvae to the shore is important for population replenishment and intertidal community dynamics but its variability at most scales is not well understood. We tested the relationship between nearshore mussel larval abundance and intertidal settlement rates over several years at multiple spatiotemporal scales in Oregon and New Zealand. Abundance of competent larvae nearshore and intertidal recruitment rates were simultaneously quantified using collectors mounted at different depths on moorings 50–1100 m from shore, and at adjacent rocky intertidal sites. Total mussel larval abundance and oceanographic conditions were also measured in some locations. At all scales, abundance of nearshore mussel larvae was unrelated to intertidal recruitment rates. In the intertidal, patterns of mussel recruitment were persistent in space, with sites of consistently high or low recruitment. In contrast, nearshore competent larval abundance showed generally similar abundances among sites except for a high, and spatially-inconsistent, variability in Oregon during 1998 only. On moorings, recruitment tended to be greater on midwater collectors than shallower or deeper. Finally, on moorings larval abundance in traps and recruitment on collectors was unrelated. These results suggest that (1) among sites, the size of the nearshore larval pool is relatively uniform while onshore recruitment varies and is unrelated to larval abundance, (2) temporal variability in nearshore larval availability is not strongly expressed onshore, (3) vertical stratification of competent larvae nearshore is strong and may influence transport and recruitment, and (4) within-coast variability in onshore recruitment is strongly driven by processes occurring locally within the surf zone that need to be studied to understand coastal recruitment dynamics.

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## 1. Introduction

Most coastal benthic organisms have a complex life cycle that includes a planktonic larval stage and a benthic adult stage (Scheltema, 1986). As a consequence, both pre-settlement (i.e., larval transport, survival and physiological condition in the water column) and post-settlement (i.e. predation, competition, facilitation, thermal and desiccation stress) processes can be important in shaping coastal ecological communities (Connell, 1985). After decades of focusing primarily on the influence of post-settlement factors, in the 1980s ecologists turned their attention towards the influence of propagule inputs on populations and communities (Caley et al., 1996; Gaines and Roughgarden, 1985; Grosberg and Levitan, 1992; and see review, Levin, 2006; Lewin, 1986; Underwood and

Denley, 1984; Underwood and Fairweather, 1989). Since then, investigating the role of recruitment relative to other factors in structuring communities (supply-side ecology *sensu* Lewin 1986) has been a central focus of ecological research across multiple spatiotemporal scales (Connolly and Roughgarden, 1998; Gaines and Bertness, 1992; McQuaid and Lawrie, 2005; Menge et al., 2004; Menge et al., 2003; Navarrete et al., 2005; Petraitis, 1991; e.g., Raimondi, 1990; Rilov and Schiel, 2006b; Underwood, 2004; Underwood and Anderson, 1994).

Successful recruits in benthic coastal habitats have to overcome many hurdles (Pineda, 2000). The rate of recruitment to the shore depends on a complex suite of oceanographic and biological factors, including larval production rates, the degree of offshore transport or retention, survival rates in the plankton, onshore transport mechanisms, larval behavior and, once the larvae arrive onshore, substrate availability, settlement cues, environmental stress, predation, competition and micro-hydrodynamics. Despite the dramatic increase in research investigating this issue, and substantial new insights into the patterns and factors influencing recruitment onshore (Connolly and Roughgarden, 1998; Pineda, 2000; e.g., Pineda, 1991; Pineda and Caswell, 1997; Porri et al., 2006; Shanks, 1995; Shanks and Brink,

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2005; Shanks et al., 2003; Tapia and Piñeda, 2007) our understanding of the relative importance of the different factors regulating the supply and delivery of larvae is limited.

Recruitment rates of intertidal organisms can differ in space by orders of magnitude at multiple scales both within and between coasts (e.g., Connolly and Roughgarden, 1998; Harris et al., 1998; Ladah et al., 2005; Lawrie and McQuaid, 2001; Menge et al., 2004; Moreno et al., 1998; Navarrete and Wieters, 2000; Navarrete et al., 2005; Pineda and Lopez, 2002; Todd, 2003). Determination of the factors underlying this variability has been a major challenge. In recent years, ecologists have begun to focus on the role of oceanographic conditions in determining macroscale (>100 km) or mesoscale (10–100 km) variation in recruitment. In particular, effects of the intensity and persistence of seasonal upwelling regimes on nutrient and larval availability in coastal environments have been postulated to be of major importance (Menge et al., 2003). For example, in the persistent upwelling region of central and northern California, recruitment rates can be orders of magnitude lower compared to rates in the intermittent upwelling region of Oregon (Menge et al., 2004). A possible explanation for this large scale difference is that in Oregon north of Cape Blanco, upwelling events are frequently interrupted by “relaxation” events when northerly winds weaken or reversal events, when winds switch from north to south. This mechanism has been termed the “current reversal hypothesis” (Dudas et al. unpublished manuscript). These interruptions of upwelling-favorable winds are hypothesized to allow larvae that have accumulated near the surface offshore at upwelling fronts to return to shore and settle (Connolly et al., 2001; McCulloch and Shanks, 2003, Dudas et al. unpublished manuscript). In central and northern California, in contrast, upwelling is more persistent, relaxation events are relatively less frequent, and larvae are likely transported farther offshore, the net result of which is postulated to be low recruitment (e.g., Gaines and Roughgarden, 1985). A comparable example comes from a recent study on the Chilean coast (Navarrete et al., 2005).

A similar theory, the “onshore flow hypothesis” (Grantham, 1997), expands on these ideas. At upwelling fronts off the central California coast, the later (older) developmental stage larvae of some taxa were found deeper in the water column. Under this hypothesis, such larvae would be entrained in the deep onshore flow associated with upwelling and carried shoreward. In this scenario, off Oregon, where upwelling events are relatively short and upwelling fronts rarely move far offshore, greater numbers of larvae would be retained nearshore, than off central California where upwelling events are longer and fronts move correspondingly farther distances offshore. Grantham (1997) postulated that for some taxa it was the onshore movement of deeper waters following the resumption of upwelling that delivered larvae onshore.

Other mechanisms of across-shelf larval transport that may explain variation in recruitment include other types of wind-driven currents (e.g. switching wind directions across an embayment, Bertness et al., 1996), and internal waves and tidal bores (Ladah et al., 2005; Pineda and Lopez, 2002; Shanks and Wright, 1987). Variation in the magnitude, rate or direction of these processes along the shore may explain variation in recruitment on smaller spatial scales. Short and long-term monitoring of recruitment rates shows that order of magnitude differences can occur on small spatial scales of 10s–100s m (Ladah et al., 2005; McCulloch and Shanks, 2003; Porri et al., 2006; Rilov and Schiel, 2006b, Menge, unpublished data). A variety of other factors could underlie such variability including effects of bottom topography or coastal geomorphology, the distribution and behavior of larvae in the water column post-settlement and variation in mortality tied to environmental stresses during low tides (Caceres-Martinez and Figueras, 1998; Dobretsov and Miron, 2001; Grosberg, 1982; Miron et al., 1995). For example, stratification of larvae in the water column resulting from physical or biological processes may affect onshore delivery and subsequent recruitment (Pineda, 2000) if currents are also stratified (Marta-Almeida et al., 2006; Shanks and Brink, 2005).

Regardless of the across-shelf transport mechanism, hypothetically, recruitment rates should reflect the size of the nearshore larval

pool. A recent short-term study on larval distribution of two barnacle species at increasing distances from one intertidal site in southern California revealed a temporal coherence between cyprid abundance nearshore and onshore settlement in one of the species (Tapia and Piñeda, 2007). In contrast, a study from South Africa suggests that on the scale of 100–1000 m, mussel larval availability nearshore is unrelated to onshore recruitment (Porri et al., 2006). Both of these studies used vertical plankton net tows to measure larval abundance. Several limitations arise however when using vertical hauls: (1) they give no information on the vertical distribution of the larvae, which as noted above can affect transport, (2) they are snapshots of larval abundance relevant only to the hours or minutes when they were taken, and (3) in mussels, they capture all sizes including both competent (to settle) and precompetent larvae. Nonetheless, these last two studies represent the first attempts to test the coupling between the larval pool (i.e., the abundance of larvae in the inner shelf region, see Pineda, 2000) and onshore recruitment of intertidal organisms.

Here we integrate data from five studies that were designed to test the relationship between the relative size of the nearshore larval pool of intertidal mussels and onshore recruitment rates. The studies spanned multiple spatial and temporal scales in two biogeographic regions, Oregon and New Zealand. In all cases, we used mussel settlement collectors on moorings instead of plankton nets to assess the relative abundance of competent larvae and we placed them at different depths to evaluate their depth distribution. Mussels are dominant organisms on many rocky shores worldwide and are important ecologically. They serve as ecosystem engineers (i.e., providing habitat for other species), are prey for a multitude of organisms on the shore and are a central component of community structure (e.g., Lawrie and McQuaid, 2001; and see review in, Menge and Branch, 2001; Navarrete and Menge, 1996; Petraitis, 1998). They are also of commercial value in many locations worldwide. For these reasons, they have been a major focus of efforts to understand the relative influence of pre- and post-recruitment factors in determining their abundance (Leonard et al., 1998; McQuaid and Lindsay, 2005; Menge et al., 1994; Menge et al., 2004; Menge et al., 1997a; Menge et al., 2003; Navarrete et al., 2005).

### 1.1. Hypotheses

To examine the relationship between the relative size of the inner shelf (<30 m water depth, about 0.05–2 km offshore) larval pool and recruitment onshore in the context of local oceanography (where possible), we tested three hypotheses:

**H<sub>1</sub>.** At local (site) scales, the larval pool and onshore recruitment are coupled. Onshore mussel recruitment is proportional to competent larval availability (the larval pool) just beyond the surf zone (50–1000 m offshore). Prediction 1 thus states that onshore recruitment rates and nearshore larval abundance will be positively correlated.

**H<sub>2</sub>.** At coastal (among site) scales, larval pool abundance and onshore recruitment are synchronized. Inner shelf oceanographic events involved in onshore larval transport, such as upwelling relaxations and/or current reversals, are synchronous alongshore at scales of 10–100 km (e.g., Kirinich et al., 2005). Prediction 2 thus states that a) relative larval abundance in the water column will be temporally positively correlated among sites within coasts in the inner shelf at scales of 10–100s of km, and that b) onshore recruitment (or settlement) will be temporally positively correlated among sites at this spatial scale.

**H<sub>3</sub>.** Total larval abundance determines the magnitude of competent larval settlement in nearshore waters. The number of competent mussel larvae at different depths should be proportional to total (competent plus precompetent) mussel larvae abundance at similar depths unless ontogenetic shifts in vertical position exist. Prediction 3 thus states that within the larval pool in the inner shelf area, total

193 recruitment to collectors (competent larvae) will be positively correlated  
 194 to the total number of mussel larvae caught in plankton traps (competent  
 195 plus precompetent). Hypotheses 2 and 3 could only be tested with the  
 196 data from the Oregon 1998 and 1999 sampling (see below).

## 197 2. Methods

### 198 2.1. Protocols and Definitions

199 Our studies were carried out in the rocky intertidal and the inner shelf  
 200 area at the edge or outside the surf zone (the zone between the outer-  
 201 most breakers and the area of the wave uprush which varies in width  
 202 depending on shoreline topography and sea conditions). The inner shelf  
 203 ranges in depth from about 10 to 30 meters and at our sites and extends  
 204 from shore about 50–100 m out to ~2 km. Following Connell (1985) we  
 205 define settlers as larvae immediately post settlement (up to ~48 hr after  
 206 attachment) and recruits as settlers that have survived a period of post-  
 207 settlement life (two days - month) in the adult habitat. Since most of our  
 208 data came from collectors that were replaced on time intervals of a few  
 209 days to a few weeks, we consider most individuals as recruits.

210 Unlike many other well-studied intertidal species such as barnacles  
 211 that have a morphologically distinctive settlement stage (e.g., the cyprid  
 212 in barnacles), it is difficult to distinguish mussel larvae that are ready to  
 213 settle (competent) from precompetent larvae using simple morphology.  
 214 For our purposes it was important to distinguish the abundance of  
 215 competent larvae from total larval abundance, as many of the larvae  
 216 found in the inner shelf may be precompetent. We separated competent  
 217 and precompetent larvae by combining two methods of sampling in the  
 218 inner shelf: mussel recruit collectors, which presumably estimate  
 219 numbers of competent larvae only (because they attach with their  
 220 byssus), and larval traps, which provide an estimate of the relative  
 221 numbers of all mussel larvae occurring at different sites.

222 Mussel recruit collectors (plastic-mesh ovoid pot scrubbers or  
 223 “Tuffies”, see Menge et al., 1994; Menge et al., 1999) were used both  
 224 intertidally and on inner shelf moorings to quantify recruitment of  
 225 competent mussel larvae in both habitats. These collectors mimic the  
 226 fine foliose algae that are favored settlement substrata for mussels  
 227 (Menge, 1992; Paine, 1976). They have been used successfully by re-  
 228 search groups in the USA, New Zealand, South Africa and Chile (Menge  
 229 et al., 2004; e.g., Menge et al., 2003; Navarrete et al., 2005; Porri et al.,  
 230 2006; Rilov and Schiel, 2006b). On moorings, 4–5 collectors were  
 231 screwed or cable-tied to the ends of the arms of PVC pipe frames  
 232 constructed in the shape of an “X”. The frames were deployed with the  
 233 arms of the X parallel to the surface of the ocean and were attached to  
 234 the mooring line at two or three depths (Fig. 1). Intertidally, collectors  
 235 were fastened with lag screws threaded through the mesh and into  
 236 wall anchors in holes drilled in the rock. Depending on the study,  
 237 collectors were placed in the middle or lower edge of the mussel bed  
 238 along a ~20 m stretch of shore parallel to the water’s edge. Collector  
 239 placement was haphazard, and we attempted to place them at least  
 240 two meters apart on gently sloping benches. Retrieved collectors were  
 241 stored in -20 ° C freezers until processing. Recruits were extracted  
 242 from the collectors by soaking them briefly in bleach or rinsing with a  
 243 strong jet of water, sieved through a 100 µm mesh (New Zealand 2004),  
 244 180 µm and/or 250 µm mesh (Oregon 1998, 1999, New Zealand 2000),  
 245 and were counted under a dissecting microscope. Because more than  
 246 90% of the recruits were >250 µm long regardless of region or interval  
 247 duration we treat all these samples as comparable for our analysis.

248 Using settlement collectors a concern might be that they do not  
 249 represent the relative abundance of competent larvae in the water at a  
 250 specific site/depth/period, because competent larvae that are present  
 251 may choose not to settle in the collector or not survive in the collectors  
 252 long enough to be detected. A recent study in Oregon revealed that the  
 253 number of mussel settlers in collectors were correlated with the  
 254 number of large (250–350 µm) but not small (<250 µm) mussel larval  
 255 in traps (Rilov et al. unpublished data; see Discussion). We conclude

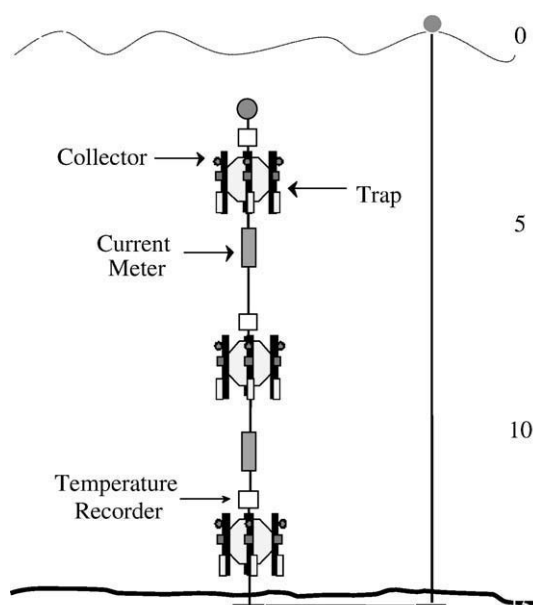


Fig. 1. An example of the mooring design (1998 set-up in Oregon) with plankton traps, mussel recruit collectors, temperature loggers and current meters.

that collector data provide a good proxy of the relative abundance of  
 competent larvae in the water column.

During the 1998–1999 Oregon studies (see below), relative larval  
 abundance was measured on the inner shelf using plankton traps (Yund  
 et al., 1991) that were also attached to the frames on the moorings at  
 approximately the same depths as the collectors. The traps were clear  
 acrylic tubes 75 cm long and 5.2 cm wide and filled with a 10% formal-  
 dehyde in seawater solution. These traps entrain zooplankton passing  
 over them, likely including precompetent larvae. Plankton samples were  
 sieved (53 µm mesh) and stored in ethanol until processing. Mytilids can  
 be distinguished with certainty from other bivalve larvae only when  
 they are >250 µm (G. Rilov, personal observations) thus only larvae  
 above this size were categorized as mytilids and used in the analysis.

During the 2004 New Zealand study (see below), larval abundance  
 was measured once (May 13, 2004) at high tide. Samples were  
 collected from a boat near the moorings by pumping 1000 liters of  
 water for 2.5 min at 0, 1.5 and 6 m depths. At shallow sites (see below)  
 only the upper two depths were sampled. Sampling involved lowering  
 an intake hose to each depth. Water was pumped through an ex-  
 changeable cod-end filter with a 100 µm mesh attached to the pump  
 outflow valve. A single cod-end was used for each sample. Cod-ends  
 were stored with their sample inside Ziploc bags in a -20 ° C freezer  
 and were later sorted and counted in the laboratory. Unlike the in-  
 tegrated measure of larval availability using traps (which integrate  
 over time), pumping, like plankton tows, represents a snapshot of  
 larval availability during the pumping period.

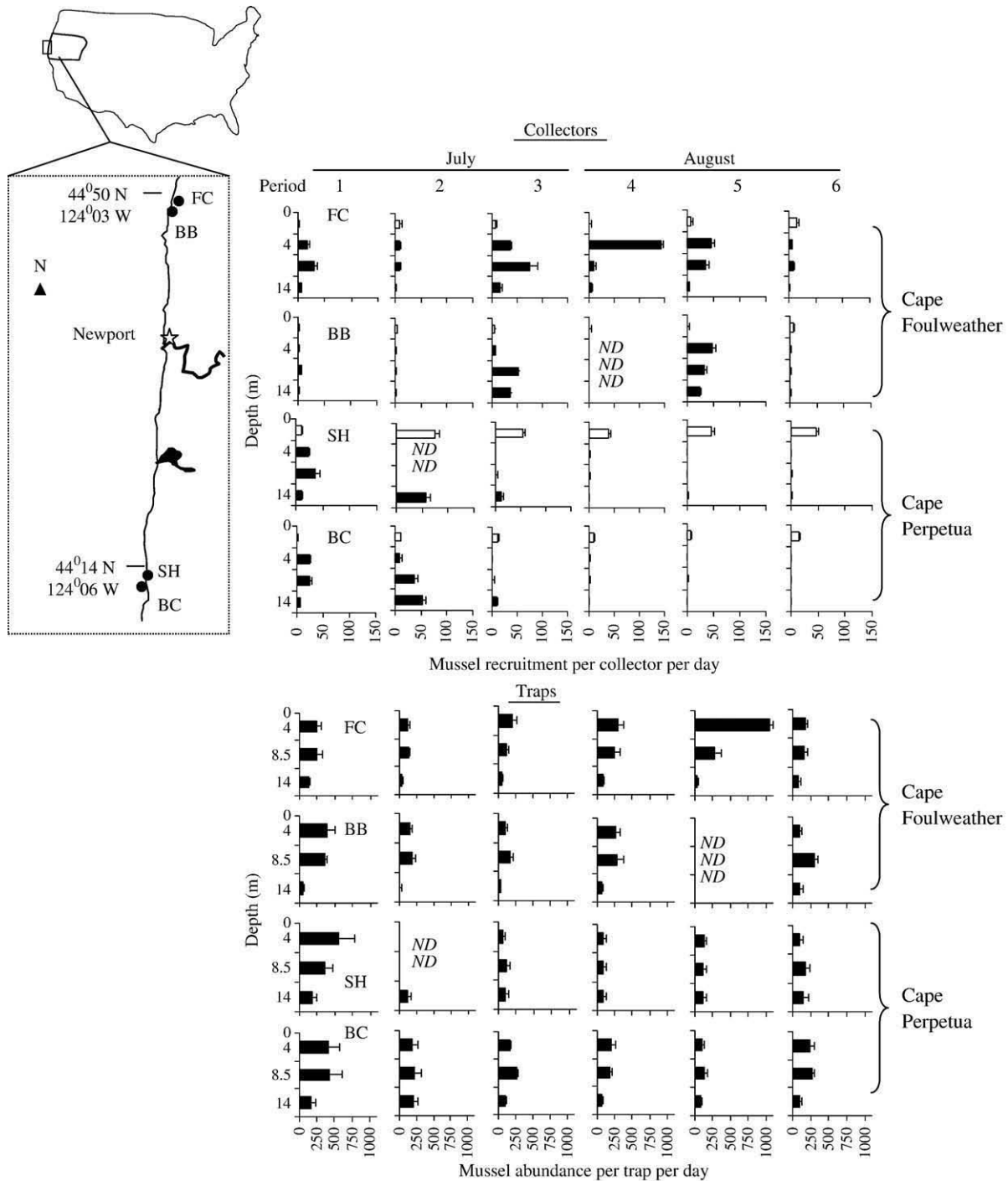
### 2.2. Species and sampling design

The mussel species sampled were mostly mytilid mussels but were  
 different species in each hemisphere (Oregon: *Mytilus californianus*,  
*M. trossulus*; New Zealand: *M. galloprovincialis*, *Perna canaliculus*,  
*Xenostrobus pulex*, and *Aulacomya maoriensis*). Although some report  
 success in distinguishing *M. californianus* from *M. trossulus* morpho-  
 logically (Martel et al., 2000), this was unreliable in our system. Thus,  
 all Oregon analyses used total mussel numbers and for consistency  
 New Zealand data are also presented as total mussels.

We used a nested sampling design in two different biogeographic  
 regions, Oregon and the South Island of New Zealand. These regions  
 were chosen because they represented similar types of ecosystems and

294 were at similar latitudes in the Pacific Ocean but in opposite and pre-  
 295 sumably evolutionarily independent hemispheres (42–45° north and  
 296 south, respectively). All sites were selected to represent contrasting  
 297 oceanographic conditions. In Oregon, the coast north of Newport (Fig. 2)  
 298 has a relatively narrow continental shelf, the California current is rela-  
 299 tively close to the coast, phytoplankton concentrations tend to be rela-  
 300 tively low and on average, summer surface currents in the inner shelf  
 301 tend to be southward, flow at higher velocity, and move offshore (Barth  
 302 and Wheeler, 2005; Kosro, 2005; Menge et al., 1997b) (Menge et al.,  
 303 2008). South of Newport, the continental shelf is broader, forming the

Heceta and Stonewall Banks, the California Current is farther offshore, 304  
 phytoplankton concentration tends to be relatively high, and summer 305  
 surface currents in the inner shelf tend to be more variable in direction, 306  
 of low velocity, and fluctuate between shoreward and seaward move- 307  
 ments (Barth and Wheeler, 2005; Kosro, 2005; Menge et al., 1997b; 308  
 Menge et al., 2008). Both Oregon coasts (north and south of Newport) 309  
 are generally upwelling-dominated in summer, the time during which 310  
 this study was done. In New Zealand, weak to moderate upwelling 311  
 characterizes sites on the west coast of the South Island, while down- 312  
 welling characterizes sites on the east coast (Menge et al., 2003). 313



**Fig. 2.** Oregon coast, summer 1998: Average (+SE) mussel recruitment and larval abundance on moorings and mussel recruitment on adjacent intertidal sites (all adjusted to recruits or larvae/collector or trap/day; n=4 collectors/traps per depth). ND=no data. Length of sampling period (interval in days) during period 1 was 10 d for the northern sites and 8 d for the southern, period 2, 11 d and 15 d, period 3, 15 for both, period 4, 8 d and 10 d, period 5, 4 for both, and period 6 14 for both. Open bar at zero depth shows onshore recruitment and black bars show recruitment at the 3 depths on the moorings. Upper panel shows settlement collector results, lower panel shows larval traps.

314 Sampling was conducted in all studies during the summer months when  
315 most mussel species peak in recruitment (Menge et al., unpubl. manu-  
316 script, unpubl. data; Rilov et al. unpubl. data).

317 Up to six sites were sampled in Oregon and up to five in New Zealand.  
318 In addition to having contrasting oceanographic conditions the sites also  
319 reflected more localized variation in substratum type. In Oregon, sites  
320 nested within the southern coast were embedded within sandy beach  
321 habitat that extended subtidally while sites nested within the northern  
322 coast were more distant from sandy beaches and have rocky substrata  
323 subtidally. In New Zealand, west coast sites were mostly sand-associated  
324 and east coast sites included both sand-associated and rocky-reef associ-  
325 ated sites. All intertidal sites were wave-exposed rocky benches.

326 Because there were some important distinctions among the stud-  
327 dies, below we describe each, organizing them first by geographical  
328 region and then chronologically.

### 329 2.3. Oregon 1998

330 In Oregon, the first study examined the relationship between  
331 intertidal recruitment and inner shelf larval abundance. Study sites in  
332 1998 (Fig. 2) were Fogarty Creek (FC; 44°50'40"N, 124°03'60"W) and  
333 Boiler Bay (BB; 44°49'80"N, 124°03'60"W) in the northern coast on  
334 Cape Foulweather, and Strawberry Hill (SH; 44°15'14"N, 124°07'59"W)  
335 and Bob Creek (BC; 44°14'40"N, 124°06'60"W) in the southern coast on  
336 Cape Perpetua. Sites within coasts were separated by ~500 m. The  
337 study was conducted between early July and early September 1998. At  
338 each site, single moorings were deployed at the 15 m isobath (approx-  
339 imately 600–1100 m from the shore) and collectors were mounted at  
340 three depths: 4, 8.5 and 14 m. Collectors on moorings and onshore  
341 were exchanged every 3–19 days (average interval length was 9.3 days)  
342 for a total of six sampling periods. Interval length was dictated by sea  
343 conditions at the bar in Newport, Oregon which often exceeded the  
344 seaworthiness of the research vessel (the RV *Sacajawea*).

### 345 2.4. Oregon 1999

346 In 1999, we expanded the 1998 study to include six sites along the  
347 central Oregon coast (Fig. 5). We selected three replicate sites within each  
348 of the northern and southern coasts. The three northern sites were FC (see  
349 above) and Whale Cove (WC; 44°47'40"N, 124°04'20"W) in the Cape  
350 Foulweather area (5.5 km apart), and Yaquina Head (YH; 44°40'24"N,  
351 124°04'28"W) 12.5 km to the south. The three southern sites were Seal  
352 Rock (SR; 44°29'58"N, 124°05'05"W) and two sites in the Cape Perpetua  
353 area, Yachats Beach (YB; 44°19'20"N, 124°06'26"W), 20 km south of SR  
354 and SH (see above), 8 km south of YB. Sampling was conducted between  
355 early July and late August 1999. Overall, four periods of different intervals  
356 (averaging 11.8 days) were sampled during summer 1999.

357 In 1998 and 1999, physical properties of the water in the nearshore  
358 environment were quantified with sensors mounted on the moorings.  
359 Temperature was measured using Onset XTI data loggers at 4, 8.5 and  
360 14 m depths sampling at one minute intervals in 1998 and two minute  
361 intervals in 1999. During 1998, current velocities were measured using  
362 Oregon Environmental Instruments vector-averaging current meters  
363 (VACMs) at 4 and 13 m depths. Currents were measured for one of  
364 every four minutes. During 1999, only one VACM was deployed at 10 m  
365 depth on each mooring. Current velocities were rotated into along- and  
366 across-shelf axes defined by the principle axis of flow (calculated using  
367 depth-averaged velocities). To facilitate comparison with biological  
368 samples, current direction was averaged for each mooring sampling  
369 period for each site and by depth. The currents were then correlated  
370 (across all sites and periods) with mussel recruitment on collectors  
371 onshore, on the mooring collectors at the three depths and with the  
372 number of larvae in traps at the three depths. We present graphically  
373 only the across-shore current data as these are the most relevant for  
374 across-shore transport of larvae but correlations were also conducted  
375 with along-shore currents. As across-shore currents are much slower

than along-shore ones and sometimes close to the resolution of the  
instrument, the results thus should be taken with caution.

### 2.5. Oregon 2005

379 To detect potential correlations between inner shelf larval abun-  
380 dance and onshore supply on the temporal scale of recruitment pulses  
381 (Pineda, 2000), in 2005, we conducted daily sampling at two locations  
382 (separated by ~150 m) within one site, FC, between 17–26 August. We  
383 deployed two moorings in 12–14 m depth (350–500 m from shore) to  
384 conduct near-surf zone sampling. Collectors onshore were exchanged  
385 daily for the full ten days. Moorings were deployed for only the first six  
386 days during which collectors were replaced every day except 22  
387 August when adverse sea conditions prevented sampling.

### 2.6. New Zealand 2000

388 To examine coastal differences in larval abundance and recruit-  
389 ment in New Zealand, we sampled at three sites on the east coast and  
390 at two sites on the west coast of the South Island (see map in Fig. 1 in  
391 Menge et al., 2003 and Fig. 10 below). East coast sites, from north to  
392 south were Raramai (RR; 42°26'54"S, 173°34'58"E), Box Thumb (BT;  
393 43°35'04"S, 172°47'23"E), and Shag Point (SP; 45°28'06"S, 170°49'38"E).  
394 RR and BT were 180 km apart and BT and SP were 260 km apart. West  
395 coast sites were Twelve Mile Beach (TMB; 42°18'59"S, 171°16'32"E) and  
396 Jackson Head (JH; 43°57'39"S, 168°32'27"E), 290 km to the south. As in  
397 Oregon in 1998 and 1999, in early January 2000, recruitment collectors  
398 were deployed at 3 depths (3, 9 and 14 m) on inner shelf moorings at the  
399 15 m isobath and at adjacent intertidal sites. Collectors were exchanged  
400 twice, with intervals lasting between 23–31 days.

### 2.7. New Zealand 2004

401 To examine variation in larval abundance and recruitment on a more  
402 local scale, and in relation to subtidal substratum type, we established four  
403 study sites in the vicinity of the BT site on the east coast of the South Island  
404 near Christchurch. All were within a 2.3 km stretch of coast and included  
405 Cave Rock (CR; 172°45'34"E, 43°33'53"S), Moki Point (MP; 172°46'38"E,  
406 43°34'48"S), Taylor's Mistake (TM; 172°46'33"E, 43°34'52"S) and Black  
407 Rock (BR; 172°47'01"E, 43°35'01"S). CR and TM were island-like rocky  
408 benches located in a sandy beach with sandy subtidal areas whereas MP  
409 and BR were rocky benches with adjacent rocky subtidal reefs (see Rilov  
410 and Schiel, 2006a). In this study, moorings were deployed at two distances  
411 from the shore (50–70 m and 500–900 m) adjacent to each intertidal site.  
412 This allowed a comparison of competent larval abundance at different  
413 distances from shore. Collectors were mounted at two depths (0.5 and  
414 5 m) at most sites except at CR and TM, where the nearshore moorings  
415 were at 2 m depth at low tide and therefore the closer moorings included  
416 only the 0.5 m collectors. From early January to late May 2004, we  
417 exchanged collectors weekly to biweekly, depending on sea conditions.  
418 From late May to December 2004 (the austral winter and spring), we  
419 altered this schedule to week-long deployments per month. Mussel re-  
420 cruitment rate was adjusted to number per day. Here, we present data  
421 from week-long deployments in each month from February to May.

### 2.8. Data analysis

422 Recruitment data were expressed as average number of mussels  
423 settled per collector/depth/site/day. Most analyses used a mixed-model  
424 analysis of variance (ANOVA) with sites nested within coasts. Site was  
425 treated as a random factor and coast and depth were treated as fixed  
426 factors. Because (1) the recruits obtained from each sample period were  
427 likely to be from independent water masses, and (2) there were insuf-  
428 ficient degrees of freedom if the entire set from each site was analyzed  
429 and periods added as a factor, we analyzed each sampling period  
430 separately. Water masses were assumed to be independent, therefore we  
431  
432  
433

**Table 1**  
Oregon, summer 1998

	df	Period					
		1	2	3	4	5	6
<b>Collectors Source</b>							
Cape	1	1.67		<b>95.19**</b>		<b>79.42*</b>	2.65
Site(Cape)	2	<b>22.45**</b>	<b>7.34*</b>	0.25	<b>10.62*</b>	0.68	3.67
Depth	2	<b>17.03**</b>	0.31	4.10	1.75	1.09	0.59
Site*Depth	4	2.18	<b>16.85***</b>	<b>24.42***</b>	<b>3.68*</b>	<b>24.02***</b>	<b>7.01***</b>
Cape*Depth	2	2.55		2.34		2.51	0.56
Error	26-36 <sup>a</sup>						
<b>Traps Source</b>							
Cape	1	<b>62.06*</b>		0.002	1.63		0.07
Site(Cape)	2	0.05	0.08	9.38*	<b>10.70*</b>	1.92	4.84
Depth	2	5.41	3.63	5.30	<b>9.70*</b>	1.53	3.12
Site*Depth	4	0.21	0.49	0.49	0.24	1.14	0.47
Cape*Depth	2	0.71		3.17	1.43		0.37
Error	25-36 <sup>a</sup>						

F-ratios from ANOVAs conducted on the effect of cape, site (random, nested in Cape) and depth on recruitment to collectors and abundance of larvae in plankton traps on moorings. Data were  $\ln(x+1)$  transformed to approach normality. \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ . Where variances were heteroscedastic significance levels were designated as  $p < 0.025$ . F-ratios in bold are significant. For periods 2 and 4 for collectors and 2 and 5 for traps data was missing for some sites therefore Cape was not tested.

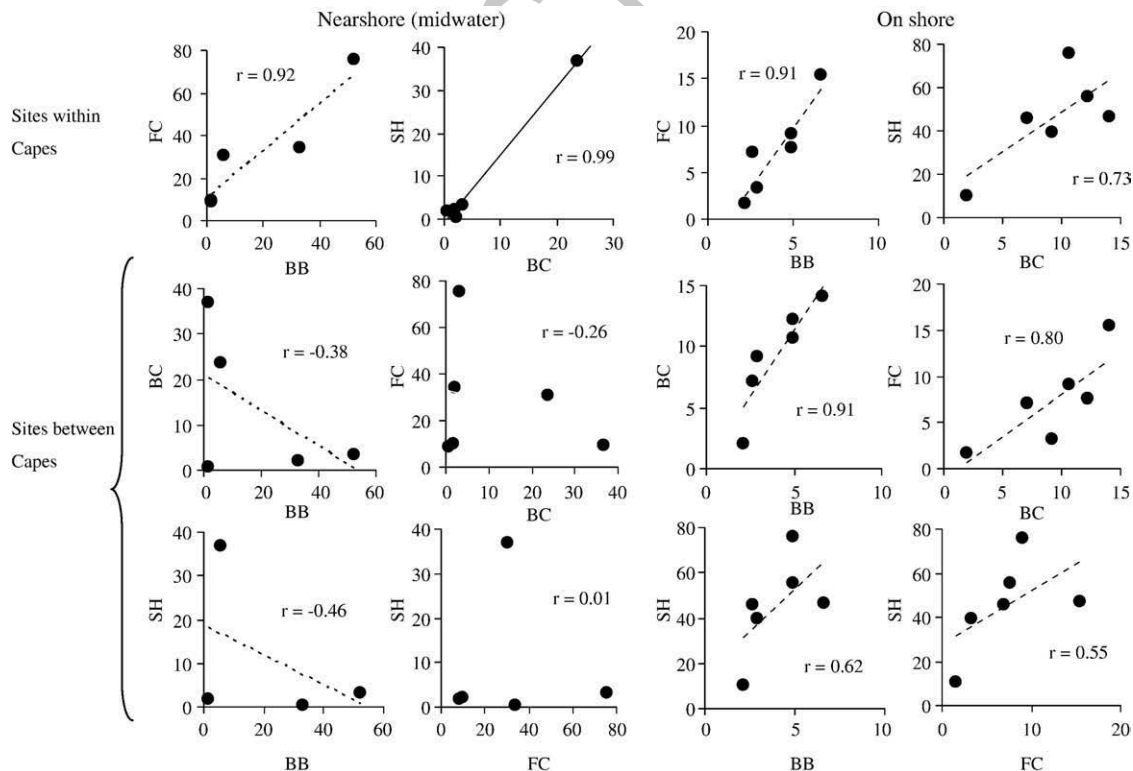
<sup>a</sup> Most degrees of freedom were 36 but some were lower due to loss of collectors.

present analyses without using the Bonferonni correction. To meet assumptions of normality, all data were transformed ( $\ln(x+1)$ ). Homogeneity of variances was evaluated using Cochran's test. When variances were heteroscedastic we still used parametric analyses because significance levels were usually very high (so that the probability of Type I errors was likely to be low). As recommended by Underwood (1997), when variances were heteroscedastic, we were conservative in our interpretations, using a p value of 0.025 instead of 0.05 as our level of significance. Analyses of

biological data were performed using the STATISTICA 7 (Statsoft) package and currents were calculated using Matlab (version 7.0.4.365).

Distance between collectors (and traps) on moorings at each depth was 0.6–1.2 m (restricted by the feasible size of the PVC pipe frames). We are aware that this distance is not ideal for separation between replicates, but deploying and frequently monitoring multiple sets of single moorings with single collectors at each site was logistically unfeasible. We recognize that the four collectors or traps per frame could be considered by some as “pseudoreplicates” (Hurlburt, 1984). We thus first using collectors or traps as replicates and the second using per-mooring means across collectors or traps as a single replicate.

In the first analysis, examination of the raw data in each sampling period revealed considerable variation in recruitment density or larval abundance among the collectors or traps, respectively, on a single frame. For example, the mean coefficient of variation (CV) of recruitment among collectors within a frame during the Oregon 1999 study was 37%. With this amount of variability within a site, in many cases means of recruitment and larval abundance on different moorings located within coasts did not differ (see Results) but differences between depths or coasts were frequently detected. This suggests that, at least when recruitment is integrated over several days or weeks, at scales of km, variation at similar depths in the inner shelf is normally not greater than variability on a single frame, and that variation between collectors on a single frame does not mask real differences among depths, sites or coasts. These findings make us confident in our results and their interpretation. Nonetheless, to avoid potential pseudoreplication, in the second analysis, we treated individual moorings for each site as single replicates (averaging data across collectors) to test the significance of coast (except for Oregon 2005 and New Zealand 2004 when coast was not relevant), depth and period on larval recruitment and abundance in the inner shelf. In this analysis, we calculated the mean of the  $\ln(x+1)$ -transformed data from the 4 collectors/traps per collector array at each depth per mooring per period as a single replicate and ran ANOVAs with



**Fig. 3.** Relationship between mussel recruitment rates at different sites along the Oregon coast on moorings (midwater depth) or on intertidal rocks in summer 1998. Solid lines indicate significant correlations ( $p < 0.05$ ), while dashed lines indicate nonsignificant trends.

476 coast and period as fixed variables. Finally, to test the correlation  
477 (Spearman Ranked correlation) between onshore and mooring recruitment  
478 values on pooled data from all studies, we used data standardized  
479 to rate of recruitment per day.

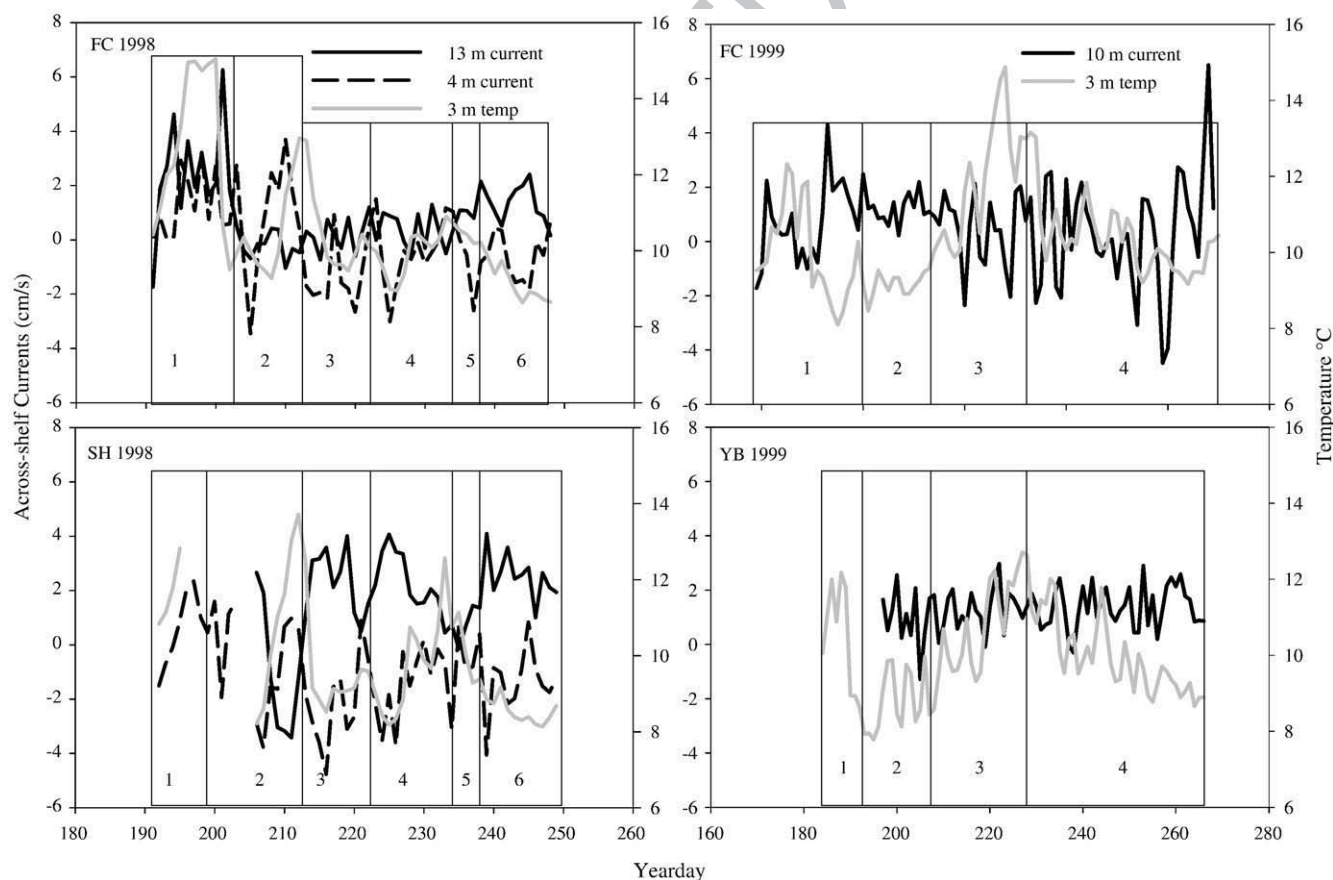
### 480 3. Results

#### 481 3.1. Oregon 1998

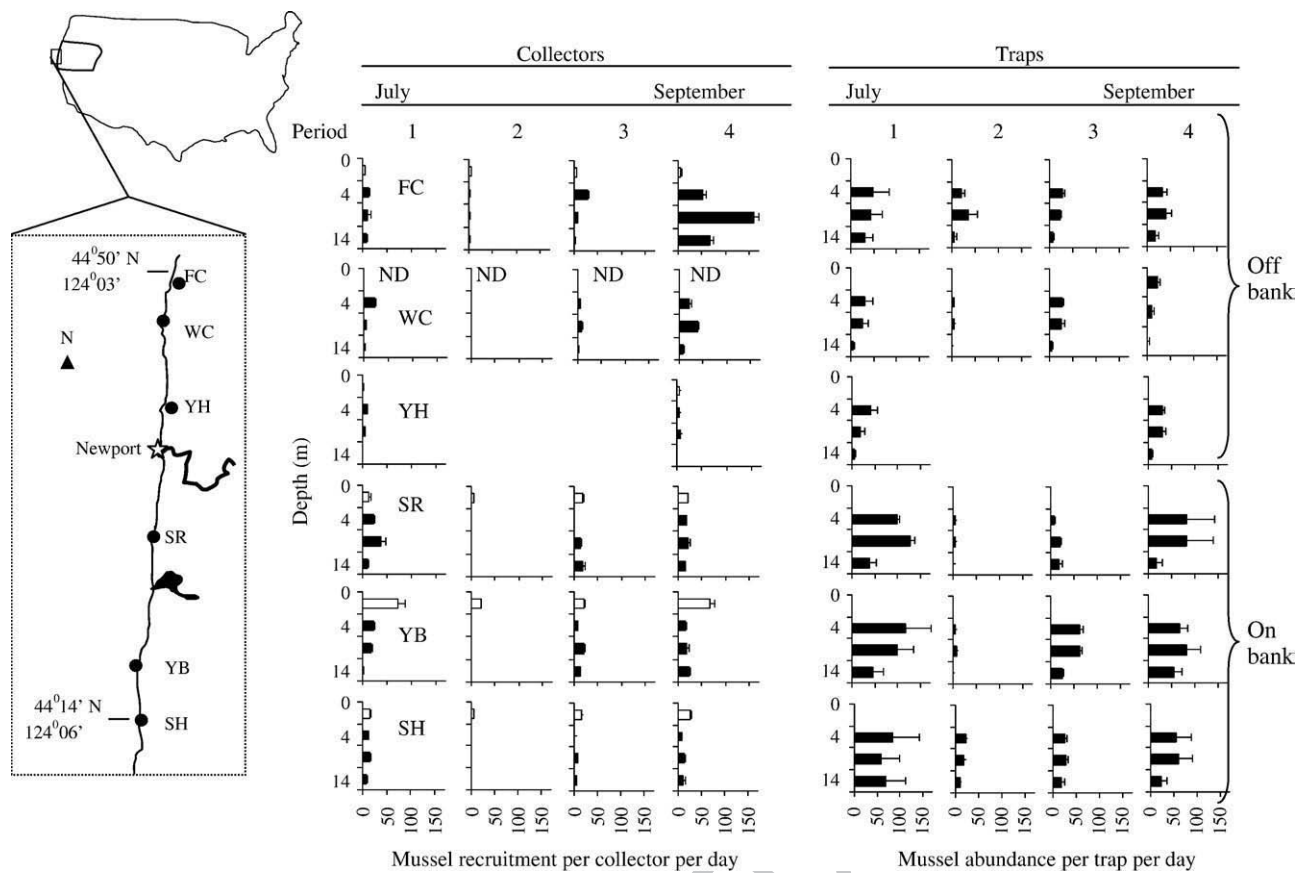
482 In 1998, recruitment varied across all scales in space, depth and  
483 time (Fig. 2). First, recruitment rates to collectors on the moorings  
484 were unrelated to those onshore (the correlations between onshore  
485 recruitment and recruitment on 14, 8.5 and 4 m collectors were weak  
486 and insignificant). Second, recruitment rates on moorings differed  
487 between capes and among sites and the highest values alternated  
488 between capes during the study period. In the first two weeks (most of  
489 July), recruitment to the moorings appeared to be greater at the Cape  
490 Perpetua than the Cape Foulweather sites, mostly due to higher values  
491 at SH in the first period (site effect  $F_{2,4}=22.45$ ,  $p<0.01$ , Table 1, Fig. 2),  
492 and to greater values at BC in the second period (site effect  $F_{2,4}=7.34$ ,  
493  $p<0.05$ , Table 1, Fig. 2). SH data from the second period were not  
494 analyzed because shallow and mid depth data were lost, although the  
495 SH bottom depth recruitment was greater than at northern sites. In  
496 contrast, recruitment was greater at the Cape Foulweather sites than  
497 at the Cape Perpetua sites in periods 3–5 (end of July and most of  
498 August), with a strong coast effect in both periods 3 and 5 ( $F_{1,2}=95.19$ ,  
499  $p<0.01$ , and  $F_{1,2}=79.42$ ,  $p<0.05$ , respectively Table 1, Fig. 2). In week 4,  
500 the site effect was strong ( $F_{2,4}=10.62$ ,  $p<0.05$ , Fig. 2; Cape Perpetua  
501 only due to lost data at BB).

502 Recruitment also frequently differed among depths. Generally, 502  
503 recruitment was greatest in midwater (8.5 m) and/or bottom (14 m)  
504 collectors except for periods 4 and 5 when it was greatest at the  
505 shallower depth (4 m) at the Cape Foulweather sites, with exceptionally  
506 high values at FC at period 4 (depth x site interaction,  $F_{4,36}=24.01$ ,  
507  $p<0.01$ , Table 1, Fig. 2). In 16 out of 22 cases, recruitment to at least one of  
508 the deeper collectors (8.5, 14 m) was greater than to the shallow (4 m)  
509 collectors, and in only 4 cases it was the opposite (in some periods/sites  
510 the overall recruitment was low therefore the differences are difficult to  
511 see on Fig. 2). Post hoc analysis (not shown) demonstrated that in most  
512 cases differences among depths were statistically significant. Using  
513 mooring means per depth as replicates and including period as a factor,  
514 recruitment was context dependent, varying with cape x period  
515 ( $F_{5,31}=21.66$ ,  $p<0.001$ ) and cape x depth ( $F_{2,31}=18.66$ ,  $p<0.05$ ). The  
516 cape x period interaction is a result of the switch in maximal recruitment  
517 rates between capes during the study period (Fig. 2). When we averaged  
518 recruitment over depths, sites and periods, recruitment was 4 times  
519 higher at CP than at CF during periods 1–2 ( $28\pm 5.6$  SE and  $7.2\pm 2.5$ ,  
520 respectively) and 16 times lower during periods 3–5 ( $2.4\pm 0.8$  and  $38.1\pm$   
521  $9.2$ , respectively). This result also suggests that coasts with different  
522 oceanographic regimes (the two capes) did not have consistent  
523 differences in competent larval abundance in the inner-shelf.

524 In contrast to the fluctuating patterns offshore, onshore recruitment  
525 was considerably higher at one site in Cape Perpetua, SH, at all periods  
526 except for period one (site x period interaction  $F_{10,96}=12.62$ ,  $p<<0.001$ ,  
527 Fig. 2). Averaging over all periods, recruitment at SH was 5 times or more  
528 higher compared to the other sites ( $46\pm 8.8$  SE per day, vs.  $9\pm 1.7$ ,  $7\pm 2$ ,  $4\pm$   
529  $0.7$  at BC, FC and BB, respectively). There was no cape effect because  
530 recruitment values at the other Cape Perpetua site, BC, were low and



**Fig. 4.** Across-shelf current velocity and surface water temperature (°C) in the inner shelf at Fogarty Creek (FC), a Cape Foulweather (northern) site, and Strawberry Hill or Yachats Beach, Cape Perpetua (southern) sites, during the 1998 and 1999 Oregon studies. Currents were measured at two depths in 1998 and one depth in 1999. The different deployment periods of mussel settlement collectors and plankton traps on the moorings are separated by vertical lines and numbered. Currents moving shoreward are  $>0$ , and currents moving offshore are  $<0$ .



**Fig. 5.** Oregon coast, summer 1999: Average (+SE) Mussel recruitment and larval abundance on moorings and mussel recruitment on adjacent intertidal sites (all adjusted to recruits or larvae/collector or trap/day;  $n=4$  collectors/traps \* depth<sup>-1</sup>). ND=no data. Length of sampling period (interval in days) during period 1 varied between 13-20 d, period 2, 7-14, period 3, 14-15, period 4, 13-52. At YH, collectors and traps were exchanged only once, and the means for period 1 were calculated for the entire 47 days that the mooring was out until mid August. Open bar at zero depth shows onshore recruitment and black bars show recruitment at the 3 depths on the moorings.

very similar to those at the Cape Foulweather sites. Onshore recruitment was always 3–7 times greater at SH than at the nearby BC site. Similarly, onshore recruitment at FC was usually ~2 times greater than at the nearby BB.

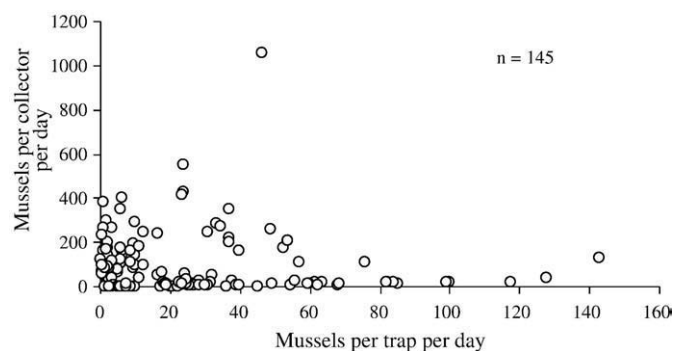
**Table 2**

Oregon, summer 1999

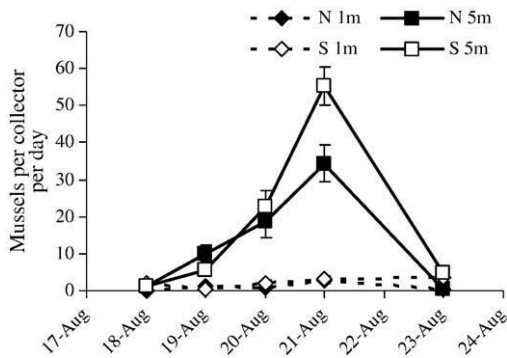
	df	Period			
		1	2	3	4
<b>Collectors Source</b>					
Coast	1	2.66	7.10	0.30	2.54
Site(Coast)	3	1.11	<b>10.50***</b>	1.40	<b>15.18***</b>
Depth	2	5.74*	0.55	0.97	<b>7.19*</b>
Site*Depth	6	<b>13.74***</b>	<b>2.70*</b>	<b>15.34***</b>	<b>2.72*</b>
Coast*Depth	2	1.10	3.65	5.40*	4.61
Error	45				
<b>Traps Source</b>					
Coast	1	<b>12.67*</b>	0.00	0.76	3.54
Site(Coast)	3	2.05	<b>37.83***</b>	<b>7.07*</b>	<b>6.87*</b>
Depth	2	<b>5.95*</b>	<b>36.16***</b>	<b>11.45***</b>	<b>12.28***</b>
Site*Depth	6	0.45	0.46	<b>2.63*</b>	0.69
Coast*Depth	2	0.63	3.19	4.63	0.47
Error	45				

F-ratios from ANOVAs conducted on the effect of coast (on- or off the Heceta bank), site (random, nested in coast) and depth on recruitment and abundance of larvae in plankton traps on moorings in four study periods. Data were  $\ln(x+1)$  transformed to approach normality. \*= $p<0.05$ , \*\*= $p<0.01$ , \*\*\*= $p<0.001$ . Where variances were heteroscedastic significance levels were designated as  $p<0.025$ . F-ratios in bold are significant. This analysis did not include Yaquina Head because period 1 extended all the way to period 4 for all other sites.

Interestingly, when recruitment was high overall, mussel recruitment was generally greater on moorings than intertidally at all sites but SH (Fig. 2). Recruitment on moorings ranged up to an order of magnitude greater than to the intertidal. For example, during period 4 at FC,  $143 \pm 5.9$  mussels per day recruited to the collectors at 4 m on the mooring but only  $3 \pm 1$  recruited to intertidal collectors. Differences in immersion time might explain some, but likely not all of this difference. Mooring collectors are always underwater and whereas intertidal collectors are underwater only about 50% of the time. But this ~two-fold difference in immersion time is far less than the ~48-fold difference in recruitment, so it seems likely that additional factors are necessary to explain differences between mooring and intertidal recruitment.



**Fig. 6.** Relationship between average mussel larval abundance in larval traps and average mussel recruitment rates in collectors on the moorings, Oregon coast; summers of 1998-99.



**Fig. 7.** Average (+SE) mussel recruitment rates to collectors mounted at two depths (1 & 5 m) on two moorings north (N) and south (S) at Fogarty Creek, OR, over 6 consecutive days in August 2005. Collectors were not exchanged on 22 August due to weather conditions so data for the 23rd were divided by two and are thus an “average” for days 22 and 23.

547 Unlike the very clear spatiotemporal patterns of recruitment on  
 548 moorings, differences in numbers of mussel larvae in the plankton traps  
 549 were less apparent (Fig. 2). During period 1, larval abundance was  
 550 greater at Cape Perpetua (cape effect;  $F_{1,2}=62.06$ ,  $p<0.05$ , Table 1). Depth  
 551 distributions were inconsistent (in 13 of 22 cases, larval abundance was  
 552 higher at 8.5 m or deeper and in 8 cases it was higher at 4 m), and larval  
 553 abundance varied by depth only in period 4 when it was highest near the  
 554 surface (depth effect;  $F_{2,4}=9.69$ ,  $p<0.05$ , Table 1). Sites also differed only  
 555 during period 4 when mussel larval abundance was lower at SH compared  
 556 to the other sites ( $F_{2,4}=10.69$ ,  $p<0.05$ , Table 1). Using moorings as  
 557 replicates and including period as a factor, larval abundance was context-  
 558 dependent (cape x depth interaction,  $F_{2,31}=6.47$ ,  $p<0.01$ ), due  
 559 mainly to the greater numbers in the shallow traps in Cape Foulweather.  
 560 Finally, larval abundance was not correlated with onshore recruitment  
 561 ( $r=-0.1$  to  $-0.29$  depending on depth,  $p>0.05$  in all cases).

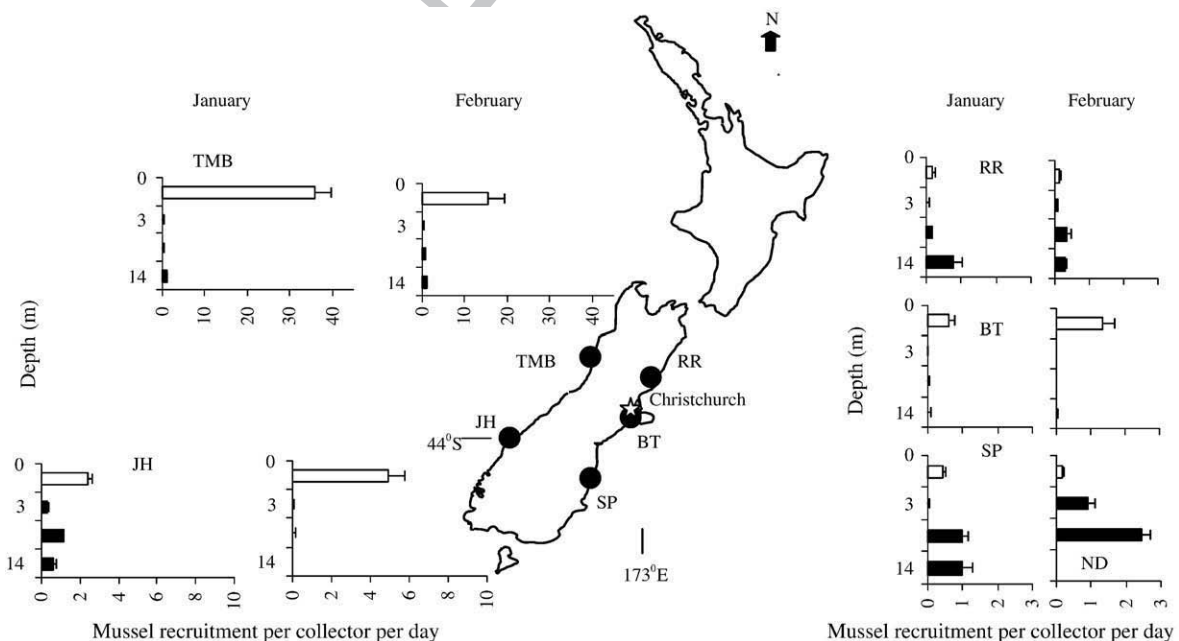
562 To determine if recruitment rates (on moorings and onshore) were  
 563 synchronized among sites (Hypothesis 2), we calculated pairwise  
 564 Pearson correlation coefficients between all sites for mooring (at all  
 565 depths) and onshore data (only mid-depth collectors are shown Fig. 3).

566 Despite several high correlation coefficients (nearshore in sites within  
 567 capes and onshore among most sites), only mooring recruitment at SH  
 568 and BC were correlated (at all depths). Other pairwise comparisons  
 569 likely would have been stronger if we had more sample periods but  
 570 correspondence was good in at least 1/3 of the cases with  $r$  near 0.8.

571 The physical data from the mooring instruments revealed interesting  
 572 temporal and spatial patterns (Fig. 4). During most of period 1 and into  
 573 period 2, across-shelf currents at Cape Foulweather moved primarily  
 574 onshore in both bottom and surface layers and water temperatures were  
 575 high (Fig. 4), patterns indicative of downwelling. This pattern changed  
 576 during the next 3 periods, with little across-shelf movement near the  
 577 bottom and mostly offshore transport at the surface (Fig. 4). At Cape  
 578 Perpetua, data were unavailable for period 1 and most of period 2 from  
 579 the bottom current meter and the temperature sensor due to equipment  
 580 failure. During periods 3–5 surface waters were mostly moving offshore  
 581 while bottom waters were moving onshore, indicative of upwelling.  
 582 Warm temperature spikes occurred when currents reversed (the end of  
 583 period 2) or were near zero (end of period 4 and into 5), a pattern typical  
 584 of downwelling or relaxation. On moorings, correlations between mean  
 585 current direction per depth (averaged over each sampling period for  
 586 both cross-shore and along-shore vectors) and either recruitment  
 587 (collectors) and/or total abundance (traps) revealed that: 1) shallow  
 588 (4 m) shoreward currents were positively correlated with the abundance  
 589 of larvae in the deeper (14 m) traps ( $r=0.47$ ,  $p<0.05$ ), and 2) shallow  
 590 poleward currents were positively correlated with abundance of larvae  
 591 in midwater (8 m) traps ( $r=0.58$ ,  $p<0.05$ ).

3.2. Oregon 1999

592 In summer 1999, as in 1998, recruitment rates on the moorings  
 593 were unrelated to those onshore ( $r=-0.05$  to  $0.1$  between onshore  
 594 recruitment and recruitment on 4, 8.5 and 14 m collectors,  $p>0.05$ ;  
 595 Fig. 5). On moorings, the most consistent effect on recruitment was  
 596 depth, the effect of which always varied with site (Fig. 5, Table 2; depth  
 597 x site interaction). Where recruitment differed with depth, recruit-  
 598 ment rates were almost always lowest on the bottom collectors.  
 599 Recruitment at the upper two depths was either similar or varied  
 600 inconsistently. During periods 2 and 4, when overall recruitment was  
 601



**Fig. 8.** Average (+SE) mussel recruitment rates per day on collectors located onshore and mounted on moorings at three depths at three east coast and two west coast sites located around the South Island of New Zealand; summer 2000. Open bar at zero depth shows onshore recruitment and black bars show recruitment at the 3 depths on the moorings. Note differences in scale among sites.

**Table 3**  
South Island of New Zealand, summer 2000

Source	df	Period	
		January	February
Coast	1	1.32	0.03
Site(Coast)	3	3.85	<b>21.18**</b>
Depth	2	4.79	3.70
Site(Coast)*Depth	6	<b>4.66***</b>	<b>3.12*</b>
Coast*Depth	2	0.27	0.10
Error	42 <sup>a</sup> -45		

F-ratios from ANOVAs conducted on the effect of coast, site (random, nested in coast) and depth on recruitment of larvae to collectors on moorings in 2 study periods. Data were ln(x+1) transformed to approach normality. \* = p<0.05, \*\* = p<0.01, \*\*\* = p<0.001. Where variances were heteroscedastic significance levels were designated as p<0.025. F-ratios in bold are significant.

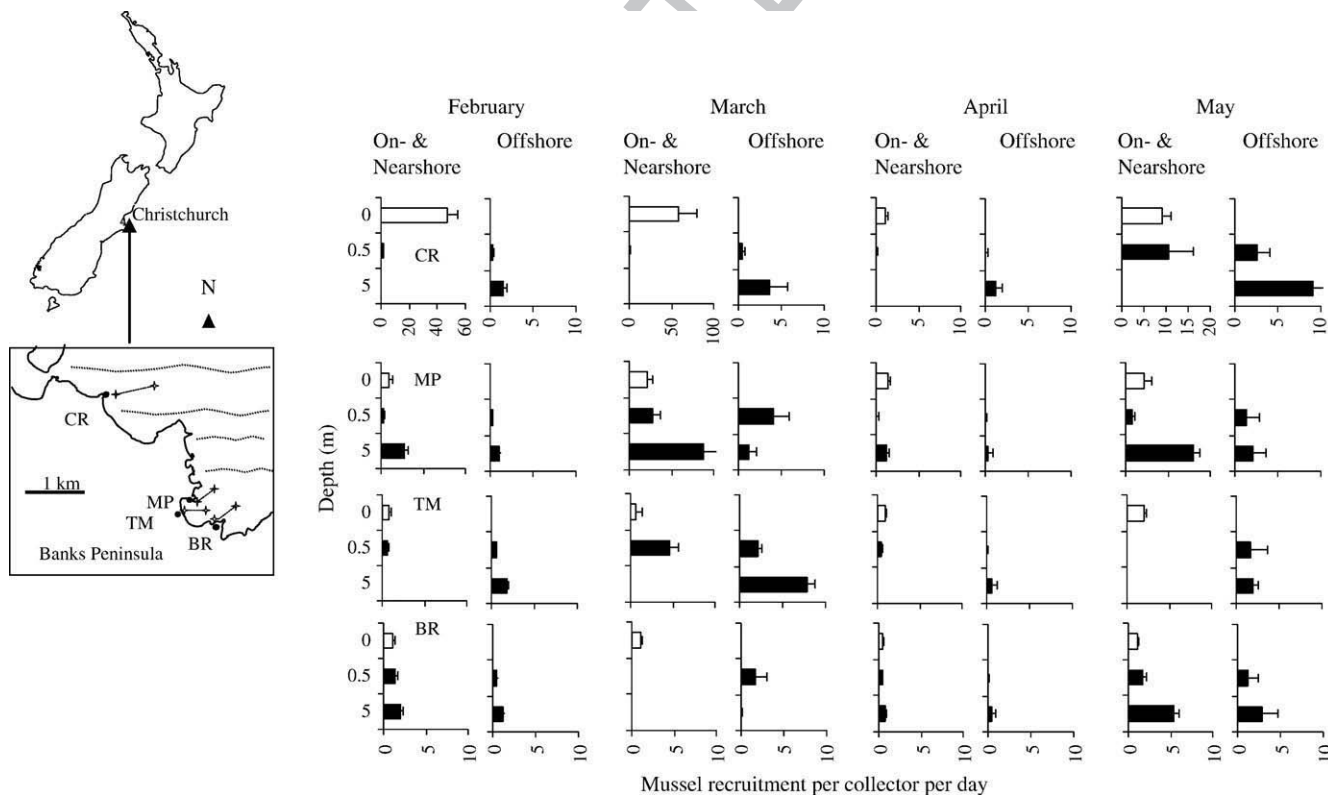
<sup>a</sup> The three February Shag Point deep collectors were lost, which resulted in a smaller n and thus a smaller error degrees of freedom.

low, values were highest on the FC mooring (period 2 site effect,  $F_{3,6} = 10.5$ ,  $p < 0.001$ ; period 4 site effect,  $F_{3,6} = 15.18$ ,  $p < 0.001$ ). Analysis using mooring means as replicates and including period as a factor, revealed that recruitment varied with depth (maximal at mid water depth;  $F_{2,36} = 4.22$ ,  $p < 0.05$ ) and by period x coast ( $F_{3,36} = 5.25$ ,  $p < 0.01$ ) with the highest recruitment levels during period 4 in the northern coast. This demonstrates again that the two coasts did not have consistent differences in competent larvae abundance at the inner-shelf waters.

In contrast to the mooring results, recruitment onshore throughout the entire study was greater at the southern sites than at the northern sites (Fig. 5). Recruitment also varied strongly among sites within coasts and the highest values were measured at YB during periods 1 and 4 (site x period interaction,  $F_{12,93} = 2.52$ ,  $p < 0.01$ , coast x period interaction,  $F_{3,12} = 3.80$ ,  $p < 0.05$ , respectively).

Patterns of total mussel larvae abundance as measured in mooring traps were more consistent in 1999 than in 1998. Lowest densities were almost always in at 14 m (Table 2, Fig. 5). Larval abundance varied among sites and between coasts (Table 2). During periods 1 and 4, overall abundance was almost three times higher at the southern than at the northern sites, although it was not significantly higher in period 4 because of high variance ( $F_{1,3} = 12.67$ ,  $p < 0.05$ ,  $F_{1,3} = 3.54$ ,  $p > 0.05$ , respectively). During periods 2 and 3, abundance varied by site; it was greater at FC and SH during period 2 (site effect,  $F_{3,6} = 37.83$ ,  $p < 0.001$ ), and at YH during period 3 but only at the shallower two depths (site x depth effect,  $F_{6,45} = 2.63$ ,  $p < 0.05$ ). Analysis using moorings as replicates (including period as a factor) revealed that larval abundance varied by period ( $F_{3,36} = 16.23$ ,  $p < 0.001$ ; lowest values during period 2), depth ( $F_{2,36} = 14.31$ ,  $p < 0.001$ ; lowest values at the bottom traps), and coast ( $F_{1,36} = 13.41$ ,  $p < 0.001$ ; higher values in the southern coast). In contrast to 1998, in 1999 total larval abundance in traps and onshore recruitment were positively correlated at all three depths ( $r = 0.51$  to  $0.56$ ,  $p < 0.05$  in all cases). However, this correlation was mostly driven by two exceptionally high recruitment dates in YB where larval abundance was also very high. When these two dates are omitted, the correlation disappears. Using the data from Oregon 1998 and 1999, mussel larval abundance in mooring traps was uncorrelated with recruitment on mooring collectors at any year or depth (pooled data show in Fig. 6).

The physical data from the mooring instruments show that currents in the northern coast fluctuated throughout the time period, but were weakly shoreward during the first two periods and weakly seaward during most of the last two periods (Fig. 4). No correlation was found between either (mooring) collector or trap data and the across-shore and along-shore currents. Two major warming events were recorded during the 1999 deployment, most notably at the northern site.



**Fig. 9.** Average (+SE) mussel settlement rates per day to collectors located onshore and mounted on nearshore moorings at two distances (50-70 m and 500-900 m) and two (for some sites and distances) depths at four sites within 2 km of shoreline near Christchurch, New Zealand east coast, summer 2004. Open bar at zero depth shows onshore recruitment and black bars show recruitment at the 2 depths on the moorings. Crosses on the map show location of nearshore moorings.

648 3.3. Oregon 2005

649 In this study, intertidal mussel recruitment was very low (0–1  
650 mussels per collector/day on average) throughout the entire 10-d  
651 period. On moorings, mussel recruitment varied by day and depth but  
652 not between moorings (Fig. 7; date x depth interaction;  $F_{4,80}=22.18$ ,  
653  $p<0.01$ ). At 5 m depth, recruitment increased from near zero on the  
654 first day to between 35–55 mussels per day per collector in August  
655 21st and then dropped to almost zero two days later (Fig. 7). At 1 m  
656 depth, recruitment was very low throughout.

657 3.4. New Zealand 2000

658 As in Oregon, onshore recruitment rates were not related to inner  
659 shelf recruitment rates on moorings (Fig. 8,  $r=-0.12$  to  $0.58$ ,  $p>0.05$ ).  
660 When on- and nearshore recruitment rates were compared between  
661 coasts, recruitment rates to the intertidal sites were orders of mag-  
662 nitude higher on the west than on the east coast, but recruitment rates  
663 on moorings were similar among all five sites (Fig. 8). On moorings,  
664 mussel recruitment varied among sites by depth (site x depth inter-  
665 action; January -  $F_{6,45}=4.66$ ,  $p<0.001$ , and February -  $F_{5,42}=3.12$ ,  
666  $p<0.05$ , Table 3). At most sites, recruitment was higher at depth (8.5 or  
667 14 m), but varied considerably among sites on the deeper collectors.  
668 For example, at BT on the east coast where intertidal recruitment was  
669 relatively high, recruitment on the deep collectors was low. At SP,  
670 where intertidal recruitment was extremely low, recruitment on  
671 moorings was higher than at the other east-coast sites. On the west  
672 coast in February, TMB had much higher recruitment on moorings and  
673 intertidally than JH (or any east coast site). When using moorings as  
674 replicates and including month as a factor, mooring recruitment did  
675 not vary with coast, site or depth ( $p>0.05$ ).

676 3.5. New Zealand 2004

677 As with the large-scale study in New Zealand and the Oregon  
678 studies, recruitment on moorings was not related to intertidal recruit-  
679 ment in the small-scale New Zealand study (Fig. 9;  $r=-0.17$  to  $0.11$ ,  
680  $p>0.05$ ). Recruitment onshore varied by 1–2 orders of magnitude in  
681 some weeks, primarily due to the much higher recruitment rates at  
682 CR, but among-site variation was much lower on the moorings. On  
683 moorings, mussel recruitment varied by depth (February, April, and  
684 May) or by both site and depth (Table 4). The dominant pattern was  
685 higher recruitment on midwater (5 m) vs. near surface (0.5 m) col-  
686 lectors (Fig. 9). In March, recruitment was higher at the surface in MP  
687 and BR which generated the site x depth interaction ( $F_{3,32}=15.45$ ,  
688  $p<0.001$ ). In May, exceptionally high recruitment at 5 m at CR led to a  
689 strong site effect independent of depth ( $F_{3,32}=9.73$ ,  $p<0.05$ ). Using  
690 moorings as replicates and including period as a factor, recruitment  
691 varied by period ( $F_{3,24}=8.39$ ,  $p<0.001$ ; low values in April) and depth  
692 ( $F_{1,24}=6.75$ ,  $p=0.015$ ; low values at the surface).

693 To evaluate how recruitment on moorings varied with distance  
694 from shore, we analyzed differences in recruitment between near and

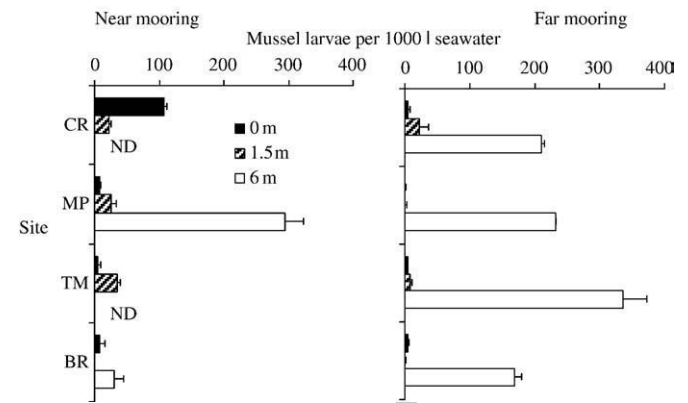


Fig. 10. Average mussel larvae densities (larvae per 1000 liters of seawater +SE) at different depths at two distances from four onshore sites near Christchurch, New Zealand. Samples were not taken at the 6 m depth at the nearshore moorings at CR and TM because the bottom at these sites was too shallow. n=3 pump samples per depth/distance.

695 far moorings by depth (4 sites for surface, and 2 sites for 5 m depth). In  
696 surface collectors, recruitment was twice as high on the near moorings  
697 (50–70 m from shore) than as on the far moorings (500–900 m from  
698 shore,  $F_{1,140}=4.66$ ,  $p<0.05$ ). In the 5 m collectors, recruitment was  $>3\times$   
699 higher on the near than on the far moorings ( $F_{1,106}=30.36$ ,  $p<0.001$ ).  
700 Recruitment also differed among sites ( $F_{1,106}=9.12$ ,  $p<0.01$ ) with near  
701 densities usually higher at MP than BR (Fig. 9).

702 To compare recruitment patterns on moorings by depth with  
703 point-in-time vertical distributions of mussel larvae, we pumped  
704 plankton samples at several sites near and far from shore on May 13,

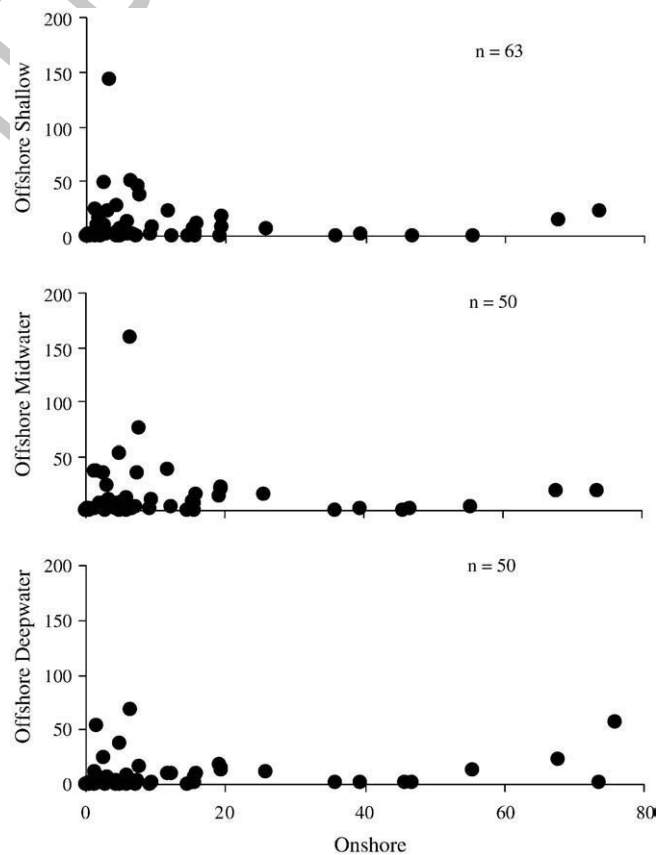


Fig. 11. The relationship between recruitment to onshore mussel collectors vs. collectors in shallow (3–5 m), medium (8.5–9 m) or deep (13–14 m) depths on nearshore moorings in Oregon and New Zealand. Values were adjusted to number of mussels per collector per day.

t4.1 **Table 4**  
t4.2 East coast of the South Island, New Zealand in summer 2004

Source	df	Period			
		February	March	April	May
Site	3	3.15	0.97	2.48	<b>9.73*</b>
Depth	1	<b>63.83**</b>	0.02	<b>25.92**</b>	<b>22.66*</b>
Site x Depth	3	0.35	<b>15.45***</b>	1.06	0.51
Error	32				

t4.5 F-ratios from ANOVAs conducted on the effect of site (random) and depth on recruitment  
t4.6 of larvae to collectors on moorings at four sites. Data were  $\ln(x+1)$  transformed to  
t4.7 approach normality. \* =  $p<0.05$ , \*\* =  $p<0.01$ , \*\*\* =  $p<0.001$ . Where variances were  
t4.8 heteroscedastic significance levels were designated as  $p<0.025$ . F-ratios in bold are  
t4.9 significant.

2004. In all cases except one, there was considerably greater larval abundance at 6 m than in shallower depths (Fig. 10). For the far stations, recruitment varied by depth among sites (depth x site interaction;  $F_{3,23}=4.43$ ,  $p<0.01$ ), with larval abundance at 6 m being higher at MP than at the other three sites. At the two sampling stations close to the nearshore moorings where deeper samples could be collected, recruitment also varied by depth between sites (depth x site interaction;  $F_{3,15}=16.54$ ,  $p<0.001$ ), with larval abundance higher at the surface at CR than at 1.5 m.

### 3.6. Analysis of pooled data

As with the more detailed analyses, no relationship was evident in data pooled across all studies (both Oregon and New Zealand) between recruitment onshore vs. recruitment on moorings at any of the three depths (Fig. 11). This analysis does not include the surface collectors in the New Zealand 2004 as there were no comparable samples in the other studies.

## 4. Discussion

### 4.1. The surf zone as a semi-permeable barrier to onshore recruitment

Although they historically have worked in different portions of the marine environment, on different scales in space and time, and with somewhat different motivations, the issue of variability in recruitment has plagued marine ecologists and fishery biologists for decades. Investigating this issue in all of the habitats a larva encounters as it is transported towards shore, including three zones - the intertidal, the surf zone and the area seaward of the surf zone - offers potential for better resolution of the processes involved in the coupling between pelagic larval populations and benthic populations of settlers, recruits and adults. Sampling is relatively inexpensive in inner shelf systems because ships either are unnecessary or are small and less costly. As a result of the lower cost of sampling in coastal (vs. offshore) habitats, and their easier access, the efficacy of sampling the entire life history of the organisms of interest, and in particular, sampling the pre-metamorphic larval stages, is higher. Despite these advantages, however, progress in understanding benthic-pelagic coupling in high-energy, wave-swept coastal environments has proceeded relatively slowly. Impediments have included, but are not limited to, mismatches in both spatial and temporal scales between events occurring on the shore and those occurring across the inner, middle and outer shelf, and the difficulty of sampling and working in the high energy environments of the inner shelf, especially the surf zone.

To our knowledge, the present study represents the most intensive and extensive attempt to examine benthic-pelagic coupling in temperate coastal locations. We believe that the results we present are of particular interest and represent a significant advance. In particular, the finding that recruitment patterns onshore generally do not reflect patterns of abundance of competent mussel larvae in the nearshore (as measured by recruitment to collectors at distances of a few tens to 100's of meters) is striking. Even more intriguing is that this pattern was seen across all scales sampled, from days to weeks, among sites, coasts and even hemispheres. The consistency in the distribution pattern of nearshore mussels (the strong depth stratification of competent larvae) and in the lack of nearshore-onshore relationship at all these scales (and most datasets) indicates that, despite some limitations with the data (see below), this result is real. The consistent lack of a relationship between competent propagule numbers onshore and the seaward side of the surf zone suggests that for mussels at least, the key to understanding how propagules are transported shoreward lies within the surf zone itself. In other words, our data suggest that the surf zone is a "semi-permeable" barrier to recruitment of mussel larvae to the intertidal zone. That is, despite temporally variable and sometimes relatively uniform larval abundances along the coast, recruit-

ment tends to be consistently high at some sites and low at others suggesting differential transport through the surf zone, or differential success in settlement in the intertidal.

A potential alternative, or additional explanation for the decoupling between on- and nearshore recruitment is that larvae settling at a site come not from directly offshore but are advected from upstream by alongshore currents. Although this process is undoubtedly important in transporting larvae, it cannot explain the relatively consistent ranking of onshore recruitment abundance among sites over time even at relatively small spatial scales (see Figs. 2, 5, 8 and 9). Further, the alternation between upwelling and downwelling conditions means alongshore currents shift between flowing northward and southward along the coast, and might be expected to shift the among-site rank order of recruitment in time if the currents have switched direction for long enough. Such temporal shifts were not observed, and we suggest that sampling of larvae directly offshore reflects larval abundances that are averaged in the alongshore direction.

What factors are responsible for the semi-permeability of the surf zone? Firm answers to this question are not yet clear. Our data offer limited insight into mechanisms, which is the subject of ongoing research. Below we summarize the results in the context of the predictions from our three hypotheses, discuss potential mechanisms that could help explain the decoupling between larval abundance and recruitment, and examine the significance of these results for the dynamics of these coastal ecosystems.

### 4.2. Tests of predictions

#### 4.2.1. Prediction 1

*Onshore recruitment rates and nearshore larval abundance will be positively correlated.* In none of studies were intertidal recruitment rates a reflection of competent larval abundance just offshore indicating that the number of competent mussel larvae nearshore (the larval pool) is not a good predictor for onshore recruitment. There was one case (Oregon 1999) where total larvae in traps correlated with onshore recruitment but this correlation was driven by two data points where both values were very high. Thus, most data are not consistent with prediction one.

#### 4.2.2. Prediction 2

*a) Larval abundance in the water column should be positively correlated among sites and coasts in the inner shelf on scales of 10s of km;*  
*b) larval recruitment will be correlated among onshore sites at this spatial scale.* The lack of relationship in rates of recruitment of mussels on nearshore moorings between sites located at different coasts (Cape Perpetua and Cape Foulweather, Oregon 1998 data) falsifies part a of this prediction but the apparent positive correlation in recruitment between sites onshore supports part b. This result indicates that the processes that affect the abundance of competent larvae nearshore are for the most part decoupled from the processes that deliver those larvae to the rocky intertidal.

#### 4.2.3. Prediction 3

*In the inner shelf, recruitment to mooring collectors will be positively correlated with the number of mussel larvae caught in plankton traps.* Contrary to prediction, the number of larvae caught in the traps and the number that recruited on the collectors were uncorrelated (Oregon, 1998, 1999 data). This could result from either a much stronger stratification of competent than of precompetent larvae in the water column or from a preference of competent larvae for settlement at specific depths, at particular distances from shore.

Additionally, we have noticed interesting regional patterns in nearshore mussel larval abundances. In Oregon, recruitment to collectors in the inner-shelf habitat often differed between the two coasts but the differences were not spatially consistent. During some periods it was higher in one coast and at other periods it was higher in the other. On the South Island of New Zealand, and in strong contrast to

828 the large between-coast difference in intertidal recruitment (Fig. 8,  
829 see also Menge et al., 1999; 2003) recruitment to moorings in the  
830 inner shelf did not differ between the west and east coasts.

#### 831 4.2.4. Caveats

832 There are several limitations to our dataset that warrant comment.  
833 As we note below, however, we do not believe that these issues  
834 compromise our conclusions.

- 835 1) *Mismatch in scales of sampling and of events in the inner shelf.*  
836 Although oceanographic conditions can change on the scales of  
837 hours to days to weeks, equipment and logistical limitations at the  
838 time prevented sampling on the shorter scales of days. Possible  
839 consequences are differential post-settlement mortality (or poten-  
840 tially facilitation) among sample periods and inability to resolve  
841 the processes generating the observed patterns. Data from more  
842 recent work show that daily settlement in our larval collectors was  
843 positively correlated with weekly recruitment (Dudas et al.  
844 unpublished data), suggesting that post-settlement mortality was  
845 density-independent and thus that the impact of the various post-  
846 settlement processes was proportionally constant.
- 847 2) *Design limitations.* On the moorings, collectors and trap replicates  
848 nearshore were spaced close to each other on the same sampling  
849 unit, generating a potential “pseudoreplication” situation (Hurl-  
850 bert, 1984). We addressed this issue by analyzing results using both  
851 individual collectors and moorings as replicates. Use of averages  
852 across collectors by mooring means that the mooring, not collector,  
853 is the replicate and eliminates the pseudoreplication issue. Our  
854 analysis using moorings as replicates showed that most patterns  
855 remained statistically significant at the coastal and water depth  
856 levels, suggesting that our results are robust.
- 857 3) *Confounding of pattern due to lack of taxonomic resolution.* Due to  
858 difficulty in distinguishing between mussel species at the larval and  
859 recruit stages (especially in Oregon), we used total mussel number  
860 in our analyses. We are aware of the fact that different species may  
861 recruit at different times of the year or be located at different depths  
862 offshore. Nevertheless, the consistency of ranking of recruitment  
863 rates onshore and the similarity in patterns of recruitment on  
864 moorings (very low at shallow water and mostly highest at  
865 midwater) suggest that (a) either one species is dominating the  
866 patterns; or (b) the different species have similar patterns of depth  
867 preference, times in the plankton and settlement. Studies address-  
868 ing this issue using genetic techniques in Oregon are underway; in  
869 New Zealand, species can be identified and analyses at the species  
870 level will be the subject of a future publication.

#### 871 4.3. The disconnect between onshore and nearshore propagule variation

872 A variety of temporal and spatial patterns emerged from our data  
873 that suggest why nearshore larval supply and onshore recruitment  
874 appear unrelated. We believe that these results can guide the direction  
875 of future studies needed to decipher the mystery of larval supply,  
876 delivery and recruitment to the shore.

877 As has been shown previously in several geographic locations (e.g.,  
878 Connolly et al., 2001; Menge et al., 2004; Menge et al., 1999; Porri et al.,  
879 2006) intertidal mussel recruitment can vary dramatically and  
880 consistently among sites even if they are only a few hundred meters  
881 apart. As we have shown in contrast, larval abundance just beyond  
882 the surf zone can be quite similar among sites, even if they are located  
883 on coasts of contrasting oceanographic conditions (e.g., the South Island  
884 of New Zealand, northern and southern parts of the central Oregon  
885 coast). Not surprisingly, given the highly labile water column envi-  
886 ronment, among-site or between-coast differences in larval abun-  
887 dance that did occur were not temporally persistent, at least in Oregon.  
888 For example, in Oregon in 1998, when larval abundance was high at  
889 Cape Perpetua it was low at Cape Foulweather and vice versa. However,

in broad terms, intertidal recruitment is generally synchronized in  
time across sites (e.g., Connolly and Roughgarden, 1998; Farrell et al.,  
1991; Menge et al., 1999). Thus, while the concentration of competent  
mussels can vary along the coast, the processes that move them  
shoreward such as upwelling-relaxation or downwelling events  
(Farrell et al., 1991; Wing et al., 1998), often operate on a coast-wide  
scale on a relatively straight coastline such as the central Oregon coast  
(Kirincich et al., 2005). Nonetheless, availability of larvae in the inner  
shelf cannot explain variation in mussel population replenishment  
patterns onshore, at least on the meso-scale. A similar result was  
recently reported on the scale of 100s of m for *Perna perna* in South  
Africa (Porri et al., 2006).

One explanation for the apparent lack of coupling between larval  
abundance in the inner shelf and onshore recruitment rates is that  
locally persistent differences in conditions on the site scale (10s–100s m)  
affect the magnitude of intertidal recruitment. Because the abundance of  
nearshore competent larvae is either relatively similar or not consis-  
tently different within coasts, local-scale processes seem most likely to  
modulate onshore recruitment among sites, thus accounting for the  
among-site consistency in rank of recruitment densities (e.g., Connolly  
et al., 2001).

What are these local-scale processes? Candidate mechanisms in-  
clude factors underlying the delivery process from the inner shelf  
through the surf zone (e.g., wave action, hydrodynamics, larval beha-  
vior or both) and site-specific intertidal conditions (e.g., rock type,  
substrate availability, settlement cues, environmental stress, and  
shoreline geomorphology). Below, we examine some of the patterns  
apparent in this study that suggest potential mechanisms involved.

Shanks and Brink (2005) demonstrated the importance of the  
vertical position of bivalve larvae to cross-shelf transport. Under-  
standing the consequences of larval positioning in the water column  
on transport and settlement is thus key in future studies of coastal  
population replenishment. Our mooring data suggest that vertical  
distribution of mussel larvae in the water column was relatively con-  
sistent. In 55 out of 77 cases from both Oregon and New Zealand,  
recruitment on mooring collectors was higher in the midwater and/or  
near-bottom depth compared to 19 cases where it was the opposite (a  
notable exception was FC in weeks 4–5 in 1998). The New Zealand  
small scale study, where moorings were deployed at two different  
distances from the shore, also showed that abundance of competent  
larvae (or perhaps their readiness to settle) increased closer to shore  
(50–70 m compared to 500–900 m offshore), and more so at 5 m depth  
than near the surface. These results indicate that competent larvae are  
frequently highly stratified in the water column even very close to  
shore (<100 m) where the water has traditionally been assumed to be  
well mixed due to surf action. Miron et al. (1995) found higher  
densities of intertidal barnacle cyprids (competent larvae) at 4 m  
compared to near-surface water very close to shore, a distribution that  
affected the barnacle's settlement zonation onshore. However this  
study was conducted in a protected bay and may not represent bar-  
nacle distribution in the water column near exposed shores. Grantham  
(1997) also found the highest densities of barnacle cyprids at depth at  
upwelling fronts and noted similar ontogenetic changes for crab,  
asteroid, and echinoid larvae.

Another intriguing finding in our study in Oregon, at least, was the  
total lack of relationship between the number of larvae in the traps and  
the number of settlers in the mooring collectors just cm away from the  
traps. Examination of the data indicates that this is because most larvae  
in the traps were caught in the near-surface to midwater depths while  
recruitment was denser at midwater and near-bottom depths. Thus at  
least in Oregon, the implication is that as they develop into com-  
petency, mussel larvae swim down or sink to midwater depths  
therefore becoming a bigger fraction of the total larvae at those depths.  
Alternatively, it is also possible that a greater proportion of the  
midwater competent larvae choose to settle compared to shallow ones.  
We cannot evaluate whether the higher recruitment to midwater

depth collectors is passive or active, but since midwater settlement is usually higher than bottom settlement, behavior seems to be a more plausible explanation. Since most larvae in traps were close to settlement size (about 250  $\mu\text{m}$ ), most larvae at all depths should be at a “competent” size, and thus the hypothesis that larval behavior underlies the denser settlement at midwater depths seems even more likely. A recent study where mussel larvae were differentiated to finer size bins showed that settlement of mussels in collectors strongly correlated with the number of 250–350  $\mu\text{m}$  larvae in traps but not with those of the 230–250  $\mu\text{m}$  further supports the importance of competency (Rilov et al. unpublished manuscript). The fact that in some cases there was higher recruitment to collectors at shallower waters suggests that it is not the effect of depth itself (e.g. pressure or light) that determines settlement. It is possible that in these cases, strong water mixing moved most of the competent larvae nearer to the surface from greater depths and this is where most eventually settled.

The evident shift in positioning in the water column in Oregon is opposite to what was found for *Mytilus edulis* larvae in gulf in the White Sea (Russia) where most larvae were found in the first 3 m below surface and pediveligers tended to move shallower to about 1.5 m towards the peak time of settlement (Dobretsov and Miron, 2001). This difference indicates that the vertical distribution of larvae of intertidal mussels in the water column can be species-specific, as they appear to be for barnacle cyprids (Grantham, 1997; Grosberg, 1982).

As Grantham (1997) hypothesized, larvae moving to depth – either by active movement or simply by sinking – may be retained closer to shore and moved shoreward during upwelling. Crab larvae off the Iberian coast, another upwelling system, exhibit this behavior, migrating vertically to deeper waters when ready to settle (Marta-Almeida et al., 2006). Similarly, in North Carolina, bivalve larvae found below the thermocline are transported shoreward during upwelling (Shanks and Brink, 2005).

The proximity to the shore of stratified waters and the thickness of the deep and surface layers are issues underlying this “conveyor belt” model of larval transport. Recent evidence along the Oregon coast indicates that water as shallow as 8 m can be stratified with respect to across-shelf currents, i.e., surface (down to 3–4 m) and bottom waters move in opposite directions (see Fig. 4 in, Kirincich et al., 2005). The steady increase of mussel settlement on collectors only at 5 m depth during the summer 2005 study in Oregon could have been a result of onshore transport of competent mussel larvae from deeper to mid water during the strong upwelling that occurred throughout the 10-day sampling period. Alternatively, or in conjunction, this peak settlement at 5 m may have been a result of competent larvae “riding” the edge of an internal wave(s) or bore(s) (Pineda, 1991) at this depth.

Although our measurements of across-shore currents show very dynamic patterns, the correlation analysis between larval abundance and current direction for the 1998 and 1999 data yielded little insight into transport mechanisms. This is probably a result of the mismatch between the temporal resolution of the physical data (high) and the biological data (low) as suggested by Schiel (2004). One significant result was an increase in larval abundance in traps at 14 m during shoreward shallow water movement during 1998 in Oregon. This may be an indication that during downwelling, mussel larvae accumulate near the bottom on the inner shelf. The other significant result from that year was an increase in mussel larvae in midwater traps with increasing southward shallow water movement. As southward currents are dominant during the prevailing summer upwelling conditions, movement of larvae from the north at this water level is plausible (although we cannot confirm this as we did not have current meters at this water level). A more in-depth analysis of this dataset, including barnacles, suggests that upwelling relaxation and/or current reversals appear to affect larval transport. Unfortunately, because of the scale mismatch the exact timing of recruitment pulses in the context of the different mechanisms acting in concert or individually could not be pinpointed (Dudas et al. in review). It is clear that in order to test the mechanisms of transport in detail, the biological sampling

must be conducted appropriately for the scale of the events being examined, i.e., the temporal and spatial scale of transport and settlement pulses that could be in the order of hours to days (Pineda, 2000). A recent example is the study of Tapia and Piñeda (2007) who examined the stage-specific distribution of barnacle larvae and onshore settlement every day for 7 days off one site in Southern California with some evidence of correspondence between cyprid abundance nearshore and settlement.

One possible explanation for the decoupling between nearshore larval abundance and onshore settlement rate might be that a significant portion of the midwater competent mussels actually settle on subtidal rocks. The fact that intertidal mussels settle subtidally on artificial substrates at mid to near-bottom depths provides evidence for potential settlement of intertidal mussels on natural subtidal reef substrates. If this proves to be the case, then in seascapes that include continuous intertidal and subtidal reefs, many of the competent larvae that approach the shore at mid to near-bottom water levels could potentially settle subtidally and therefore be mostly “lost” to the intertidal population unless they detach and resettle later higher on the shore. In New Zealand, intertidal species frequently occur as patches or beds on subtidal reefs (G. Rilov personal observations) and in Oregon preliminary sampling indicates the presence of intertidal mussel recruits within algal turf on bedrock a few meters deep. Conversely, in seascapes where intertidal benches are surrounded by shallow sandy bottoms, competent larvae that approach the shore presumably have little choice but to settle intertidally. This could potentially result in consistent higher settlement levels on rocky benches that are located in more sandy areas. Indeed, sites in Oregon that are found at the Heceta Bank coast are more “sandy” (D’Antonio, 1986; Menge et al., 1994; Trowbridge et al., 1996) and generally have higher settlement levels than sites in the northern areas. Similarly, in New Zealand, the rocky benches at TMB on the west coast are embedded in a shallow sandy/pebble beach and had by far the highest settlement rates onshore, whereas all three sites on the east coast during the 2000 study and JH on the west coast, are continuous with subtidal reefs and had much lower settlement rates. At the same time all sites on both coasts had comparable numbers of competent larvae nearshore. These potential seascape-settlement relationships are also evident on a smaller scale; near Christchurch in New Zealand the highest settlement rates occurred at CR on an isolated rocky bench located at a gently sloping sandy beach with no adjacent subtidal reefs, whereas the other three sites are part (or are very close to, TM site) of a larger rocky shore with steeper slopes and more subtidal reefs. This “seascape-settlement hypothesis” is similar to Pineda and Caswell’s (1997) “decreased-substrate settlement-intensification hypothesis”. These authors suggested that the amount of substrate available for settlement influences recruitment because settlement is higher in areas where substrate is limited (e.g., by sand) than in areas where it is not (Pineda, 1994; Pineda, 2000; Pineda and Caswell, 1997; Pineda et al., 2002). In our hypothesis, we emphasize that subtidal substrate limitation facilitates intertidal settlement. In New Zealand at CR, where the bottom is shallow and sandy very close to shore, water that was pumped 70 m from shore had more larvae at the surface than at 1.5 m whereas in all the other nearby sites larvae were more abundant deeper. Possibly, at CR, mussel larvae that found no available substrate subtidally are forced to the surface. Further testing of the seascape hypothesis seems warranted.

## 5. Conclusions

Our results document some intriguing patterns and raise a number of questions. One suggestion is that larger-scale (10s of km) coastal oceanographic processes affect the timing of settlement events, while smaller-scale differences in coastal morphology modify these processes, resulting in localized differences in the magnitude of settlement. In order to fully understand the relationship between the nearshore larval pool

and onshore transport and settlement we must, in conjunction with studying nearshore oceanography, attempt to open the *very-nearshore*, surf zone “black box” that has been least investigated by both oceanographers and marine ecologists. Such efforts should facilitate the refinement of larval transport models that have so far been limited to the areas beyond the 20 m isobath and help decipher the largely unexplained variability in settlement rates to the shore.

The study of processes that operate on a local scale, and determine population replenishment, also has implication for conservation of coastal ecological communities and should, for example, influence the selection, design and management of marine protected areas. Furthermore, understanding the processes driving patterns of larval transport and recruitment is increasingly urgent given recent evidence that the impacts of climate change are accelerating and may affect the circulation patterns that drive local transport mechanisms (Harley et al., 2006). Global warming is predicted to influence upwelling conditions either by weakening upwelling intensity (Vecchi et al., 2006) or by intensifying it (Bakun and Weeks, 2004). The study of transport processes at all appropriate scales should thus be a top priority for both marine ecologists and conservationists.

## Acknowledgments

We thank R. Barrell, captain of the R/V Sacajawea, G. Hudson, J. Pamplin and M. Foley who assisted with the mooring fieldwork and F. Jones and his ship operation staff who coordinated our boat trips, helped load and provided storage space during the 1998–99 Oregon studies. D. Pilsbury and J. Simpkins provided advice and assistance during the mooring design process and generously provided materials to construct the first prototypes. R/V *Kalipi* and R/V *Elakha* boat crews: J. Barth, A. Dale, S. Holmes, C. Holmes, M. Robart and K. Shearman, and the intertidal crew: R. Driscoll, R. Hilgris, J. Tyburczy, B. Martin, D. McCoy, R. McCoy and K. Milligan helped greatly during the 2005 Oregon study. Many thanks to our Marine Ecology Research Group colleagues at the University of Canterbury in New Zealand, D. Taylor, P. South and R. Taylor, for invaluable help in the field, and to D. Tattle for help in mooring construction and boat work. This research was supported by the David and Lucile Packard Foundation, the Andrew W. Mellon Foundation (to B.A. Menge and J. Lubchenco and to D.R. Schiel), including a post-doctoral fellowship to G. Rilov, an NSF (SGER) grant (OCE97-29396) to B. A. Menge and the New Zealand Foundation for Research, Science and Technology (to D. Schiel). This is contribution number 292 from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans, funded primarily by the Gordon and Betty Moore Foundation and the David and Lucile Packard Foundation. [SS]

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