

Settlement intensification and coastline topography: understanding the role of habitat availability in the pelagic–benthic transition

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ABSTRACT: Among the factors that influence intertidal settlement of rocky shore invertebrates, habitat availability has a direct effect on potential settlement per unit area. Consequently, the amount of suitable habitat available is relevant to explanations of intertidal distributions and abundance. Results concerning the direction of the relationship between the availability of habitat and settlement have, however, been contradictory. Several studies have concluded that settlement rates are positively correlated with free space, whereas others have identified inverse relationships, typified by the settlement intensification hypothesis based on the finding that barnacle settlement has a negative non-linear relationship with habitat availability. Combining a simple method of measuring alongshore rocky habitat availability with intertidal mussel settlement data from 20 sites and 4 sampling occasions, we examined the relationship between these 2 factors at 3 spatial scales (10, 100 and 1000 m) to test for an intensification effect and to identify the scale(s) at which it may take place. Sites were split between bay and open coast areas, allowing additional tests of habitat availability patterns between bays and open coast areas. Significant negative settlement–habitat correlations were identified on 3 of the sampling occasions, and regression analyses confirmed that these relationships were mostly exponential in nature, with as much as 45% of the variation in settlement explained by rocky habitat availability. This finding of settlement intensification highlights the need to understand fully settlement data, particularly in relation to the interpretation of benthic–pelagic links and large-scale patterns of mussel settlement.

KEY WORDS: Settlement rate · Intertidal · Mussel · *Perna perna* · Residence time · Bays · Larval abundance · Benthic–pelagic coupling

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INTRODUCTION

In the marine environment, the influence of habitat availability on abundance and distribution patterns stems not only from post-settlement consequences of space limitation, but also from direct effects on settlement rates (e.g. Connell 1985, Roughgarden et al. 1985, Bertness et al. 1992, Hills & Thomason 1996). Although post-settlement effects are relatively well known, fewer studies have been dedicated to exam-

ining the relationship between habitat availability and settlement rate. Moreover, little consensus exists in the literature, showing the nature of the habitat–settlement relationship to be variable among and within taxa (e.g. Pineda & Caswell 1997, Holbrook et al. 2000, Jeffery 2000, Boström et al. 2010). Consequently, characterising the relationship between habitat availability and settlement rate for particular taxa and spatial scales is necessary, particularly because such study engenders predictive information.

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Broadly, the intensity and importance of the relationship between habitat and the abundance of a species depends on the degree to which the species is specialised for a particular habitat and, to a lesser extent, on characteristics of its lifestyle, such as whether it is sedentary or mobile (Munday 2002, Wood & Pullin 2002). The relatively high degree of habitat specialisation, and limited mobility, of sessile or sedentary benthic marine invertebrates inhabiting hard substrata make aspects of habitat quality and availability particularly pertinent. For these organisms, habitat availability, along with other small-scale environmental features such as micro-hydrodynamics, hold a pivotal place within the hierarchy of factors affecting their populations as they mediate the transition from pelagic to benthic life (Pineda 1994, Cowen & Sponaugle 2009).

Also within the hierarchy of factors affecting settlement are those that influence the supply and retention of larvae (Pineda 2000). These include effects of large or mesoscale topographic features such as bays and headlands, which have been linked to a variety of larval and benthic settlement or recruitment patterns (e.g. Gaines & Bertness 1992, Archambault & Bourget 1999, Helson & Gardner 2004). In South Africa, it has previously been shown that adult mussel abundance is greater in bays than on the open coast (von der Meden et al. 2008). A concern with this work is that log-spiral bays, like the ones in the study area, may generally have less rocky habitat than open coastal areas because of the sandy beaches typically present in the lee of headlands (*sensu* Yasso 1965, Field & Griffiths 1991). As it is possible that the amount of rocky habitat at a location could be related to the wider topographic context of the coastline, we are potentially presented with 2 confounding factors: coastline topography (bay versus open coast) and the amount of rocky habitat typically present in each 'topographic' habitat. Both factors may affect settlement rate.

This asserts the need for caution when inferring patterns of larval supply from settlement data and, conversely, the need for caution when invoking supply-side explanations for settlement patterns. In this latter context, the influence of coastline topography has been repeatedly explained in terms of oceanographic supply-side processes rather than in terms of associations with habitat availability. Commonly, these explanations include retention and larval accumulation in the lee of headlands and bays resulting in higher settlement or recruitment rates in these areas (Lagos et al. 2005, McQuaid & Phillips 2006, Roughan et al. 2005, von der Meden et al. 2008).

To separate topographic effects on settlement from effects of habitat availability, characterisation of the habitat–settlement relationship and the quantification of rocky habitat in relation to coastline topography (bay versus open coast areas) is necessary. Here, we characterise the relationship between habitat availability and settlement rate across multiple bay and open coast sites, enabling an assessment of the role that habitat availability may have in setting up topography-related patterns. For the purposes of this paper, the term 'habitat availability' refers broadly to the amount of rocky habitat relative to completely uninhabitable areas of sand, rather than to detailed measures of biotic cover within rocky areas.

Generally, the marine literature is split between studies showing that settlement (both total settlement on a given feature of habitat not standardised by its area, and settlement rate per unit area of the habitat) increase, usually linearly, with the amount of habitat available (positive relationship), and those that show the opposite. Positive linear relationships between habitat area, or volume in the case of coral, and settlement have been demonstrated for reef fish (Holbrook et al. 2000, Schmitt & Holbrook 2000, but see Shima 2001), intertidal invertebrates (Minchinton & Scheibling 1993, Hills & Thomason 1996) and macroalgae (Reed et al. 2004). In contradiction, negative relationships have likewise been shown for hard-bottom fauna including barnacles (Bertness et al. 1992, Pineda 1994, Osman & Whitlatch 1995, Pineda & Caswell 1997) and for seaweed-associated invertebrates (Boström et al. 2010), whereas other studies have found no significant relationship at all (e.g. Jeffery 2000).

When comparing such studies, 2 aspects of experimental design become important: (1) standardisation of settlement rate by area and (2) the location of settlement sites within the surrounding matrix. The first has obvious importance, but in some cases such as investigations of reef fish, it is not possible to present per-area settlement rates, making comparisons difficult (e.g. Holbrook et al. 2000, Boström et al. 2010). Secondly, settlement sites isolated by uninhabitable matrix, such as coral surrounded by sand, can have as much as double the settlement or recruitment as comparable habitat located on contiguous reef pavement (e.g. Caselle & Warner 1996, Holbrook et al. 2000). This means that studies such as these, showing a positive relationship between habitat availability (i.e. volume of coral) and settlement (where settlement is not reported as a rate per unit of habitable area), may in fact support the idea of intensification caused by isolation of habitat (see Holbrook et al. 2000).

One of the most comprehensive studies dedicated to elucidating the habitat–settlement relationship is that of Pineda & Caswell (1997), in which the settlement intensification hypothesis is put forward and corroborated through mathematical modeling and laboratory experimentation. Essentially, this hypothesis holds that as the area of suitable settlement habitat decreases, the settlement rate per unit area of that habitat will increase (become intensified) given constant larval supply. In their work, Pineda & Caswell (1997) recognize the potentially confounding effects of gregarious settlement behaviour, the influence of residence time and the importance of the spatial scale of habitat relative to that of the larval pool. Although subsequent studies have alluded to, or discussed, the possibility of settlement intensification, few have directly addressed questions surrounding the scales of habitat isolation or the field applicability of this important aspect of larval settlement.

Using an extensive settlement data set for the intertidal mussel *Perna perna* (20 sites, sampled over 4 mo), we examine the relationship between rocky habitat availability and settlement rate on standard units of artificial substrata. We do this under field conditions, considering multiple spatial scales (m to km) and minimizing the effects of gregarious behaviour by using only primary settlement rates recorded on conspecific-free standard artificial units of substratum. With habitat availability quantified across sites, we also test for any topography-related bias in the amount of rocky habitat between bay and open coast sites.

MATERIALS AND METHODS

Larval settlement

Settlement data for *Perna perna* were gathered between March 2005 and March 2006 at 20 sites on the south coast of South Africa, covering ~500 km of coastline (Fig. 1). In terms of coastline topography, 10 sites were located within bays (all of similar size and of log-spiral form) and 10 were located on the open coast (Fig. 1). At each site, 3 standard units of artificial settlement habitat in the form of plastic mesh pot-scourers were placed 0.5 to 1 m apart among mussel beds on low intertidal rocks on spring tides (e.g. Menge 1992, Navarrete et al. 2005). Located within the lower balanoid zone, these rocks lie within the preferred zone of the study species and receive the bulk of the species settlement (Porri et al. 2007). This allowed quantification of mussel settlement rate per collector, with each collector representing a standard settlement area and substratum type, placed within a broader settlement scenario of varying amounts of rocky habitat. An analogous method has been used to investigate barnacle settlement (Pineda 1994). Collectors were deployed on 4 occasions: autumn April 2005, winter July 2005, spring October 2005 and summer January 2006. By necessity, the retrieval of collectors across the 500 km study area took 3 d. In the laboratory, collectors were rinsed and all material collected in a 75 µm sieve was examined using a dissecting microscope. A graduated ocular micrometer was used to measure shell lengths. Although collectors remained on the rocks for 1 mo at a time on each sam-

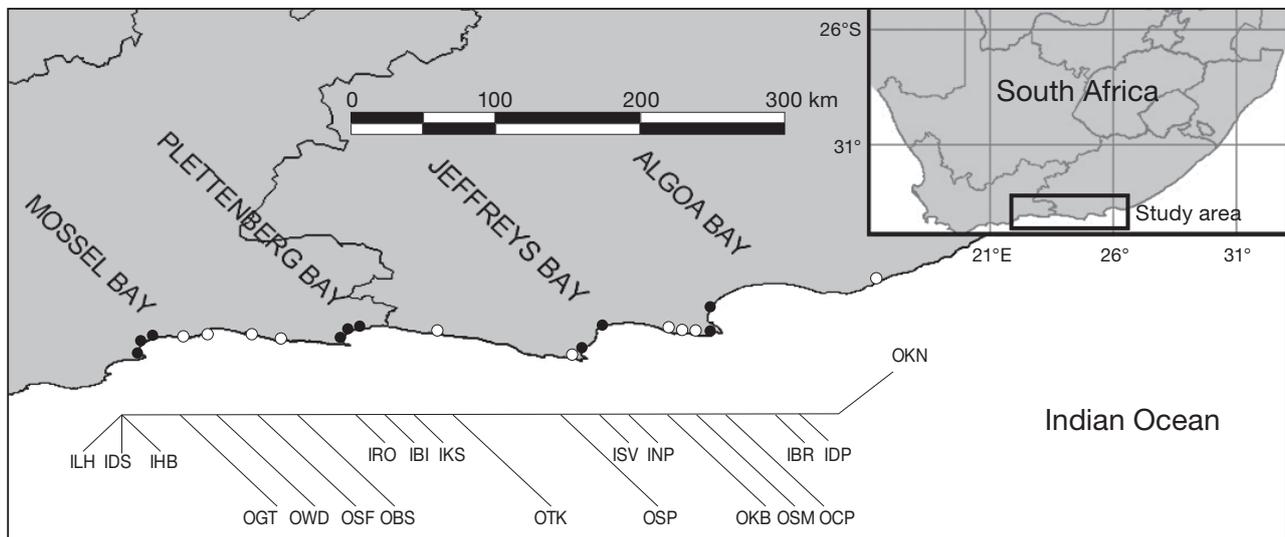


Fig. 1. Study sites along the south coast of South Africa. Bay sites (●) are those with the prefix 'I' and open coast sites (○) are those with the prefix 'O'

pling occasion, for the purposes of this study, only *P. perna* settlers <360 μm were identified and enumerated. This size selectivity, based on size at larval competency and local growth rate, meant that only newly settled 'primary' settlers having arrived within the last 2 d of deployment were considered (Bayne 1964, Bownes 2005). Primary settlement rates were therefore calculated by dividing the number of primary settlers on a collector by 2, giving the settlement rate per day per collector in each case.

Habitat availability estimation

At each site a simple one-off retrospective measure of alongshore rock availability was undertaken during spring tide at 10, 100 and 1000 m scales in November 2010 (Fig. 2). In each case, measurements were centred on the low-shore settlement location and followed the contour of the rock at approximately this tidal height, thereby measuring availability of the most relevant habitat for the study species (*sensu* Porri et al. 2007). Measurements were not made of the width of the mussel zones because these are relatively constant within the region (Reaugh-Flower et al. 2011, C. E. O. von der Meden pers. obs.). For the 10 and 100 m scales, a tape measure was used to quantify the length of habitat made up by rock along 5 and 50 m transects, respectively, on either side of the settlement location. The contour height was continually maintained by staying within the low-shore mussel zone and by continual visual reference to the low water mark. Where uninhabitable substrata (e.g. sand) were encountered, the line of measurement continued directly across to the next available rocky habitat at the same tidal height (see Fig. 1). The same approach was applied at the 1 km scale, but measurements were made using Google Earth[®] images (Eastern Cape, South Africa; 33° 31' S, 27° 04' E to 34° 16' S, 22° 20' E; www.google.com/earth/index.html, accessed 16 October 2010).

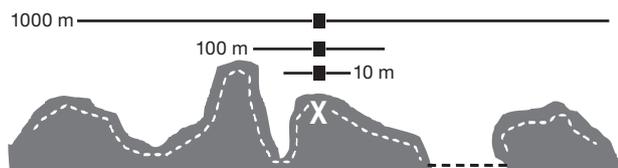


Fig. 2. Hypothetical plan view representation of the alongshore measurement of rocky habitat availability. Settlement location is represented by 'X' with measurements (white dashed line), following the contour of the rock, taken on either side. The black dashed lines show the measurement of straight-line distance across unsuitable habitat. Solid black lines illustrate the successive scales of measurement centred on settlement location

Known ground features were used to verify that the correct low-shore mussel zone was being measured in the remote images. To check the accuracy of these remotely sensed data, the 100 m scale measurements were repeated remotely and ground-truthed against the 100 m scale field data. The percentage of total alongshore distance at each scale made up by rocky habitat (regardless of the biota covering it) relative to non-rock (water or sand) was calculated, providing an estimate or index of rocky habitat availability hereafter referred to as percent rocky habitat. The intention here was simply to obtain an indication of the amount of generally habitable versus completely uninhabitable shore that exists at each study site. Although biotic cover can influence settlement at small scales, filamentous algae, conspecifics and barnacles are all suitable for mussel settlement (e.g. Griffiths 1981, Lively & Raimondi 1987, Lasiak & Barnard 1995, Erlandsson & McQuaid 2004, McQuaid & Lindsay 2005).

Data treatment and statistical analysis

A *t*-test compared the Google Earth and ground-truth measurements made at the 100 m scale to check the validity of remotely measured data. Normality and homogeneity of the variances of the data were examined using Kolmogorov-Smirnov (KS) and Levene tests, respectively. With this established, Spearman's rank correlations were used to preliminarily assess correlations between percentage rock and mean settlement rates for each sampling occasion and spatial scale. To examine the relationship further, linear, exponential and quadratic regression models were fitted to the raw data for each scale. Statistically influential data points (i.e. outliers with high leverage) were checked using Cook's distance procedure and the adjusted R^2 values and ANOVA results were compared, establishing which of the regression models best described the data.

To test for a topography-related bias in habitat availability, the percentage rocky habitat data from the 10 bay sites were compared with that from the 10 open coast sites using separate *t*-tests for each of the 3 spatial scales surveyed.

RESULTS

Ground-truthing and Spearman's rank correlations

The ground-truthed and remotely sensed data from the 100 m scale were normally distributed with

homogeneous variances (KS $d = 0.15$, $p > 0.05$; $d = 0.19$, $p > 0.05$, respectively; Levene's $F_{1,36} = 1.23$, $p > 0.05$). The 100 m scale Google Earth data ($\bar{x} \pm SE = 74.1 \pm 5.9\%$) were not significantly different from the ground-truthed 100 m scale measurements ($\bar{x} \pm SE = 72.8 \pm 5.2\%$; $t = 0.15$, $df = 36$, $p = 0.88$), validating the use of the remotely measured 1000 m habitat availability percentages.

Settlement rates and percent rocky habitat were significantly negatively correlated at all 3 spatial scales in January (1000 m: $r_S = -0.67$, $p < 0.05$; 100 m: $r_S = -0.46$, $p < 0.05$; 10 m: $r_S = -0.41$, $p < 0.05$). Similar correlations were found for the 1000 and 100 m scales in October (1000 m: $r_S = -0.64$; 100 m: $r_S = -0.44$, $p < 0.05$), but not for the 10 m scale ($r_S = -0.24$, $p > 0.05$). In July, significant but weak negative correlations were found for the 1000 and 100 m scale data, but not for the 10 m scale data (1000 m: $r_S = -0.39$, $p < 0.05$; 100 m: $r_S = -0.28$, $p < 0.05$; 10 m: $r_S = -0.18$, $p > 0.05$). Settlement rates and percent rocky habitat were not correlated in April at any spatial scale.

Regression analysis

Regression analyses were used to investigate the Spearman's rank correlations further. Various significant negative relationships were found between set-

tlement rates and percentage rocky habitat in January and October (Table 1a & b), but only weak relationships were seen in July and none in April. In January, exponential models were identified as the best fit for the 1000 and 100 m scales (adj. $R^2 = 0.44$, $p < 0.0001$; adj. $R^2 = 0.27$, $p < 0.0001$, respectively; Table 1a, Fig. 3A,B), whereas a linear model best described the 10 m scale relationship (adj. $R^2 = 0.45$, $p < 0.0001$, Table 1b, Fig. 3C). Significant exponential relationships were identified in October at each of the 3 scales (Table 1b); however, only the 1000 and 100 m scale regressions were comparable to those in January (adj. $R^2 = 0.43$, $p < 0.0001$; adj. $R^2 = 0.20$, $p < 0.0002$, respectively; Table 1b). Although significant, the adjusted R^2 value for the 10 m scale regression was low (adj. $R^2 = 0.10$; Table 1b). All adjusted R^2 values were extremely low in the July regressions (adj. $R^2 \leq 0.10$) and are not presented.

Using the strictest operational guideline for identifying highly influential data points ($D_i > 4/n$; Bollen & Jackman 1990), 2 replicates from site OBS were considered influential on the 100 and 10 m regressions for January (Cook's $D \geq 0.06$; see Fig. 3B,C). In the October data, a single point from site OGT was identified as influential on the 1000 m scale regression (Table 1b). However, with no experimental or biological reasons to remove any of these points, the regressions were not altered.

Table 1. Regression analysis results for linear, exponential and quadratic models fitted to raw settlement data for *Perna perna* from January ($n = 60$) and percentage rocky habitat availability measured at each spatial scale: 1000 m, 100 m and 10 m. The root mean square error (RMSE) is calculated for each fit. Asterisks indicate the best model in each case. Potentially influential data points are accompanied by Cook's distance (D). (a) Data from January. All influential data points were from site OBS. (b) Data from October. All influential points were from site OGT. See Fig. 1 for location of study sites

Scale (m)	Statistic	R^2	Adjusted R^2	$F_{1,58}$ (Quad. $F_{2,57}$)	p	RMSE	Cook's D
a) Data from January							
1000	Linear	0.1745	0.1602	12.259	0.0009	960.86	0.27, 0.21
	Exponential	0.4479	0.4384*	47.057	< 0.0001	1064.61	None
	Quadratic	0.1176	0.1487	6.154	0.0038	967.43	0.28, 0.22
100	Linear	0.0603	0.0441	3.7218	0.0586	1025.16	0.27, 0.21
	Exponential	0.2841	0.2718*	23.018	< 0.0001	1070.65	0.06, 0.06
	Quadratic	0.0676	0.0349	2.066	0.1361	1030.1	0.20, 0.15
10	Linear	0.4558	0.4465*	48.585	< 0.0001	780.12	1.52, 0.98
	Exponential	0.2347	0.2215	17.784	< 0.0001	919.96	None
	Quadratic	0.4635	0.4447	24.626	< 0.0001	781.34	1.28, 0.81
b) Data from October							
1000	Linear	0.1565	0.142	10.764	0.0018	214.09	1.13
	Exponential	0.443	0.4334*	46.138	< 0.0001	233.26	0.20
	Quadratic	0.2632	0.2373	10.179	0.0002	201.85	1.26
100	Linear	0.0609	0.0448	3.7672	0.0571	225.9	0.66
	Exponential	0.2115	0.1979*	15.556	< 0.0002	239.34	0.13
	Quadratic	0.1206	0.0897	3.908	0.0257	220.52	0.63
10	Linear	0.0031	-0.0141	0.182	0.6715	232.75	0.33
	Exponential	0.0848	0.0690*	5.375	0.024	240.77	0.08
	Quadratic	0.0845	0.0524	2.632	0.0807	224.99	0.69

Topographic bias

Rocky habitat availability data from bay and open coast sites were normally distributed with homogeneous variances at the 100 and 1000 m scales. Tests comparing the availability of rocky habitat between bay and open coast sites found no significant differences at either of these scales ($n = 20$, $t_{18} = 0.14$, $p = 0.89$; $n = 20$, $t_{18} = 0.11$, $p = 0.91$, respectively; see Fig. 4). At the 10 m scale, habitat availability data were not normally distributed. However, a Mann-Whitney U -test confirmed that the amount of rocky habitat did not differ between sites in bays and those on the open coast ($U = 31.5$, $n_1 = n_2 = 10$, $p = 0.17$; see Fig. 4).

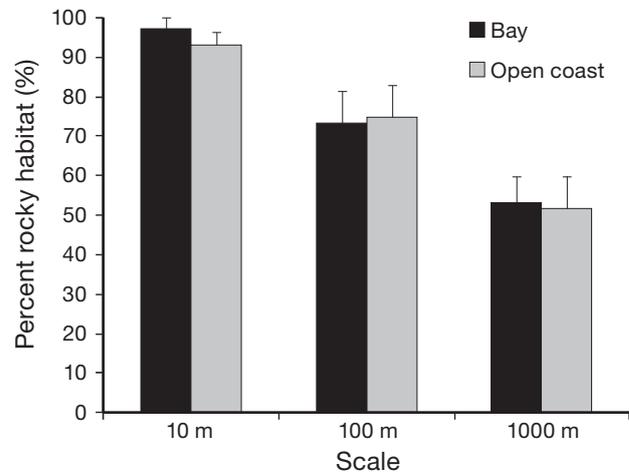


Fig. 4. Percent rocky habitat (mean \pm SE) over 3 spatial scales recorded at bay and open coast sites

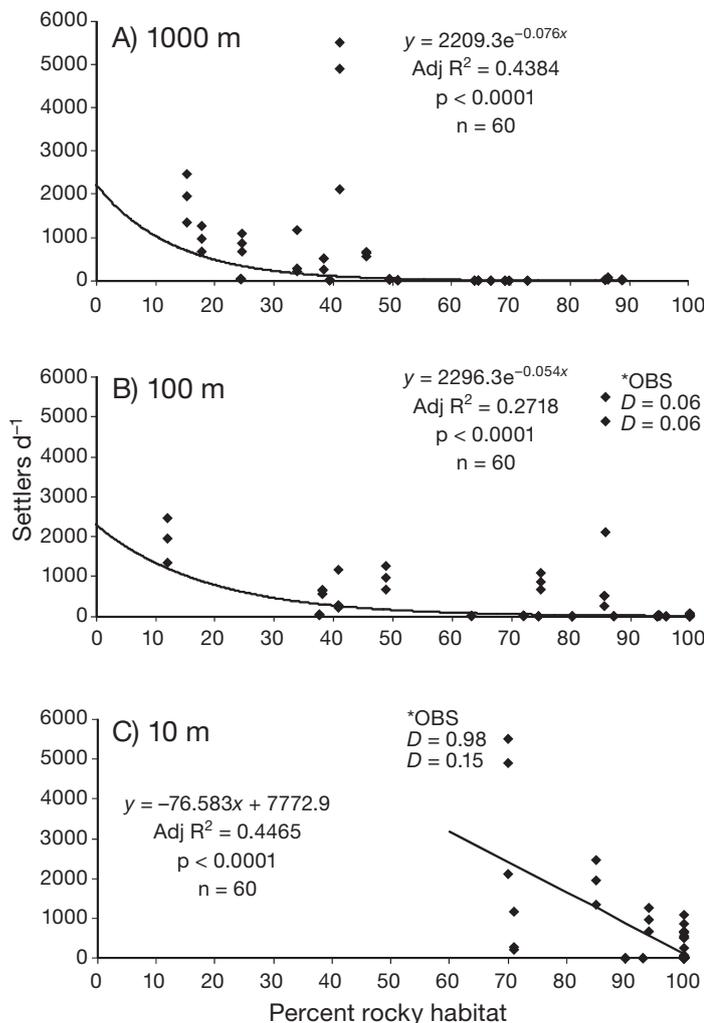


Fig. 3. Primary settlement per day per collector for January, plotted against percentage rocky habitat measured at (A) 1000 m, (B) 100 m and (C) 10 m scales around settlement locations at each of 20 sites. Regression equations, adjusted R^2 values and associated levels of significance are given. *Cook's D and site code for adjacent influential data points

DISCUSSION

As is evident from literature spanning several taxa and, to a lesser extent, a variety of spatial scales, the relationship between the amount of suitable habitat and settlement rate is variable in direction and intensity (Minchinton & Scheibling 1993, Pineda & Caswell 1997, Jeffery 2000). However, by examining settlement rates at 20 sites on 4 independent occasions and investigating 3 spatial scales, we found distinct negative, mostly non-linear, relationships between mussel settlement rates and rocky habitat availability. These relationships were evident only in the summer months (January and October) when settlement rates were relatively high (averaging 10s to 100s of settlers per day), and link settlement rate at a location to habitat variability occurring over tens to hundreds of metres surrounding that location.

Validation and contingencies of settlement intensification

Our regressions show that at the broadest scales (1000 and 100 m), settlement increases exponentially as the percentage of rocky habitat composing a shore decreases. At the 1000 m scale, 43 to 44 % of the variation in settlement was explained by rocky habitat availability. This decreased to between 20 and 27 % at the 100 m scale, and the nature of the settlement-habitat relationship changed substantially at the smallest scale (10 m). At this small scale, the relationship was described either by a linear fit, as seen in January, or by a weak exponential fit, as was seen in October.

Most pertinently, the negative non-linear nature of the settlement–habitat relationships at the 1000 and 100 m scales corroborates the settlement intensification hypothesis and model predictions of Pineda & Caswell (1997), and agrees well with data plots from several other studies, albeit from work at smaller (centimetre to metre) scales (e.g. Bertness et al. 1992, Osman & Whitlatch 1995). However, departures from this type of relationship are not precluded by previous findings or Pineda & Caswell's (1997) model. In fact, departures such as were seen in the low settlement months (April and July, when settlement averaged <5 settlers d^{-1}) and in the weaker or linear fits identified at the 10 m scale in the high settlement months seem to be indicative of some of the very mechanistic contingencies put forward in these previous studies.

(1) The lack of any strong settlement–habitat relationships in April and July presumably reflects the fact that intensification is unlikely when larval numbers are small relative to the area(s) of suitable habitat available (Pineda & Caswell 1997). (2) Changes in the settlement–habitat relationship as the scale of habitat measurements decreased (to the 10 m scale) may be linked to the scale dependency of larval–habitat interactions (*sensu* Pineda & Caswell 1997). If the spatial scale of the larval pool were small relative to the size of the habitat patch, settlement should (in the absence of other factors) occur in proportion to the amount of habitat. Alternatively, if the larval pool was larger in extent than the individual patches of habitat, then intensification of settlement on the isolated patches would be likely, with greater habitat isolation meaning stronger intensification (see Pineda & Caswell 1997). This likely explains why the 10 m scale, which incorporated little habitat isolation (usually $>70\%$ of each shore at this scale was composed of rocky habitat), produced linear or weak non-linear regression relationships (Fig. 3C, Table 1a,b).

It is also possible that our broad-scale approach and definition of habitat availability as generally suitable rocky habitat is not appropriate at the 10 m scale, where differences in biotic cover and density would perhaps be more pertinent drivers of settlement patterns and any intensification effect (e.g. Dobretsov & Wahl 2001). That previous work has identified intensification at centimetre to metre scales does suggest that a fine-scale approach, taking into account cover or density of other biota, would be useful (e.g. Bertness et al. 1992). It must be noted, however, that cover of biota other than mussels was recorded at the 10 m scale at only 4 out of the 20 sites in the present study. At these sites, the percentage length

of rock covered by algae or barnacles in our 10 m transects was usually small, being 4% at IDS, 7% at ILH and 5% at OCP, but 62% at OSP.

Although the nature of the settlement–habitat relationship is itself variable, Fig. 3A,B exemplifies the potential for site-level variability in the relationship by showing that sites with low habitat availability can have low settlement rates and, to a lesser degree, the opposite (sites with high habitat availability and high settlement rates). One possible explanation for this sort of variability in our data may be localised seasonal or episodic (storm-related) sand inundation and removal (McQuaid & Dower 1990, Pineda 1994). Periods of sand inundation could have increased intensification effects by decreasing available rocky habitat, whereas sand removal would have had the opposite effect. Such fluctuations are unlikely to have been spatially consistent but could have affected specific sites, making our one-off sampling of habitat availability somewhat of a limitation. Given the temporal and spatial unpredictability of sand movements, only high-temporal-resolution simultaneous measurement of settlement and habitat availability would allow this to be tested. Similarly, other methodological limitations that could have introduced variable settlement rates include the brief (essentially 2 d) periods of settlement survey and the slightly extended sample retrieval time (3 d). However, both these elements were unavoidable and it is unlikely, given the spatial and temporal replication used, that they affected the results strongly.

Topographic influence

Although our results highlight the potential for strong relationships between settlement and habitat availability, the absence of any topography-related (bay versus open coast) pattern in our habitat availability data eliminates habitat availability as a confounding factor in comparisons of settlement and adult abundance between the 2 topographic categories.

This lack of bias suggests that no direct influence of intensification is responsible for the topography-related patterns of adult abundance and settlement previously observed at the study sites (von der Meden et al. 2008, C. E. O. von der Meden, F. Porri, C. D. McQuaid unpubl. data), and implies that the patterns are indeed supply-side driven. However, extended residence times, such as may be common in bays (Largier 2004, Gawarkiewicz et al. 2007), which allow larval searching behaviour and re-

sampling of benthic substrata, should increase the probability of intensified settlement (Pineda & Caswell 1997).

This last contingency may mean that it is possible for coastline topography, through its effect on residence time, to influence indirectly the settlement–habitat relationship because there would be a greater likelihood of settlement intensification at sites in bays than on the open coast, even when habitat availability is comparable between sites. This indirect relationship between bays and settlement intensification may, at least partially, inform explanations of topography-related settlement patterns.

Relevance to the pelagic–benthic transition

Including settlement intensification as one of several processes mediating the pelagic–benthic transition must have implications for explanations of settlement patterns, the inference of larval supply from settlement data and, in particular, the inconsistency of correlations between nearshore larval abundance and settlement rates (e.g. Bertness et al. 1992, Gaines et al. 1985, Pineda et al. 2002, Porri et al. 2006, Dudas et al. 2009) by providing a mechanism by which sites having similar nearshore larval abundances can nonetheless have different settlement rates.

While recognising that the present study is ultimately a correlative one, requiring appropriate caution in interpreting causation (Hills et al. 1999, Shima 2001), our results suggest that knowledge of habitat availability is important, especially in situations where habitat is severely limited or isolated. Moreover, using a simple index of habitat availability, as in the present study, means that this knowledge is practicable to obtain, allowing its inclusion in settlement studies. As they are relevant under field conditions, and are possible co-variants with other physical/environmental factors (e.g. Caselle & Warner 1996), habitat availability and settlement intensification need to be considered as ecologically relevant parts of the benthic–pelagic cycle and of benthic–pelagic coupling.

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