

Spatial patterns of invertebrate settlement in giant kelp forests

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ABSTRACT: Settlement of kelp-associated organisms may vary as they are delivered to (and through) giant kelp (*Macrocystis pyrifera*) forests, with implications for local population dynamics and community structure. Previous work suggests that settlement of invertebrates with long pelagic durations would be reduced as they move from an offshore environment toward the interior of kelp forests due to dampened current flow and reduced larval delivery. We evaluated spatial variation in settlement across giant kelp forests in an extensive field study conducted over 2 yr. We collected and sorted >36 000 settling organisms and had sufficient data to explore patterns in detail for 8 taxa. Orthogastropods (snails) were the most common invertebrates and exhibited a pattern of declining settlement from the outer (seaward) to inshore edge of kelp forests. Inverse patterns were observed for *Crepidula* spp. and carideans, and other abundant taxa (non-sessile polychaetes and pectinids) showed spatial structure that differed regionally and between years. Other taxa failed to exhibit significant spatial variation in settlement. In general, settlement was lower near the sea floor than in the upper water column, and similar across locations for most groups. For some taxa, spatial variation was more apparent when the magnitude of settlement was relatively low, which may suggest that kelp forests become 'saturated' with larvae during pulses of high settlement. Our results are in contrast to previous predictions, as we observed high settlement in the interior for several species with long pelagic durations. For taxa that settled evenly across kelp-forested reefs, differential distributions of adults may be attributed to post-settlement processes. The patterns we observed here warrant additional study to address potential mechanisms for differential settlement.

KEY WORDS: Settlement · Invertebrates · Giant kelp forests · Larval filtering · *Macrocystis pyrifera* · Biogenic structure

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INTRODUCTION

Marine biogenic habitats alter both environmental conditions (Fonseca et al. 1982, Jackson & Winant 1983, Lowe et al. 2005) and biotic interactions (Irlandi et al. 1995, Arkema et al. 2009), and thus play an important role in shaping population structure and community dynamics (Bégin et al. 2004, Arkema et al. 2009). Although the presence and type of biogenic habitat influences diversity and community structure (Graham 2004, Pérez-Matus & Shima 2010), there is also the potential for species distributions and ecological processes to vary spatially within habitat

patches. For example, epifaunal abundances in seagrass beds are often higher near edges despite greater structural complexity in the interior, with distributions varying by taxa (Bologna & Heck 2002, Moore & Hovel 2010). There are also uncertainties concerning the sources of this variability, as adult distributions are influenced by a suite of processes that may vary with location within a habitat, differentially reducing the abundance of organisms. As examples, juvenile blue crabs have higher survival rates in smaller fragmented patches of seagrass because predatory adult blue crabs are less abundant in patches with more edge area (Hovel & Lip-

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cius 2001, 2002), whereas bivalves have higher settlement (Bologna & Heck 2000) coupled with greater predation-induced mortality at the edges of seagrass patches (Irlandi et al. 1995, Bologna 1999).

Recruitment (the addition of new individuals to a population) replenishes local populations but is highly variable (Caley et al. 1996) and is influenced by processes acting at multiple spatial and temporal scales (Keough & Downes 1982, Raimondi 1990, Pineda 1994). In particular, as larvae approach settlement, habitat structure may contribute to spatial variation in settlement by altering current flow (Eckman 1983, Jackson 1986), creating differential complexity and availability of suitable substrata (Foster & Schiel 1985, Bégin et al. 2004), and also providing living space for resident organisms that may decrease settlement through predation (Keough 1984, Gaines & Roughgarden 1987). In turn, this may influence the distribution and age structure of adults (Roughgarden et al. 1985, Reed et al. 2000).

On temperate rocky reefs along the California coast and elsewhere, the giant kelp, *Macrocystis pyrifera*, provides tremendous structural habitat complexity, extending from the sea floor to the water surface in forming extensive forests on rocky reefs, supporting a diverse assemblage of organisms (reviewed by Graham et al. 2007, Graham et al. 2008). The complex structure of giant kelp modifies the physical environment significantly through greatly increased drag and reduced current flow (Jackson & Winant 1983, Jackson 1998, Gaylord et al. 2007) as well as decreased light, with direct and indirect effects on benthic communities (Reed & Foster 1984, Arkema et al. 2009). Specifically, the interior of large giant kelp forests is characterized by greatly reduced flow relative to outer edges, and the delivery and settlement of organisms to or through a giant kelp forest may differ depending on the location in or near the forest (Jackson 1986), with potential effects on local populations and communities. Further, kelp forests may act as a filter for larvae (Bernstein & Jung 1979, Jackson 1986, Schroeter et al. 1996) via passive processes (reduced delivery to the kelp forest interior due to reduced flow), active processes (e.g. predation on larvae) (Gaines & Roughgarden 1987), or settlement as larvae encounter suitable substrata (Jackson 1986, Carr 1994). Variation in larval traits (e.g. pelagic larval duration (PLD), swimming ability) and settlement cues (Bernstein & Jung 1979, Keough & Downes 1982, Jackson 1986) may also play a role.

Although spatial patterns of invertebrate settlement ('settlement shadows') have been observed in seagrass beds (Orth 1992, Bologna & Heck 2000),

clear patterns of settlement in kelp forests have only been detected for common encrusting epiphytes (*Membranipora membranacea*, *Celleporella hyalina*, *Lichenopora huskiana*, and *Circeis spirillum*; Bernstein & Jung 1979). Overall, relatively few tests of a larval filtering hypothesis have been conducted in kelp forests, and results thus far have been inconsistent. For example, settlement of purple and red sea urchins (*Strongylocentrotus purpuratus* and *Mesocentrotus franciscanus*, respectively) was found to be spatially homogenous between inshore and seaward edges of giant kelp forests (Schroeter et al. 1996), and settlement of multiple echinoderm species was not influenced predictably by stands of brown kelp *Saccharina longicruris* (Balch & Scheibling 2000). Given that spatial patterns of settlement in biogenic structure have been observed in some epiphytes, but not in echinoderms, it is possible that settlement may vary spatially within kelp forests for other species due to the diversity of marine taxa and variation in their life histories, especially the highly diverse organisms that occur within kelp forests of southern California (Coyer 1984, Strathmann 1985, Graham et al. 2008).

Our objective was to determine whether settlement of multiple marine invertebrate taxa differed spatially within giant kelp forests and whether patterns were maintained between years. Therefore, we developed an array of artificial substrata as settlement collectors for a variety of invertebrate taxa and addressed 3 questions: (1) Does the settlement of invertebrates differ among locations within kelp forests, and if so, do taxa exhibit differential patterns? (2) Are spatial patterns of invertebrate settlement consistent between years? (3) Does the magnitude of settlement influence spatial patterns of settlement?

MATERIALS AND METHODS

Study system and design

Expansive subtidal rocky reefs off Point Loma in San Diego, California, USA support large stands of giant kelp that extend nearly 7 km alongshore and approximately 1 km perpendicular to shore at the widest point. These kelp forests are located on a wide rocky shelf of very low relief, and the dense stands of giant kelp attenuate currents to such a degree that the interior of the forests receives relatively low flow from alongshore or offshore currents, and is characterized by reduced bidirectional oscillatory flow

(Jackson & Winant 1983, Jackson 1986, 1998). Point Loma is an ideal study area because stands of giant kelp are sufficiently large to test a larval filtering hypothesis while variation in bottom topography is low and thus unlikely to be confounded with biogenic structure.

To detect potential cross-shelf (perpendicular to shore) and along-shore variation in settlement of invertebrates, a complete randomized block design was used in which northern and southern regions along Point Loma were established, with regions separated by approximately 1.5 km. Within each region, 3 cross-shelf transects were established randomly, spaced between 100 and 500 m apart. Three sites were then established haphazardly along each transect, with one in each of the following along-shore strata: (1) the 'outer edge', 10 m west of the outer edge of contiguous kelp forest, (2) the 'interior', approximately in the middle of kelp-forested reefs and at least 100 m east of the outer edge (this minimum distance was selected to account for narrower regions of the kelp forest), and (3), the 'inner edge', 10 m east of the inner edge of contiguous kelp forest (Fig. 1). Thus, this sampling design consisted of 2 regions, 3 cross-shelf transects within each region, and 3 sites positioned along each transect for a total of 18 sites.

At each site, 2 moorings were deployed to account for potentially high variation in invertebrate settlement within sites. The first mooring was placed

haphazardly, with the second placed 10 m south. All giant kelp within a 10 m radius of each mooring was cleared to prevent entanglement of kelp with moorings and to maintain a standardized amount of structure immediately surrounding settlement collectors. All clearings were maintained throughout sampling periods in 2009 and 2010.

Estimating invertebrate settlement

We were interested in the relative differences among locations in kelp forests and did not wish to target a specific species, so dish-scrubbing pads (S.O.S. Tuff, Clorox; hereafter Tuffys) were selected as indices of invertebrate settlement as they are a well-established method of sampling a wide variety of phyla (Leonard et al. 1998, Menge et al. 1999, Mace & Morgan 2006). Although settlement to Tuffys may differ quantitatively from natural substrates, relative differences in settlement among sites should be consistent regardless of the substrate used. Sampling of settlers was conducted every 2 wk during 2 consecutive summer-fall periods, July to October 2009 and 2010. During 2009, 1 Tuffy was placed at ~7 m depth on each of the 2 moorings per site. This depth was selected to determine spatial patterns in settlement while avoiding potential confounding effects of the kelp canopy. In 2010, 1 additional Tuffy was deployed ~2 m above the sea floor at each site to determine any depth-associated spatial patterns in settlement. The mooring used for monitoring settlement near the sea floor was randomly selected at each 2 wk sampling period. Tuffys were collected by divers every ~2 wk (Lagos et al. 2007) using a plastic bag that was sealed and then stored at -20°C until processing. All samples were passed through a 500 µm sieve in the laboratory, and any echinoderms were identified and removed for preservation in 75% ethanol while all other organisms were fixed in 10% formalin and then preserved in 75% ethanol. After preservation, samples were sorted to the lowest practical taxonomic level possible using conspicuous morphological traits. Thus the level of taxonomic resolution varied among phyla. Taxa present in very few samples and taxa that do not possess a pelagic larval stage (i.e. 'brooding' taxa) were excluded from analyses.

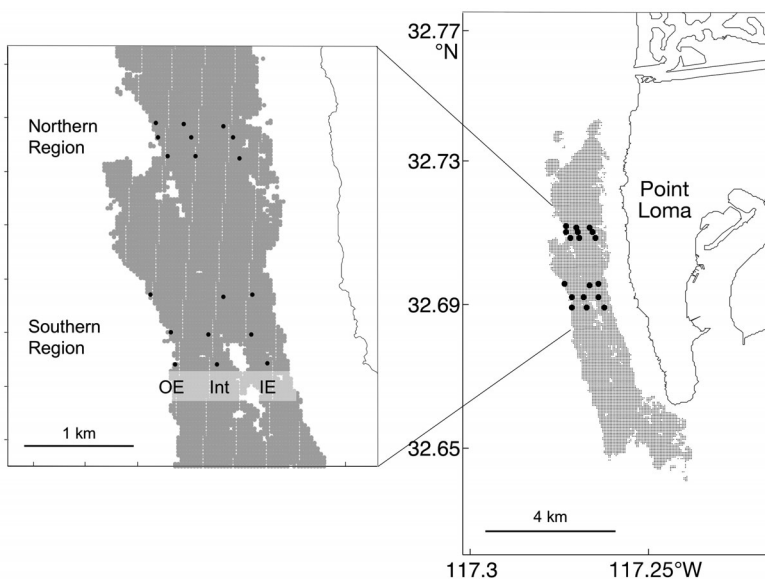


Fig. 1. Diagram of site locations at Point Loma, California, USA. Gray overlay indicates every point where giant kelp was observed at >0.13 density (via Landsat imagery) during 2009 and 2010. Invertebrate sampling sites are represented as black dots. OE: Outer Edge; Int: Interior; IE: Inner Edge

Statistical analyses

Mean settlement per 14 d for each sampling site over a 1 yr period was determined by averaging settlement between the 2 Tuffys at 7 m depth at each site for each 2 wk sample and then averaging settlement among samples at that site over the course of the entire sampling period. This provided a single point estimate of mean settlement per 14 d for 2009 and 2010 at each of 18 sites at 7 m depth (hereafter 'mean settlement'). The same procedure was used to obtain a single estimate for invertebrate settlement 2 m above the sea floor in 2010 at each of the 18 sites. Thus, our replication is at the level of sites (and not within sites) with a sample size of 6 for each location (outer edge, interior, and inner edge) and we further reduced potential within-site variability by integrating settlement over time rather than deploying additional collectors at each site.

To detect differences in overall settlement of invertebrates spatially (at 7 m depth) and inter-annually within kelp forests, a 4-factor permutational multivariate analysis of variance (PERMANOVA) was conducted based on Bray-Curtis similarities (PRIMER-E v6), followed by pair-wise comparisons between locations. PERMANOVA was used to test for simultaneous responses of all taxa to the independent variables in the sampling design. A square-root transformation was employed to reduce the contribution of highly abundant taxa in relation to less abundant taxa (Clarke & Gorely 2006). Region (north or south) and location (outer edge, interior, inner edge) were included as fixed factors, with transect (nested within region) and sampling year (2009 and 2010) as random factors. Similarity percentage analysis (SIMPER) was then used to determine the relative contributions of taxa to differences among locations and between years.

To determine whether individual taxa exhibited spatial patterns of settlement at 7 m, mean settlement for each taxon was analyzed using a 4-factor mixed-model nested ANOVA (region and location as fixed factors, and transect (within region) and year as random factors) followed by planned comparisons (Bonferroni method with corrections for multiple comparisons) to identify differences among locations (SYSTAT 12). Planned comparisons were used because of the prediction of reduced larval settlement across kelp forests according to a larval filtering hypothesis. Log transformations ($\log[x+1]$) were applied to mean settlement when necessary to improve assumptions of the model.

Sampling at depth (2 m above the sea floor) was conducted in 2010 only, with a single Tuffy deployed

per site during each 2 wk sampling period. The Tuffy at 7 m from the same mooring line as the deeper Tuffy was used in a comparison of mean settlement between depths. Mean settlement per 14 d was analyzed using a 4-factor PERMANOVA based on Bray-Curtis similarities (depth, region, and location as fixed factors, and transect nested with region as a random factor, with square-root transformation) followed by SIMPER and pair-wise comparisons as appropriate.

To assess whether settlement patterns of individual taxa might be influenced by depth, mean settlement 2010 for each taxon was analyzed using a 4-factor mixed-model nested ANOVA (region, location, and depth as fixed, and transect (within region) as random) followed by planned comparisons (Bonferroni method) of locations within each sampling depth. Rather than examining overall spatial structure, we focused only on differences between locations within each sampling depth. Log transformations ($\log[x+1]$) were applied to mean settlement when necessary to improve assumptions of the model.

To address whether observed spatial patterns of settlement differed when the magnitude (density of settlers per Tuffy) of settlement was relatively low versus high, we identified the sampling dates with the lowest (non-zero) and highest settlement within each year. We ensured that the assumptions of ANOVA were met, and that mean settlement was statistically different between these 2 dates. Spatial patterns on specific dates were unknown prior to the selection of dates. Settlement was examined using a 3-factor nested ANOVA, with region, location, and transect (region) as fixed factors, followed by planned comparisons (Bonferroni method) between locations.

RESULTS

Over 2 yr, 36 189 settling invertebrates were collected and sorted into 12 taxa. Eight taxa were suitable for detailed analyses after less abundant taxa were excluded. Snails (hereafter orthogastropods) were most abundant in our sample, followed by non-sessile polychaetes and scallops (pectinids) (Table S1 in the Supplement at www.int-res.com/articles/suppl/m485p075_supp.pdf).

There was a significant difference in the collective settlement of all taxa among locations and between years (Table 1). However, pairwise comparisons within PERMANOVA failed to detect differences between individual locations ($p > 0.05$), indicating high variability in this system. The difference among loca-

Table 1. Results of PERMANOVA for settlement of all taxa combined. Bolded values indicate significance at $\alpha \leq 0.05$.

| Source | SS | df | MS | Pseudo- <i>F</i> | p(perm) |
|--|---------|----|---------|------------------|-----------------|
| Year | 3241.00 | 1 | 3241.00 | 27.34 | <0.01 |
| Region | 205.89 | 1 | 205.89 | 1.25 | 0.41 |
| Location | 1988.70 | 2 | 994.35 | 9.15 | 0.02 |
| Transect(Region) | 321.72 | 4 | 80.43 | 0.68 | 0.67 |
| Region \times Year | 179.30 | 1 | 179.30 | 1.51 | 0.24 |
| Location \times Year | 217.24 | 2 | 108.62 | 1.14 | 0.34 |
| Location \times Region | 731.82 | 2 | 365.91 | 3.02 | 0.11 |
| Year \times Transect(Region) | 474.18 | 4 | 118.54 | 1.24 | 0.27 |
| Year \times Region \times Location | 242.62 | 2 | 121.31 | 1.27 | 0.28 |
| Residual | 1531.30 | 16 | 95.71 | | |
| Total | 9133.7 | 35 | | | |

tions was primarily due to variation in the relative abundance of orthogastropods, but non-sessile polychaetes and scallops were also important; the 3 taxa collectively contributed over 60% of the dissimilarity in each of the pairwise comparisons between locations (Table 2). These 3 taxa also were the largest contributors to the difference in settlement between years.

Each taxon was examined individually to determine its concordance with overall trends, and indeed some taxa exhibited cross-shelf patterns while many others did not (Table 3, Fig. 2). Moreover, each of the 3 gastropod taxa demonstrated differential patterns of settlement among locations. Orthogastropods were similar in settlement between the outer edge and interior ($p = 0.49$), but decreased from the outer edge to the inner edge ($p = 0.05$) and the interior to the inner edge ($p < 0.01$) (Fig. 2a). By contrast, slipper limpets *Crepidula* spp. increased from the outer edge to the interior ($p < 0.01$), and from the outer edge to

the inner edge ($p < 0.01$) (Fig. 2b). Opisthobranchs showed a more complex pattern of settlement, with interactions between location and year and between region and year (Fig. 2c). Comparisons within years and regions revealed that settlement did not differ among locations in 2010, but trends were detected in 2009, with nominally lower settlement along the inner edge (outer edge to inner edge, $p = 0.06$; interior to inner edge, $p = 0.07$).

Other taxa exhibited some variability in time and space, including spatial patterns of settlement as well as

interactions between variables. Non-sessile polychaetes (the second most abundant group) did not demonstrate a statistical difference overall among locations, and a high degree of variability was present in both years (Fig. 2d). It is worth noting that in the northern region in 2010 only, settlement was higher at the outer edge than at the inner edge ($p < 0.01$); however, this was the only difference detected between locations. The overall effect of region was nonsignificant ($p = 0.08$), as was the interaction between year, location, and region ($p = 0.10$). Pectinids differed in settlement between years, and in 2009 the interior experienced higher settlement than the inner edge ($p = 0.05$), but all locations were similar in 2010 (Fig. 2e). Other bivalves exhibited a possible trend towards higher settlement to the outer edge vs. the inner edge ($p = 0.08$), but did not exhibit a significant location effect and high variability in settlement was evident (Fig. 2f). Interactions between region and year and between transect (region)

Table 2. Results of SIMPER analysis of factors affecting overall settlement. The mean settlement per 14 d period is shown for each group. Values shown in parentheses are the percentage of dissimilarity for each comparison. Taxa are listed in order of percentage contribution to the largest dissimilarity (2009 vs. 2010). For percentage contributions to dissimilarity, each column totals to 100%. OE: Outer Edge; Int: Interior; IE: Inner Edge

| Taxa | Mean settlement | | | | | Contribution to dissimilarity (%) | | | |
|------------------------|-----------------|------|------|------|------|-----------------------------------|-----------------------|----------------------|--------------------------|
| | OE | Int | IE | 2009 | 2010 | OE vs. Int (20.41) | Int vs. IE (22.72) | IE vs. OE (24.01) | 2009 vs. 2010 (25.31) |
| Orthogastropoda | 6.69 | 7.63 | 4.79 | 5.25 | 7.49 | 28.40 | 38.46 | 30.72 | 30.53 |
| Pectinidae | 4.78 | 2.53 | 2.06 | 3.28 | 1.17 | 19.78 | 17.64 | 14.27 | 23.00 |
| Non-sessile Polychaeta | 2.07 | 4.50 | 3.88 | 4.12 | 4.64 | 17.34 | 13.35 | 15.20 | 13.81 |
| Caridea | 0.54 | 1.21 | 1.51 | 0.92 | 1.26 | 9.65 | 8.28 | 12.25 | 8.50 |
| Brachyura | 0.73 | 0.63 | 0.50 | 0.26 | 0.98 | 6.11 | 6.13 | 6.97 | 8.13 |
| Other Bivalvia | 1.08 | 1.31 | 1.47 | 1.17 | 1.40 | 6.17 | 7.41 | 7.20 | 6.31 |
| Opisthobranchia | 1.26 | 1.14 | 0.98 | 1.25 | 1.00 | 7.00 | 4.82 | 6.49 | 5.43 |
| <i>Crepidula</i> spp. | 0.53 | 0.92 | 1.11 | 0.92 | 0.79 | 5.55 | 3.91 | 6.92 | 4.29 |

Table 3. Results of 4-factor mixed model nested ANOVAs on mean settlement of individual taxa at 7 m depth over 2 yr (n = 36 for each taxa). **Bold** values indicate significance at $\alpha \leq 0.05$ (see Table S2 in the Supplement at www.int-res.com/articles/suppl/m485p075_supp.pdf for full ANOVA tables)

| Source | Orthogastropoda | | <i>Crepidula</i> spp. ^a | | Opisthobranchia | | Non-sessile Polychaeta ^a | |
|-------------------------|-------------------------|-----------------|------------------------------------|-------------|------------------------|-----------------|-------------------------------------|-------------|
| | F | p | F | p | F | p | F | p |
| Year | 98.85 | <0.01 | 2.93 | 0.11 | 1.55 | 0.28 | 2.62 | 0.18 |
| Region | 2.08 | 0.39 | 2.66 | 0.35 | <0.01 | 1.00 | 50.09 | 0.08 |
| Location | 20.85 | 0.05 | 28.74 | 0.03 | 0.68 | 0.60 | 2.19 | 0.31 |
| Transect(Region) | 3.09 | 0.15 | 0.84 | 0.57 | 0.19 | 0.93 | 1.37 | 0.38 |
| Region × Year | 0.19 | 0.67 | 1.75 | 0.20 | 7.08 | 0.02 | 0.15 | 0.71 |
| Location × Year | 0.42 | 0.67 | 0.69 | 0.52 | 3.99 | 0.04 | 1.57 | 0.24 |
| Year × Transect(Region) | 0.19 | 0.94 | 0.73 | 0.59 | 2.68 | 0.07 | 0.86 | 0.51 |
| Location × Region | 3.39 | 0.23 | 0.51 | 0.66 | 0.34 | 0.75 | 2.16 | 0.32 |
| Year × Loc. × Region | 0.69 | 0.52 | 1.14 | 0.35 | 3.16 | 0.07 | 2.67 | 0.10 |
| Source | Pectinidae ^a | | Other Bivalvia ^a | | Brachyura ^a | | Caridea ^a | |
| | F | p | F | p | F | p | F | p |
| Year | 263.70 | <0.01 | 1.00 | 0.37 | 46.70 | <0.01 | 10.68 | 0.03 |
| Region | 1.49 | 0.44 | 1.58 | 0.43 | 0.19 | 0.74 | <0.01 | 1.00 |
| Location | 0.60 | 0.62 | 2.05 | 0.33 | 3.81 | 0.21 | 8.52 | 0.11 |
| Transect(Region) | 0.96 | 0.52 | 0.23 | 0.91 | 0.82 | 0.57 | 2.51 | 0.20 |
| Region × Year | 1.26 | 0.28 | 5.91 | 0.03 | 0.18 | 0.68 | 1.87 | 0.19 |
| Location × Year | 3.49 | 0.06 | 1.49 | 0.25 | 0.36 | 0.70 | 2.00 | 0.17 |
| Year × Transect(Region) | 0.70 | 0.61 | 3.27 | 0.04 | 1.57 | 0.23 | 0.63 | 0.65 |
| Location × Region | 1.39 | 0.42 | 1.74 | 0.37 | 5.27 | 0.16 | 3.19 | 0.24 |
| Year × Loc. × Region | 0.21 | 0.82 | 1.12 | 0.35 | 0.49 | 0.62 | 1.15 | 0.34 |

^aLog transformation used to meet assumptions of normality and homogeneity of variances

and year indicate differences in along-shore larval settlement between years within this group. Brachyurans did not exhibit any significant spatial patterns in settlement, although settlement was higher in 2010 (Fig. 2g). Carideans also had higher settlement in 2010, but they demonstrated clear spatial structure in settlement, with increasing settlement towards the shore (Fig. 2h); settlement at the outer edge was lower than the interior ($p < 0.01$) and the inner edge ($p < 0.01$).

We observed temporal variation in that overall settlement of invertebrates was higher in 2010 (Table 1), but this was largely due to higher settlement of orthogastropods (Table 2). Brachyurans and carideans also settled in higher numbers in 2010, but pectinids reached their peak settlement in 2009. The spatial structure of settlement did not differ significantly between years for orthogastropods, brachyurans, and carideans, but pectinids showed higher settlement at the interior in 2009 only (Table 3). Opisthobranchs exhibited a nominal trend of cross-shelf differences in settlement in 2009, but not in 2010 (Fig. 2c), and other bivalves showed different along-shore and cross shelf patterns of settlement between years (Table 3).

The overall spatial structure of settlement among locations at 2 m above the sea floor was typically similar to that at 7 m depth (i.e. overall there was no interaction between depth and other variables detected by PERMANOVA, and pairwise comparisons showed similar structure between both depths) (Table 4). However, for all taxa, settlement was lower near the sea floor than at 7 m depth (Table 5). Orthogastropods, non-sessile polychaetes, and other bivalves (non-pectinids) were responsible for almost 70% of the dissimilarity between depths, with orthogastropods and non-sessile polychaetes each contributing approximately 30%. Upon examination of individual taxa in planned comparisons of locations within each sampling depth, only 2 taxa, *Crepidula* spp. and carideans, displayed spatial structure at 7 m depth (Table 6, Fig. 3b,h). For both of these groups, settlement at 7 m was lower at the outer edge than in the interior (*Crepidula* spp., $p = 0.05$; carideans, $p = 0.01$) and the inner edge (*Crepidula* spp., $p < 0.01$; carideans, $p = 0.02$), and statistically similar across locations sampled near the sea floor. Orthogastropods retained the same spatial structure at 7 m and near the sea floor (Fig. 3a). We did not detect

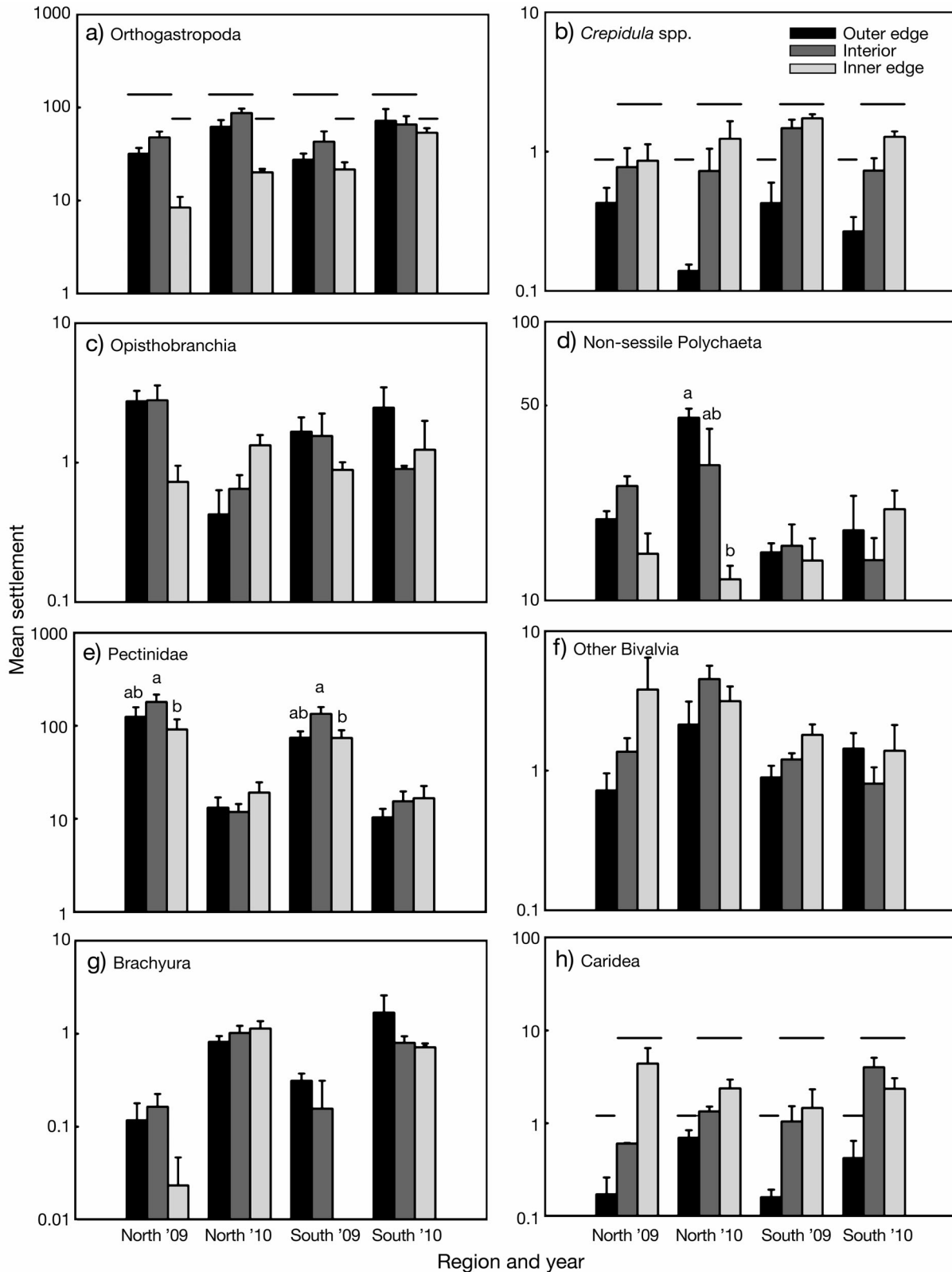


Fig. 2. Spatial and inter-annual patterns of settlement for individual taxa at 7 m depth. Bars depict mean settlement at each sampling site; error bars are standard error; lines indicate significant differences among locations overall; letter groups denote significant differences among locations within regions or years ($\alpha < 0.05$). (See Table 3 for ANOVA results)

Table 4. Results of PERMANOVA comparing settlement at 7 m vs. 2 m depth above the seafloor in 2010. **Bold** values indicate significance ($\alpha \leq 0.05$)

| Source | SS | df | MS | Pseudo- <i>F</i> | p(perm) |
|---------------------------|---------|----|--------|------------------|-----------------|
| Region | 104.72 | 1 | 104.72 | 1.03 | 0.50 |
| Location | 1863.10 | 2 | 931.57 | 7.76 | <0.01 |
| Depth | 5128.30 | 1 | 5128.3 | 36.68 | <0.01 |
| Transect(Region) | 408.12 | 4 | 102.03 | 0.85 | 0.58 |
| Region × Location | 2045.30 | 2 | 1022.6 | 8.52 | <0.01 |
| Region × Depth | 440.71 | 1 | 440.71 | 3.15 | 0.12 |
| Location × Depth | 331.82 | 2 | 165.91 | 1.38 | 0.23 |
| Transect(Region) × Depth | 559.20 | 4 | 139.8 | 1.17 | 0.33 |
| Region × Location × Depth | 405.43 | 2 | 202.72 | 1.69 | 0.14 |
| Residual | 1919.90 | 16 | 119.99 | | |
| Total | 13207 | 35 | | | |

cross-shelf spatial structure at either sampling depth for any other taxa, although an interaction between depth and region was detected in opisthobranchs, non-sessile polychaetes, and other bivalves (Table 6).

Due to high variability in settlement among sites and sampling periods, or relatively consistent settlement over time, only orthogastropods and non-sessile polychaetes were suitable for inclusion in our analysis for exploring the influence of the magnitude of settlement on spatial patterns (Table 7). High and low periods of settlement of orthogastropods were observed in both years (Fig. 4a,b), and during both periods, there were significant effects of location but the specific patterns differed: differences in settlement between the outer and inner edges of the kelp stands were detected during low but not high settlement. During low settlement, non-sessile polychaetes exhibited significant differences between regions and among locations, with lower settlement at the inner edge vs. outer edge ($p = 0.02$) and interior ($p = 0.04$) (Fig. 4c). However, no significant differences

were observed during high settlement periods ($p > 0.30$ for all comparisons), although a trend of higher settlement along the outer edge was noticeable. Overall, for the 2 taxa in which this analysis was possible, there were more pronounced spatial patterns observed during relatively low versus high settlement.

DISCUSSION

We observed a difference in overall settlement of invertebrates among locations within kelp forests and

between 2 consecutive years. Individual taxa, however, exhibited differential patterns of settlement spatially and temporally, and several taxa showed no patterns in settlement whatsoever. Our results stand in contrast to the larval filtering hypothesis as proposed by Bernstein & Jung (1979) and Jackson (1986), as several of the taxa we observed did not exhibit spatial patterns of settlement and all taxa reached the interior as well as the edges of the kelp forests in appreciable numbers. Based on their study of epiphytes on giant kelp, Bernstein & Jung (1979) suggested that species with PLDs of 2 to 4 wk would only be delivered to outer edges, whereas species with PLDs of a few hours would be retained in the interior of kelp forests. We did not detect any relationships between PLD and pattern of settlement for any of the taxa collected in our study. Taxa with the longest PLDs (>3 wk: pectinids, other bivalves, carideans, and brachyurans; Strathmann 1987), showed a mixture of similar settlement spatially as well as cross-shelf patterns, although it had been predicted

Table 5. SIMPER analysis of significant main effects. Mean settlement is shown for each group. Values shown in parentheses are the percentage of dissimilarity for each comparison. Taxa are listed in order of percentage contribution to the largest dissimilarity (7 m vs. sea floor). For percentage contributions to dissimilarity, each column totals to 100%. OE: Outer Edge; Int: Interior; IE: Inner Edge

| Taxa | Mean settlement | | | | | Contribution to dissimilarity (%) | | | |
|------------------------|-----------------|------|------|------|--------|-----------------------------------|-----------------------|----------------------|--------------------------|
| | OE | Int | IE | 7m | Bottom | OE vs. Int (24.33) | Int vs. IE (25.85) | IE vs. OE (28.21) | 7m vs. bottom (30.37) |
| Orthogastropoda | 6.37 | 7.38 | 4.90 | 7.37 | 5.06 | 29.90 | 37.82 | 29.71 | 30.69 |
| Non-sessile Polychaeta | 3.48 | 3.27 | 3.21 | 4.61 | 2.03 | 28.09 | 21.38 | 23.90 | 28.77 |
| Other Bivalvia | 1.01 | 1.03 | 0.78 | 1.39 | 0.49 | 8.08 | 10.25 | 9.70 | 10.38 |
| Caridea | 0.64 | 1.24 | 1.47 | 1.20 | 1.04 | 8.94 | 8.48 | 10.38 | 7.54 |
| Pectinidae | 0.73 | 0.81 | 0.85 | 1.08 | 0.51 | 7.21 | 7.71 | 7.12 | 7.45 |
| Opisthobranchia | 0.56 | 0.62 | 0.91 | 0.91 | 0.48 | 7.01 | 6.83 | 8.12 | 6.60 |
| <i>Crepidula</i> spp. | 0.47 | 0.86 | 0.97 | 0.79 | 0.74 | 5.63 | 4.71 | 6.14 | 4.52 |
| Brachyuria | 0.87 | 0.88 | 0.90 | 1.02 | 0.75 | 5.15 | 2.81 | 4.94 | 4.05 |

Table 6. Results of 4-factor mixed model nested ANOVAs on mean settlement of individual taxa at 7 m and 2 m off the sea floor in 2010 (n = 36 for each taxa). **Bold** values indicate significance at $\alpha \leq 0.05$ (see Table S3 in the supplement at www.int-res.com/articles/suppl/m485p075_supp.pdf for full ANOVA tables)

| Source | Orthogastropoda | | <i>Crepidula</i> spp. ^a | | Opisthobranchia | | Non-sessile Polychaeta ^a | |
|--------------------------|------------------------|-----------------|------------------------------------|-----------------|------------------------|-----------------|-------------------------------------|-----------------|
| | F | p | F | p | F | p | F | p |
| Depth | 38.05 | <0.01 | 1.13 | 0.30 | 15.08 | <0.01 | 82.44 | <0.01 |
| Region | 3.22 | 0.09 | 3.76 | 0.07 | 0.18 | 0.68 | 0.29 | 0.60 |
| Location | 17.92 | <0.01 | 11.97 | <0.01 | 4.08 | 0.04 | 0.07 | 0.94 |
| Transect(Region) | 0.85 | 0.51 | 0.71 | 0.59 | 1.29 | 0.32 | 0.35 | 0.84 |
| Region × Depth | 0.18 | 0.68 | 0.02 | 0.89 | 8.29 | 0.01 | 5.57 | 0.03 |
| Location × Depth | 0.10 | 0.91 | 5.25 | 0.02 | 1.51 | 0.25 | 1.85 | 0.19 |
| Transect(Region) × Depth | 0.53 | 0.71 | 0.98 | 0.45 | 1.49 | 0.25 | 0.65 | 0.63 |
| Location × Region | 15.21 | <0.01 | 1.29 | 0.30 | 8.49 | <0.01 | 8.97 | <0.01 |
| Depth × Loc. × Region | 1.08 | 0.36 | 1.08 | 0.37 | 1.69 | 0.22 | 0.97 | 0.40 |
| Source | Pectindae ^a | | Other Bivalvia ^a | | Brachyura ^a | | Caridea ^a | |
| | F | p | F | p | F | p | F | p |
| Depth | 13.60 | <0.01 | 69.59 | <0.01 | 8.99 | 0.01 | 1.93 | 0.18 |
| Region | 0.44 | 0.52 | 4.63 | 0.05 | 0.37 | 0.55 | 3.73 | 0.07 |
| Location | 0.62 | 0.55 | 1.17 | 0.34 | 0.05 | 0.95 | 10.25 | <0.01 |
| Transect(Region) | 1.29 | 0.32 | 1.38 | 0.28 | 1.05 | 0.41 | 0.69 | 0.61 |
| Region × Depth | 0.39 | 0.54 | 6.04 | 0.03 | 0.35 | 0.56 | 1.31 | 0.27 |
| Location × Depth | 1.14 | 0.34 | 1.73 | 0.21 | 2.00 | 0.17 | 2.62 | 0.10 |
| Transect(Region) × Depth | 0.53 | 0.72 | 2.82 | 0.06 | 1.13 | 0.38 | 0.68 | 0.61 |
| Location × Region | 1.62 | 0.23 | 1.28 | 0.31 | 0.00 | 1.00 | 1.39 | 0.28 |
| Depth × Loc. × Region | 0.27 | 0.77 | 2.35 | 0.13 | 0.88 | 0.43 | 1.01 | 0.39 |

^aLog transformation used to meet assumptions of the model

that species with long PLDs would not be delivered to the kelp forest interior in significant numbers (Bernstein & Jung 1979, Jackson 1986). Similarly, of taxa with PLDs ranging from 1 to 3 wk (*Crepidula* spp., orthogastropods, and non-sessile polychaetes, Strathmann 1987), the gastropods demonstrated cross-shelf patterns of settlement while polychaetes only showed a pattern in one region in one year. Within larger taxonomic groupings, variability in settlement patterns was observed: carideans showed a pattern of settlement but brachyurans did not, and scallops showed a pattern in one year but other bivalves did not. These observations conflict with predictions of spatial settlement in kelp forests based on PLD alone, and indicates that more general characteristics of life history may not be a predictor of patterns of settlement observed in our study.

In support of some version of a larval filtering hypothesis, we did observe reduced settlement of orthogastropods along the inner edge, but settlement between the outer edge and interior was similar. This pattern was partially repeated in non-sessile polychaetes but not consistently between years or regions, and an inverse pattern was observed in

Crepidula spp. and carideans. It is evident that high numbers of settlement-stage larvae are reaching the interior of wide kelp forests despite strongly dampened flow in the interior of these forests (Jackson 1986). The presence of spatial gradients in these taxa indicates that similar processes may be acting on these species and that giant kelp exerts a slight filtering effect in some conditions.

The lack of spatial structure in several taxa, however, and the variability in settlement observed within regions and between years indicate that other mechanisms influencing settlement should be considered. Predators may prefer or avoid habitat edges (Connell & Kingsford 1998, Hovel & Lipcius 2001, 2002), and predation on settlement-stage larvae while in the water column could result in spatial patterns of settlement that reflect differential predator abundance within kelp forests (Gaines & Roughgarden 1987), rather than a passive filtering effect. Spatial patterns of settlement could also result from variation in settlement cues, including changes in understory algae (Birrell et al. 2008, Arkema et al. 2009, Matson et al. 2010) and conspecifics (Scheltema et al. 1981, Toonen & Pawlik 2001, Donahue

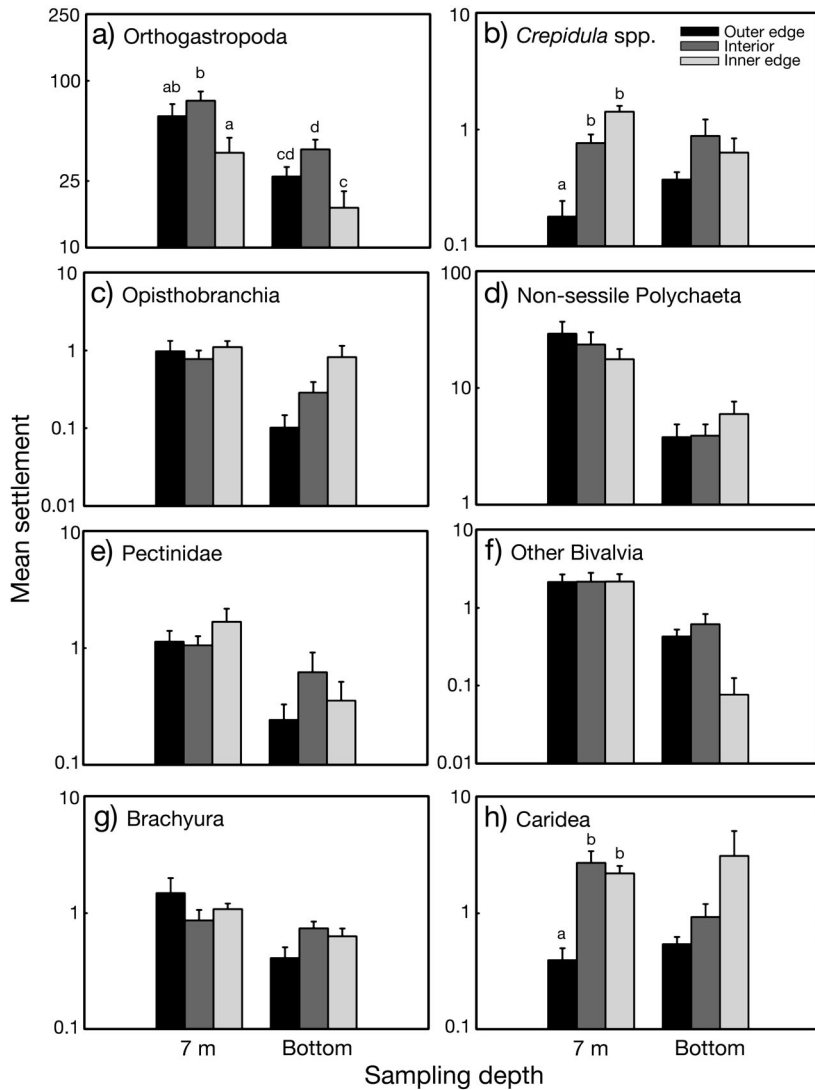


Fig. 3. Spatial patterns of settlement between 7 m depth and 2 m above the sea floor for individual taxa in 2010. Bars depict mean settlement at each sampling site; error bars are standard error; letter groups denote significant differences among locations within each depth ($\alpha < 0.05$). (See Table 6 for ANOVA results)

2006), or to changes in light levels (Olson 1985, McFarland 1986).

The variation in spatial patterns of settlement observed among the 3 gastropod taxa in this study is notable. Settlement of snails reflected a pattern consistent with larval filtering, with the exception that significant numbers of larvae were delivered to the interior, so the effectiveness of giant kelp as a filter may be limited. We now know larvae can behave in response to settlement cues (Kingsford et al. 2002, Matson et al. 2010) and the patterns of settlement observed here may reflect delivery of larvae from offshore, passive transport through kelp forests, and evenly dispersed settlement cues throughout the for-

est. Indeed, most of the snails observed (family Rissoidae) are micrograzers on macroalgae (McLean 2007) and thus may respond to cues from the kelp itself. By contrast, slipper limpets *Crepidula* spp. exhibited an opposite gradient, with decreasing settlement towards the outer edge of giant kelp stands. The adult distribution of this species may provide an explanation: the species sampled is likely to be *Crepidula nivea*, which occurs intertidally (McLean 2007). If the majority of larvae were spawned in the intertidal, settlement-stage larvae could be most abundant inshore of the kelp forest with reduced delivery to the outer edge. In addition, settlement-stage larvae of this species and congeners are attracted to adult females (due to protandrous hermaphroditism; Coe 1953, Collin 2000), so the observed patterns of settlement may reflect the distribution of adult conspecifics. Settlement of opisthobranchs was variable in space and time, which may reflect the variety of habitat types and life histories within this diverse group (Strathmann 1987, Botello & Krug 2006) and the interaction of species-specific behaviors and physical processes. Targeted sampling of individual species of opisthobranchs might be beneficial in resolving some of the variability observed in this group.

Variation in spatial patterns of settlement was also observed within decapods, with different patterns observed between carideans and brachyurans. Carideans were the only group outside of gastropods to show consistent differences in settlement among locations. Most of these shrimp were hippolytids, which have intertidal to subtidal distributions and are abundant on kelps (Kuris et al. 2007). Their patterns of settlement suggest stronger delivery from inshore of kelp forests (if larval filtering is occurring). The stands of kelp along Point Loma are separated from shore by a wide area, so larval delivery via along shore currents is possible. Brachyuran crabs were uncommon in our samples and did not show strong evidence for spatial patterns in settlement. Settlement of decapods can be extremely variable through time (Lough 1976, Eggleston & Arm-

Table 7. Results of 3-way nested ANOVA on mean settlement of relevant taxa for individual sampling dates with 'low' and 'high' settlement. **Bold** values indicate significance ($\alpha \leq 0.05$)

| Taxon Source | Low settlement | | | | | High settlement | | | | |
|-------------------------------|----------------|----|--------|-------|-----------------|-----------------|----|----------|------|-------------|
| | SS | df | MS | F | p | SS | df | MS | F | p |
| Orthogastropoda | | | | | | | | | | |
| 2009^a | | | | | | | | | | |
| Region | 0.17 | 1 | 0.17 | 0.37 | 0.56 | 1.04 | 1 | 1.04 | 1.99 | 0.20 |
| Location | 10.87 | 2 | 5.44 | 11.90 | <0.01 | 6.62 | 2 | 3.31 | 6.36 | 0.02 |
| Transect(Region) | 0.62 | 4 | 0.16 | 0.34 | 0.84 | 1.68 | 4 | 0.42 | 0.81 | 0.56 |
| Loc. × Region | 1.23 | 2 | 0.61 | 1.34 | 0.31 | 2.35 | 2 | 1.17 | 2.26 | 0.17 |
| Residual | 3.66 | 8 | 0.46 | | | 4.16 | 8 | 0.520 | | |
| 2010 | | | | | | | | | | |
| Region | 8.77 | 1 | 8.77 | 0.36 | 0.57 | 25511.28 | 1 | 25511.28 | 4.53 | 0.08 |
| Location | 871.81 | 2 | 435.91 | 17.94 | <0.01 | 84830.39 | 2 | 42415.20 | 7.54 | 0.02 |
| Transect(Region) | 165.61 | 4 | 41.40 | 1.70 | 0.24 | 40613.38 | 4 | 10153.34 | 1.80 | 0.25 |
| Loc. × Region | 98.38 | 2 | 49.19 | 2.03 | 0.19 | 23085.80 | 2 | 11542.90 | 2.05 | 0.21 |
| Residual | 194.39 | 8 | 24.30 | | | 33763.17 | 6 | 5627.20 | | |
| Non-sessile Polychaeta | | | | | | | | | | |
| 2010^a | | | | | | | | | | |
| Region | 1.32 | 1 | 1.32 | 7.83 | 0.02 | 1.97 | 1 | 1.97 | 2.46 | 0.17 |
| Location | 2.79 | 2 | 1.39 | 8.27 | 0.01 | 3.02 | 2 | 1.51 | 1.88 | 0.23 |
| Transect(Region) | 1.01 | 4 | 0.25 | 1.50 | 0.29 | 2.28 | 4 | 0.57 | 0.71 | 0.61 |
| Loc. × Region | 1.06 | 2 | 0.53 | 3.15 | 0.10 | 1.28 | 2 | 0.64 | 0.80 | 0.49 |
| Residual | 1.35 | 8 | 0.17 | | | 4.80 | 6 | 0.80 | | |

^aLog transformation was used to meet assumptions of the model

strong 1995), and focused sampling using species-specific collectors over longer time scales may help to resolve the cause of the discrepancy between these taxa.

Non-sessile polychaetes, the second most abundant group, only settled differentially among locations in the northern region in 2010. The northern and southern regions were separated by approximately 1.5 km, and along-shore flow from the north may have been a stronger source of larvae than cross-shelf flow in 2010. Diversity in life histories (e.g. settlement habitat, gregarious settlement) could be responsible for some of the variability observed. These spatial differences emphasize the potential for variation in settlement processes over a relatively small scale.

As with decapods, the 2 bivalve taxa did not exhibit similar patterns of settlement. Pectinids showed some spatial structure in 2009, with peak settlement in the interior of the forest. Individuals large enough to identify were entirely *Leptopecten latiauratus* (Coan & Valentich-Scott 2007). This abundant scallop settles opportunistically and gregariously on blades of giant kelp (Morton 1994), so patterns of settlement could reflect the density of conspecifics. Other bivalves settled in relatively low numbers and were too small to positively identify to species, but they did show an interaction between year and re-

gion and between year and transect, indicating that settlement along shore was variable between years. As with polychaetes, along-shore currents from the north may have resulted in variation in larval delivery. These differences between taxa and regions highlight the heterogeneous nature of large kelp forests and the potential for ecological processes to differ within them.

Spatial patterns of settlement were consistent at 2 m above the seafloor. There were no taxa that displayed a pattern at depth that was not observed at 7 m, and settlement was lower near the sea floor than at 7 m (upper water column) for all taxa. Orthogastropods showed the same spatial structure at both sampling depths, but for *Crepidula* spp. and carideans, the differences between locations observed at 7 m depth were not present 2 m above the seafloor. Many of the species collected in our study are found in the kelp forest canopy or settle to giant kelp, so many larvae may have already settled at this depth in the water column, explaining the low settlement observed. This would be a form of vertical larval filtering, and additional sampling at multiple depths in the water column would test this hypothesis. We can say that the patterns observed at 7 m were likely due to cross-shelf position rather than overall depth at each site as most spatial patterns of settlement were unchanged with depth.

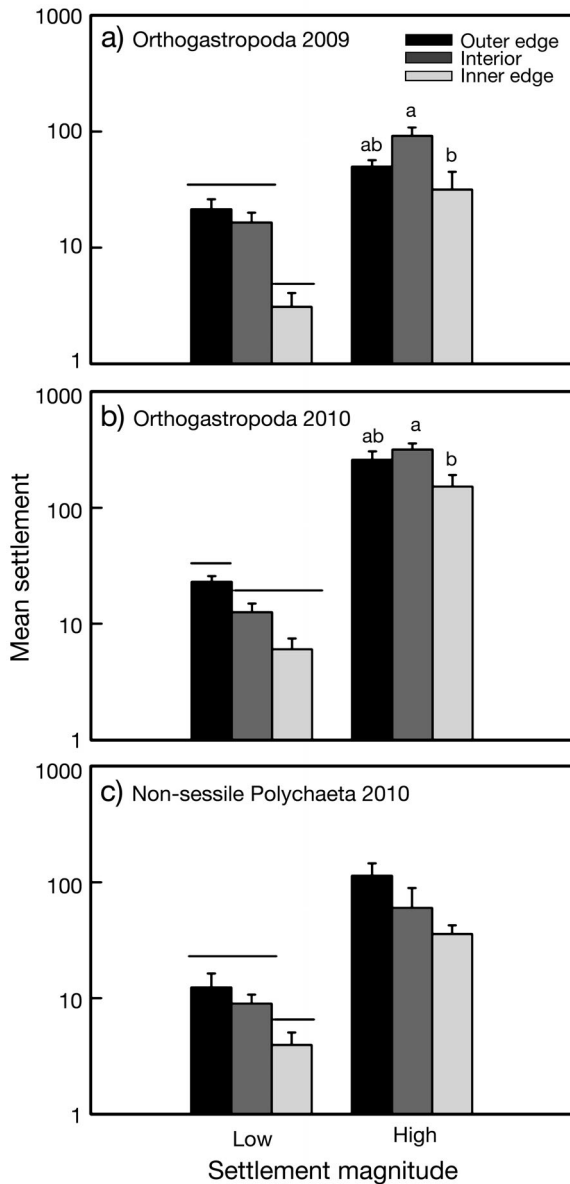


Fig. 4. Influence of the magnitude of settlement on patterns of settlement of invertebrates among locations. Bars depict mean settlement at each sampling site; error bars are standard error; lines indicate significant differences among locations at low settlement; letter groups denote significant differences among locations at high settlement ($\alpha < 0.05$). (See Table 7 for ANOVA results)

Greater spatial structure in settlement was observed during low settlement as opposed to high settlement within years for the 2 taxa that were suitable for analysis. Periods of low settlement were consistent with a more pronounced gradient of decreasing settlement towards shore, whereas this trend was less clear during relatively high settlement. Non-sessile polychaetes showed significant differences among locations during low settlement, but trends were

non-significant during high settlement. For orthogastropods, the magnitude of the low settlement pulse was slightly larger in 2009, and the outer edge and interior received similar settlement. In 2010, however, the interior received lower settlement than the outer edge. During both high settlement pulses in each of these years, high abundances of settlers were observed in the interior. For this taxon, the magnitude of settlement may determine whether the kelp forest becomes 'saturated' with settling larvae. When larvae are at low densities, giant kelp may dampen currents sufficiently to reduce delivery to the interior or inner edge of kelp forests. At higher densities, there is a greater probability that an individual settler will be carried through kelp without encountering suitable habitat or being removed by a predator. In this way, kelp forests could be effectively 'saturated' in settlement-stage larvae when larval densities are high, creating high concentrations of settlers in the interior of kelp forests. This considers larvae as passive particles, but larval behavior and navigation in response to settlement cues should be considered as well. It is also important to note that several taxa that had low abundances overall did not show spatial structure in settlement, reinforcing the taxon-specific nature of these results.

This work is the first to our knowledge to directly observe cross-shelf patterns of settlement of gastropods, non-sessile polychaetes, scallops, and caridean crustaceans through kelp-forested reefs. Although we did not find any evidence for a consistent larval filtering effect observed across invertebrate taxa, this in itself is a significant finding, as previous work has suggested that large kelp forests should have a filtering effect on larvae. Due to our level of taxonomic resolution (versus identification to species), the patterns of settlement observed for some groups may reflect the patterns of settlement for only one or a few species, and it is possible that settlement patterns of less abundant species were obscured. However, even with this caveat the patterns of settlement documented here are ecologically relevant as they reflect the most abundant taxa, and further study could address species-specific patterns within these groups.

There is a lack of basic information on spatial distributions of invertebrate settlement in near shore ecosystems in general and kelp forests in particular, despite a high level of general interest in these areas and the importance of these invertebrates in kelp forest food webs. A paucity of data exists for less conspicuous and non-commercially harvested species, and few studies have examined the settlement of many subtidal invertebrate taxa in detail, with the

exception of work on echinoderms and other groups in which species are easily identified. The lack of spatial structure in settlement for multiple taxa is interesting given the hypothesis that such patterns should exist. We can rule out larval filtering for some taxa, and the patterns we did observe deserve additional study to determine the mechanisms responsible. Given our findings, why did Bernstein & Jung (1979) observe such clear patterns of settlement? One key difference between their study and ours is that they focused on settlement of sessile epiphytic species, whereas our study examined taxa with varied life histories and mobilities. For encrusting species (epiphytes), encounter with giant kelp is a critical stage of settlement, and larvae may begin to settle as soon as kelp is detected. The kelp may not only act as a filter, but as an important cue for these epiphytes. For more mobile species (e.g. orthogastropods), larvae may be influenced by a suite of other factors in addition to the presence of kelp habitat. In addition, giant kelp forests are highly dynamic (Dayton et al. 1992, 1999, Edwards 2004), so differences in kelp forest structure could result in variation in spatial patterns of settlement (e.g. muted patterns in years of low kelp density). There is little evidence that the structure of the kelp forests differed substantially between our study and that of Bernstein & Jung (1979).

Because Point Loma supports expansive, wide stands of giant kelp, we hypothesized that if cross-shelf patterns of invertebrate settlement occurred, they would be detectable in this system. The kelp forests of Point Loma have been extensively studied and have served as a model ecosystem for many studies of kelp forest dynamics and processes (e.g. Dayton et al. 1984, 1992) and its currents have been well defined (Jackson & Winant 1983, Jackson 1986), allowing us to ask detailed ecological questions. The spatial extent of our sampling area is large enough to encompass multiple kelp forests, and indeed there are sand channels and other features that separate stands of kelp spatially. Recent work by Cavanaugh et al. (2013) has demonstrated that population synchrony in giant kelp decreases exponentially with distance between populations, indicating that northern and southern ends of kelp forests function relatively independently. The fact that spatial patterns were observed for some taxa in these wide kelp stands provides impetus for further study in smaller forests, as well as attention to the processes involved. Because this study examines settlement of several invertebrate taxa simultaneously, including groups in which the identification of species is difficult, this study provides

a benchmark from which future studies could explore species-specific patterns. For taxa that settled evenly across kelp forests, it is highly probable that spatial gradients of settlement would also be absent in smaller stands of giant kelp. Based on this knowledge, we can make inferences concerning the relationship between patterns of settlement and the relative importance of post-settlement processes in determining adult distributions of specific invertebrate taxa and subsequent community structure.

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