

# Temporal scales of variation in settlement and recruitment of the mussel *Perna perna* (Linnaeus, 1758)

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## 1. Abstract

Population dynamics of many intertidal organisms are strongly affected by the abundance and distribution of larvae arriving on the shore. In particular, not only absolute numbers of settlers but also the degree of synchronisation of settlement can have a strong influence on whether density-dependent or density-independent processes shape adult shape populations. Temporal variation in rates of settlement and recruitment of the mussel *Perna perna* on the south coast of South Africa was investigated using a nested spatial design at different temporal scales. Variability in settlement at spring tides was examined at two temporal scales: lunar (to investigate the effect of state of the moon on settlement) and tidal (to investigate the influence of state of the tide on mussel settlement). Recruitment over neap tides was examined at one temporal scale, fortnight (to investigate the effect of date on mussel recruitment).

Strong temporal variation was evident for both settlement and recruitment, but not at all time scales. Distinct peaks of settler/recruit abundance were observed during the lunar and neap tide studies. Recruitment intensity differed over the course of the year, and pulsing of recruitment was generally synchronised among locations. However, the strength of pulsing differed dramatically among locations, giving a significant interaction between fortnight and location. The finest temporal scale, investigated in the tidal study, did not reveal a significant effect of the state of the tide on settlement. The state of the moon (new or full) was not significant as a main factor ( $p = 0.052$ ), although generally more settlers arrived on the shore during new moon. Phase of the moon appeared to have an effect on settler abundances, but only when and where densities were high.

## 1. Introduction

Sedentary intertidal organisms with a pelagic larval stage are generally considered to have open populations, as larvae normally have little chance of recruiting into the parent population ([Roughgarden et al., 1985](#)). Larvae return to the shore through settlement, which is one of the main processes regulating the dynamics and structure of benthic populations ([Roughgarden et al., 1988](#); reviewed by [Underwood and Fairweather, 1989](#) and [Balch and Scheibling, 2000](#)).

In some cases, the literature fails to distinguish settlement from recruitment, ignoring post-settlement mortality, which is often very important (Keough and Downes, 1982, Connell, 1985 and Minchinton and Scheibling, 1993). Settlement is the permanent, reversible or irreversible contact that planktonic larvae establish with the substratum (Bayne, 1964, Keough and Downes, 1982 and Lasiak and Barnard, 1995). As this contact is made, the larvae may or may not go through a phase of metamorphosis (Seed and Suchanek, 1992). Poulin and co-workers (2002) consider settlement to be the transition from the planktonic larval stage to life in the benthos.

Recruitment is less easy to define than the simple arrival of new individuals on the shore, but is essentially the number of individuals that have survived for a certain period after settlement, during which time post-settlement mortality may have occurred (Bayne, 1964, Keough and Downes, 1982 and Connell, 1985). Pineda (2000) defines recruitment rate as the rate at which juveniles join the population.

Underwood and Denley (1984) found that, with low rates of settlement, settlement itself was very important in determining the variability and composition of barnacle populations. Connell (1985) subsequently confirmed this and also observed that with high settlement rates, post-settlement processes had a strong influence on adult populations. Thus, with low intensity settlement, density-dependent processes are relatively unimportant and adult/recruit densities tend to be correlated, while density dependence tends to lead to an uncoupling of this correlation when settlement rates are high.

Many factors, both physical and biological, can influence rates of settlement in marine systems (Delafontaine and Flemming, 1989 and Pineda, 2000). Among the most important of these are factors affecting larval supply, such as the effects of hydrodynamics (Abelson and Denny, 1997 and Archambault and Bourget, 1999) and larval behaviour (Scheltema, 1974, Bourget, 1988 and Tankersley et al., 2002). Once larvae are competent to settle, the presence of suitable substrata can be indicated by either biotic or abiotic cues (Raimondi, 1988), for example surface chemical characteristics, biofilm presence, orientation of the substratum, sunlight, texture and the presence of conspecifics, especially if the species shows gregariousness (Stamps and Krishnan, 1990, Roberts et al., 1991 and Harder et al., 2002). These cues and the biological and physical factors that influence settlement operate at different spatial and temporal scales (Gaines and Bertness, 1992 and Bertness et al., 1996) and the high variability frequently observed in settlement rates can be explained by variation in this wide range of factors (Balch and Scheibling, 2000 and Jeffery and Underwood, 2000).

Mussel populations on the south coast of South Africa normally show significant correlations between adults and recruits (McQuaid et al., 2000 and Lawrie and McQuaid, 2001), although the relationship is stronger for larger recruits (Erlandsson and McQuaid, 2004), implying that these populations are recruitment limited and that rates of settlement are likely to be important in determining population densities.

In this study, we investigated temporal scales of variation in settlement and recruitment of the intertidal mussel *Perna perna*, on the south coast of South Africa, measuring settlement and recruitment at several temporal scales with a sampling design that involved collections at different states of the moon and tide.

The influence of phase of the moon on the arrival of settlers was examined by testing for differences in settlement rates over new and full moon spring tides (lunar study). The influence on settlement of day over spring tide was also tested to examine differences in settlement on days immediately before, during and after spring tide (tidal study). Finally, temporal variation in recruitment over neap tides was explored by measuring recruit abundances over neap tides (neap tide study).

## **2. Materials and methods**

Two intertidal sites 3 km apart, Kenton (KE) and High Rocks (HR) were sampled on the south coast of South Africa (33°41'S, 26°40'E). Each site had three locations, 300 m apart, all at approximately the same height on the low shore. Locations were at the edge of wave-cut platforms of Aeolian dune rock. The six locations all experience similar exposure to wave action, mostly receiving the influence of waves that have dissipated much of their energy on offshore reefs. Intertidal sand movement in the study area is seasonal and quite substantial towards the top of the shore, but none of the locations was inundated by sand during the study.

At these sites mussel distribution is patchy, but all locations had similar, relatively high cover (approximately 80%) of mussels interspersed with small patches of the foliose red alga *Gelidium pristoides*.

Settlement was investigated from March 2000 to June 2001 using kitchen scouring pads as settler-collectors. Pads were made of woven plastic, circular, about 10–11 cm in diameter and 2 cm thick. Prior to use on the shore, new pads were left in seawater for 1 or 2 weeks, to develop a natural biofilm and leach any surface chemicals.

Five pads were secured at each location, about 20 cm apart, using plastic cable ties and screws attached to the rocks. Sampling took place fortnightly, throughout the study: around full moon and new moon spring tides (lunar study). At each spring tide, pads were collected and replaced at 2-day intervals: 2 days before spring tide, on spring tide (at the lowest predicted tide) and 2 days after spring tide (tidal study). In addition, pads were left on the shore over the neap tide period, between spring tides. The pads considered for the neap tide study were collected on the first day of a spring tide cycle, after being on the shore for the duration of the previous neap tide period (i.e. 7–9 days).

Since the position of the screws securing the pads changed, due to the occasional loss of screws and pads attached to them, pads also needed to be relocated from time to time.

After collection, pads were returned to the laboratory. The samples were usually processed immediately after collection, but on some occasions, pads were frozen before analysis. Pads were thoroughly rinsed in 75- $\mu$ m filtered

water. The contents were collected in a Petri dish and examined under a dissecting microscope. Settlers of *P. perna* were identified, counted and measured to the nearest 0.001 mm, using an eyepiece graticule.

## 2.1. Statistical analysis

A single analysis considering all different scales simultaneously would have led to an unbalanced design, therefore, separate analyses were required for each temporal study, i.e. the lunar, tidal and neap tide studies, as described below. Since pads were occasionally lost, especially during storms, data sets were balanced using one of two options. If up to two out of the five pads were lost, the mean from the remaining pads was used for the missing values (this occurred in 2–5% of sampling events). Dates when three or more pads were lost at one or more locations were eliminated from the analysis.

The data were analysed using nested ANOVA to examine scales of variation due to both temporal and spatial factors. The results on spatial variability and its effect on settlement are presented in detail elsewhere (Porri et al., in press). All independent variables and the possible interactions among factors were considered to assign variability. The spatial factor site was treated as random; location was also treated as random, nested within site (Zar, 1996). Normality was examined using the Kolmogorov–Smirnov test and homogeneity of variances determined using Cochran's test (Winer, 1971, Zar, 1996 and Underwood, 1997). In all analyses, homogeneity was attained after logarithmic transformation ( $p > 0.05$ ).

Different subsets of these data were used in each of the following analyses.

## 2.2. Lunar study

This study analysed the effects of the phase of the moon (full or new moon) on the abundance of *P. perna* settlers. Analysis was based on a reduced data set of 12 dates (due to the need to balance the analysis for missing data), using only pads collected at spring tide (i.e. lowest predicted tide). From the 12 dates, the analysis was run on a data set that was further reduced to a total of 6 dates (months) for each moon, to avoid the problem of interdependence of moon and date. Six dates were randomly picked for each state of the moon. A nested ANOVA was performed with factors site and location (nested in site) crossed by moon (2 levels) and month (6 levels). The factor moon was treated as fixed; month was nested within moon and treated as random.

*F*-ratios were constructed using post-hoc pooling (Winer, 1971 and Underwood, 1997).

## 2.3. Tidal study

This examined the effect of date around spring tide, particularly the possibility that settlement differs immediately before, during and after spring tide. This study used data from pads collected 2 days before spring tide, 2 days after

spring tide and at spring tide. We refer to these days as “tides”. In this way, settlement was followed over 10 spring tidal cycles. However, to avoid the problem of interdependence of tide and date, the data set was reduced to a total of 5 dates for each tide. Five dates (months) were randomly picked for each tide (before, after and at spring tide). A nested ANOVA was performed with the factors site and location (nested in site) crossed by the factors month (5 levels) and tide (3 levels). The factor tide was treated as fixed; month was nested within tide and treated as random.

As for the lunar study, *F*-ratios were constructed using post-hoc pooling (Winer, 1971 and Underwood, 1997).

## **2.4. Neap tide recruitment study**

This examined the abundances of larvae that accumulated on pads between two consecutive spring tide cycles, for a total of 26 sampling events. The neap tide recruitment study thus examined recruitment rather than settlement, since pads were left on the shore from the last day of a spring tide cycle to the first day of the following one (7–9 days). Data were averaged to 1 day.

Nested ANOVA was used to examine scales of variation due to neap tide. The spatial factor site was treated as random, likewise location, nested within site (Zar, 1996). The temporal factor fortnight was treated as random.

## **3. Results**

### **3.1. Size at settlement**

The sizes of *P. perna* settlers collected on pads during the settlement studies (i.e. pads on the shore for 2 days) were quite variable. Occasionally, individuals of up to 2.5 mm shell length or greater were found (23% of collected settlers were larger than 1 mm), but the most common sizes ranged between 200 and 400  $\mu\text{m}$  (almost 60% of all settlers). The 200–400  $\mu\text{m}$  size class was used for the analysis of abundance of settlers at different temporal scales, because animals falling in this range were considered to be primary settlers, arriving on the shore for the first time and were morphologically indistinguishable from larvae collected in the water column (personal observation). For the neap tide recruitment study, individuals from all size classes were taken into account, because this analysis considered recruit rather than settler abundance.

### **3.2. Lunar study**

The data suggest that settlers were more abundant at both sites during new moon than full moon, although there were clear differences in abundances among locations (Fig. 1). However, the analysis of variance did not show a clear effect of moon as a main source of variability for the larvae coming from nearshore waters onto the rocks, although the *p*-value was very close to significance ( $p = 0.052$ ; Table 1). The non-significant effect of moon as a main factor could have been masked by the very low numbers of settlers collected on many occasions. Although the pattern was

less clear for two of the six locations (KEA and HRF), phase of the moon generally appeared to influence larval abundances on those occasions and at those locations where large numbers were collected (Fig. 1).

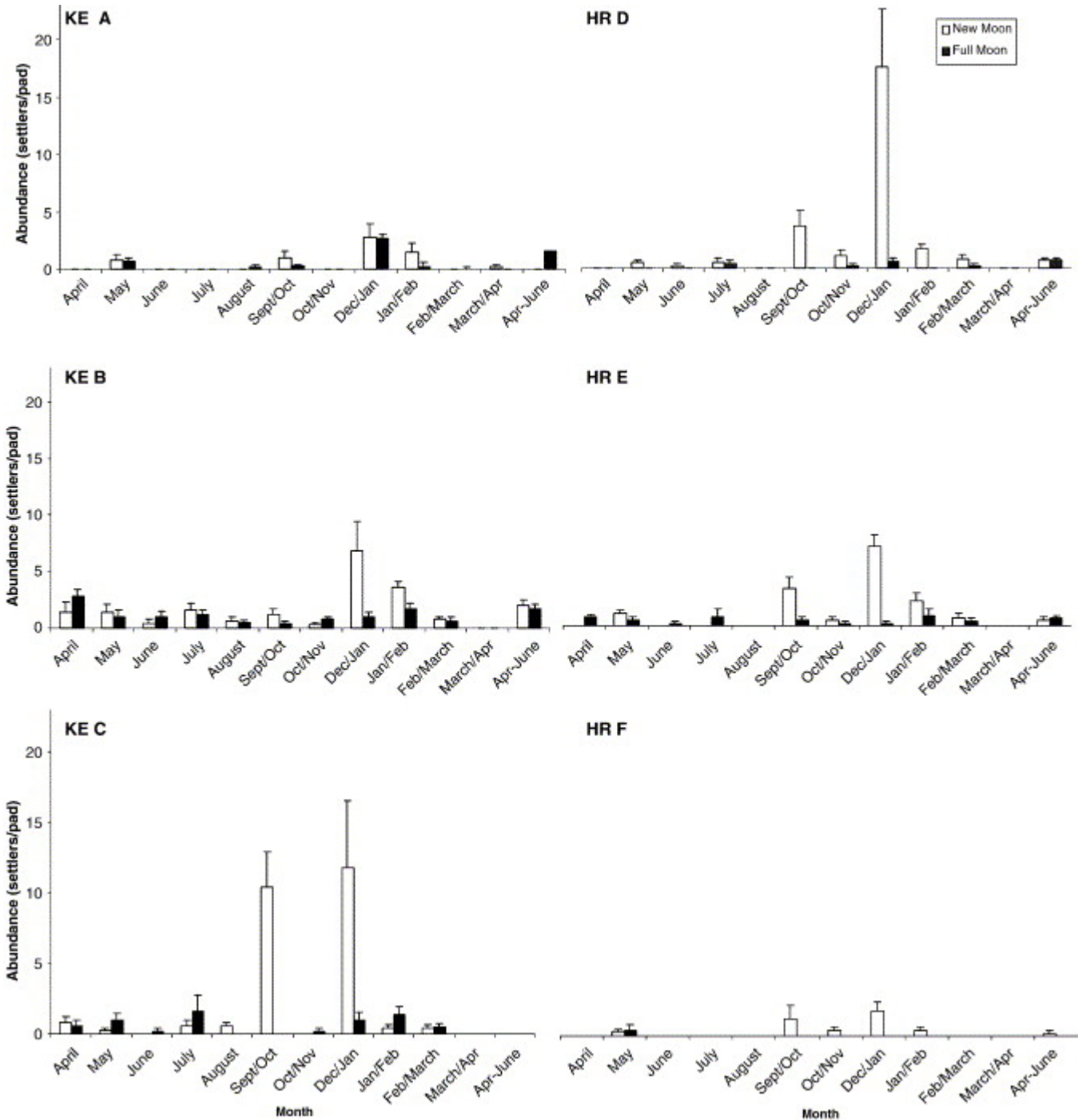


Fig. 1. Settlement of *Perna perna* at KE (locations A, B, C) and HR (locations D, E, F) at different lunar phases. Histograms indicate mean values and error bars show standard errors (S.E.).

Table 1.

ANOVA for lunar (a), tidal (b), and neap tide (c) studies

	<b>Effect</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>p</b>
<i>a) Lunar study</i>					
Moon	Fixed	1	29.77	4.84	0.052
Site	Random	1	0.73	0.32	0.60
Location (Site)	Random	4	2.27	3.49	****
Month (Moon)	Random	10	6.14	9.42	****
Month (Moon) × Location (Site)	Random	55	0.65	2.78	****
Error		288	0.23		
<i>b) Tidal study</i>					
Tide	Fixed	2	5.66	0.62	0.55
Site	Random	1	7.20	2.41	0.19
Location (Site)	Random	4	2.98	5.81	**
Month (Tide)	Random	12	9.10	17.74	****
Month (Tide) × Location (Site)	Random	70	0.51	3.34	****
Error		360	0.15		
<i>c) Neap tide recruitment study</i>					
Fortnight	Random	25	17.5639	18.02598	****
Site	Random	1	18.2126	0.64213	0.46
Location (Site)	Random	4	28.3627	13.83646	****
Fortnight × Site	Random	25	0.9744	0.47533	0.98
Fortnight × Location	Random	100	2.0499	8.26745	****
Error		624	0.247943		

*df* = degrees of freedom; MS = mean square; *F* = *F*-ratio; *p* = probability value; \*\*  $p < 0.001$ ; \*\*\*\*  $p < 0.00001$ .

### 3.3. Tidal study

The raw data showed no clear patterns, with no obvious influence of state of the tide on settler abundance (Fig. 2). This was confirmed by ANOVA, with no significant effect of state of the tide as a main effect (Table 1). The only significant interaction involved those two variables that were significant as main effects: month and location ( $p < 0.00001$ ).

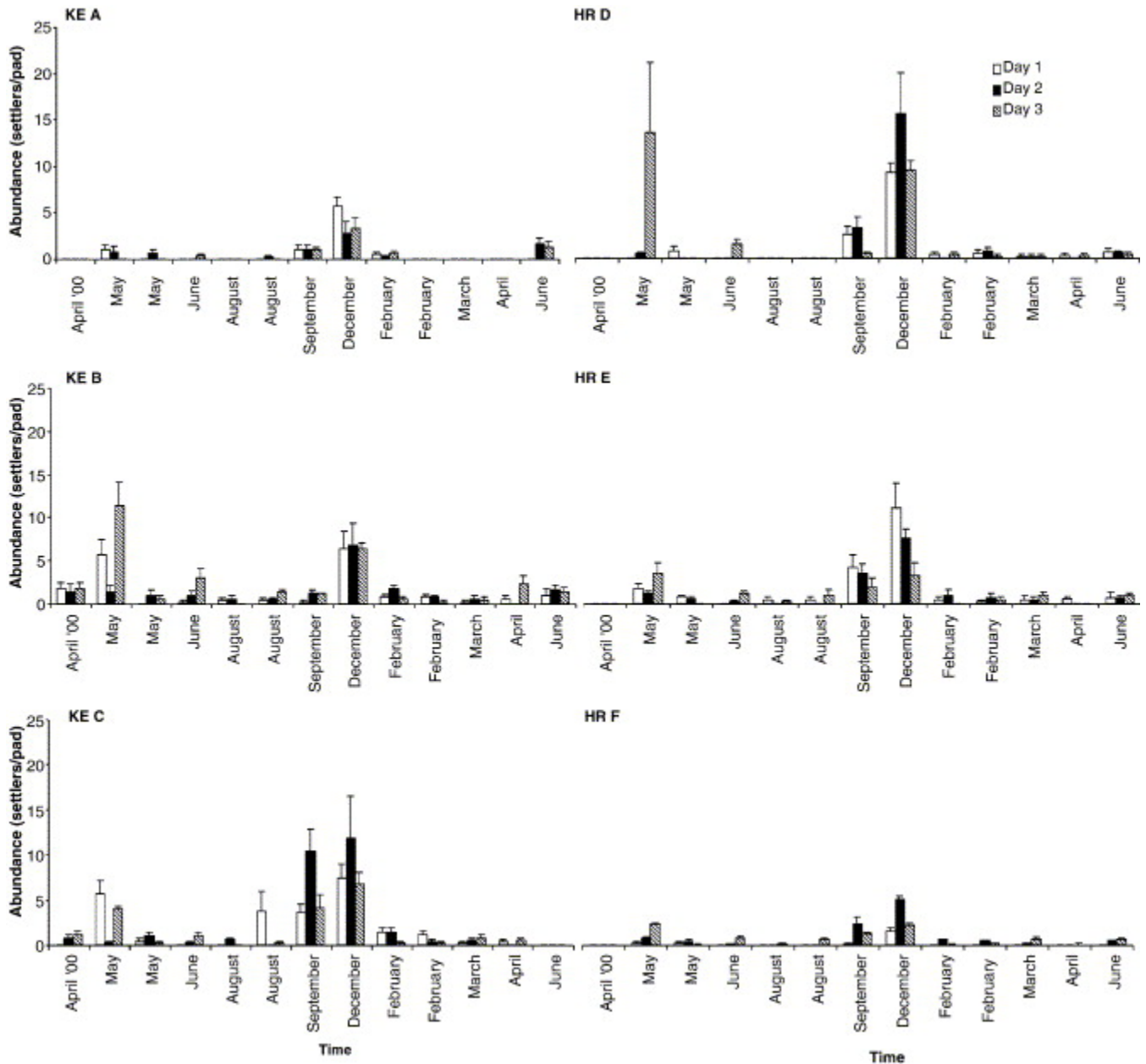


Fig. 2. Settlement of *Perna perna* at KE (locations A, B, C) and HR (locations D, E, F) on consecutive days over spring tide. Histograms indicate mean values for locations and error bars show standard errors (S.E.). Days 1, 2 and 3 of each tide represent 2 days before full spring tide, spring tide and 2 days after spring tide, respectively.



### 3.4. Neap tide recruitment study

Recruits were scarce, even when allowed to accumulate over 7–9 days. Similar patterns were observed at both sites, with main peaks on the 1st of May 2000 and 23rd of December 2000, and generally fewer recruits at HR than at KE (Fig. 3). Variability in recruit numbers was significantly affected by the interaction between fortnight and location ( $p < 0.00001$ ; Table 1).

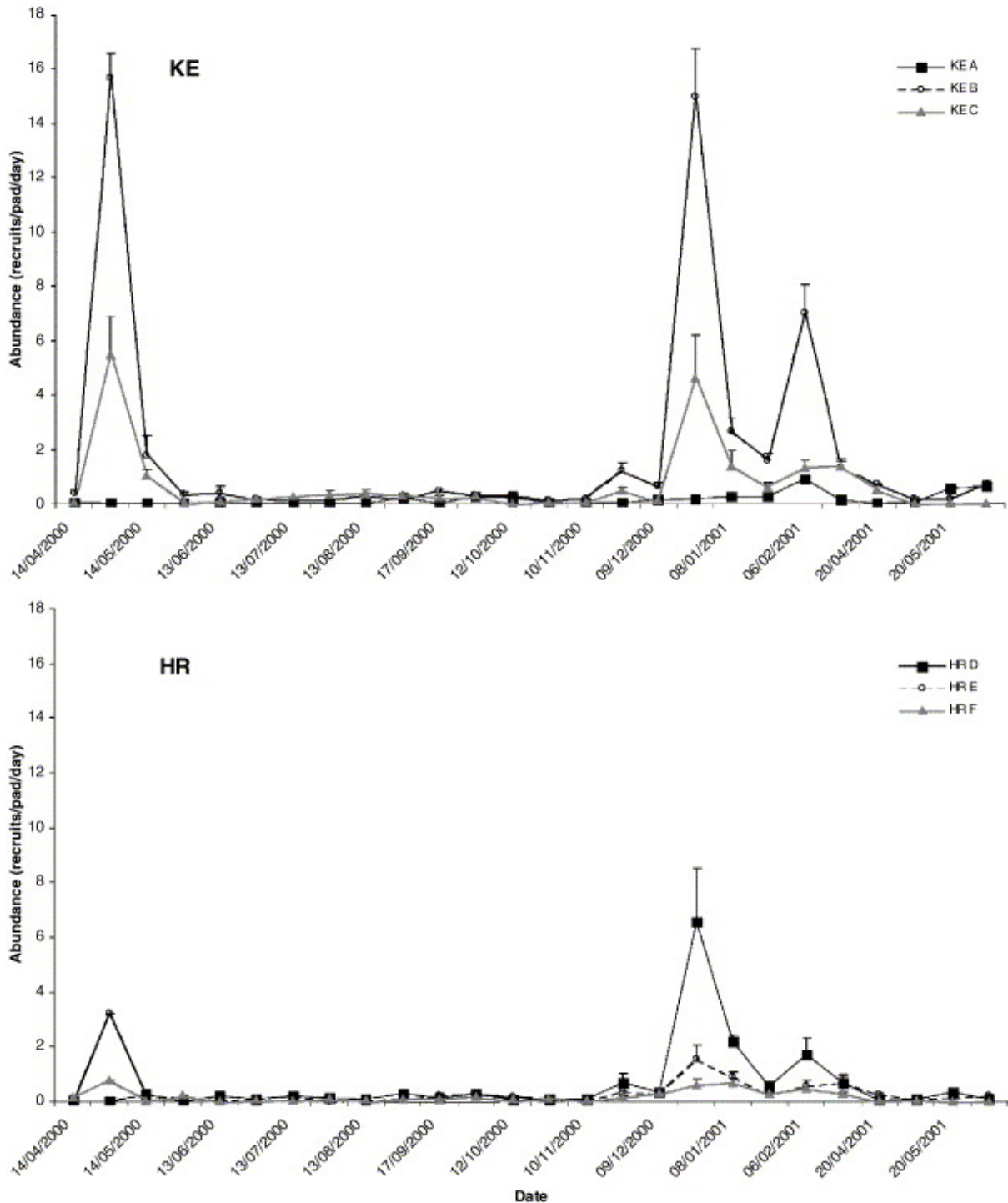


Fig. 3. Recruitment of *Perna perna* at KE (locations A, B, C) and HR (locations D, E, F) over neap tide periods. Points indicate mean values and error bars show standard errors (S.E.).

Taking the 1st of May and the 23rd of December as examples, we can see that recruit numbers differed considerably between different locations ([Fig. 3](#)), but peaks of abundance appeared at almost all locations on those dates. The significant interaction here seems to be due to the magnitude of temporal effects, rather than to actual differences in timing between locations. Thus, recruitment peaked simultaneously at almost all locations, but the strengths of the peaks differed.

## 4. Discussion

Most studies of settlement have used morphometrics to define bivalve settlers. Such categorisations can be based on measurements of laboratory-reared larvae ([Siddall, 1980](#)), descriptions of larval morphology ([Garland and Zimmer, 2002](#)), or measurements of animals found on artificial substrata ([Lasiak and Barnard, 1995](#)). Here we consider settlement to be the first arrival of larvae on the shore, although pads were collected at 48-h intervals, exposing them to four semi-diurnal tides. Recruits were regarded as individuals that had gone through morphometric changes, having been on the shore for longer than 2 days, which appears to be the minimum period during which no morphometric change occurs (personal observation).

In this study, 60% of all settlers collected were in the range of 200–400  $\mu\text{m}$  and were considered to be primary settlers. The remaining 40% of settlers collected were larger, 17% being 400  $\mu\text{m}$  to 1 mm and 23% > 1 mm. Our results could be taken to support the theory of primary and secondary settlement proposed by [Bayne \(1964\)](#). However, the theory also predicts that two different size classes of settlers should be found on different substrata: smaller individuals on filamentous material, and larger ones on adult mussel beds ([Buchanan and Babcock, 1997](#)). Both early (< 1 mm) and late (1–5 mm) plantigrades of *P. perna* occur on both substrata ([McQuaid and Lindsay, 2005](#)) and our pads collected larger individuals as well as very small settlers. A simpler explanation for the occurrence of large individuals on settlement pads is that settlers, after settling for the first time on the shore, can be dislodged, actively or passively, and reattach on local scales.

### 4.1. Lunar and tidal variability

A high degree of spatial variability was evident in both settlement and recruitment, with a clear effect of location, the smallest spatial variable investigated, as discussed in detail elsewhere ([Porri et al., in press](#)). The other major source of variation was temporal variability. Many studies have examined temporal variability in settlement of intertidal organisms (for example: [Caceres-Martínez et al., 1993](#), [Lasiak and Barnard, 1995](#) and [Balch and Scheibling, 2000](#)), but few have examined different scales of temporal variability in the same study or tried to determine which scales most influence the variability of settlement (e.g. [Bertness et al., 1996](#) and [Hunt and Scheibling, 1998](#)). Here we examined temporal variability of settlement and recruitment patterns at different scales to investigate variability in recruit densities and whether settler abundances differ at different phases of the moon or days over spring tide.

Time (as month and fortnight) was a very important factor in determining variability in settler/recruit densities in all analyses. In addition to time as a main factor, much of the variability of settler/recruit abundance was due to interaction between time and the smallest spatial scale investigated, location.

Apart from spawning cycles, high temporal variability can be driven partly by hydrodynamics (Jenkins et al., 2000) and, elsewhere (Porri et al., in press), we provide evidence of differential transport of larvae from nearshore waters to some locations rather than others. Currents can vary on large temporal scales, causing seasonal patterns in water movement, but local hydrodynamics can also change on much finer time scales, affecting the arrival of larvae on the shore (Gaines et al., 1985). Nevertheless, the data in Fig. 1 and Fig. 3 suggest that such changes in settler supply are synchronised on scales of 100 m–km (i.e. among locations and between sites).

The arrival of larvae on the shore is influenced by several factors. In the case of barnacles these include water temperature, availability of food, presence of conspecifics, algal cover and many other factors (Gaines et al., 1985 and Hills and Thomason, 1996). Larval behaviour can also be important. Changes in salinity, light and turbulence trigger a behavioural response in crab larvae so that megalopae swim during flooding of the tide at night, but settle just before low tide, when turbulence declines (Tankersley et al., 2002).

In this study, the effect of day around spring tide (before, at, or after spring tide) was investigated, to determine whether a specific day close to spring tide would influence the settlement of *Perna* possibly because of changes in tidal amplitude. The results did not show a clear effect, probably because the differences in tidal range were minimal in this particular case. The maximum tidal amplitude in the study area is about 2 m and, in this study variation, involved samples collected only 5 days apart.

The lunar study showed distinct peaks in settlement and within these periods of high settler abundances, variability appeared to be influenced by the phase of the moon, with more settlers arriving at new than at full moon. Although the effect of moon was just non-significant, there appeared to be a strong influence of the moon, particularly when settler abundances were high (i.e. at certain times and certain locations). This suggests that moon is relevant in explaining settlement variability when rates of settlement are high. The influence of lunar cycle on settlement of intertidal invertebrates has been suggested by other studies (e.g. barnacles: Pineda, 2000). In some cases, the influence of the moon probably reflects the influence of tidal amplitude as higher tides are expected around a particular phase of the moon (Reyns and Sponaugle, 1999 and Paula et al., 2001); however, this was not the case in the present study. Settlement was higher during new moons in both September/October (tidal amplitude higher during new moon) and December/January (amplitude higher during full moon; Fig. 1), suggesting that some other effect associated with the moon was important. The study carried out over neap tides highlighted the synchrony of recruitment. Peaks in recruitment occurred over neap tides in May and December at both sites, though, as with settlement, the strengths of the peaks differed among locations.

The results of this study indicate that, on this coast, the timing of mussel settlement and recruitment is extremely variable, and that there is no predictable effect driven by the state of the tide, so we conclude that tidal amplitude around spring tides has no significant effect. Peaks in recruitment, measured over neap tides however, were synchronised among locations. Likewise, there appears to have been an effect of the state of the moon, but only when and where settler numbers were relatively high, with more settlers during new moon. Under other circumstances, settler abundances were so low that there was no obvious effect of moon. Because of the extreme unpredictability of settlement, and the low numbers of settlers found, the effects of factors such as those of the moon may be masked, becoming apparent only when settler numbers are higher. We suggest that, while settlement occurs at low intensities throughout the year, rather than being strongly pulsed, the effect of moon will provide a degree of synchronisation when and where settler abundances are relatively high.

Since rates of settlement and recruitment on scouring pads were generally low throughout this study (cf. [Menge et al., 1994](#) and [McCulloch and Shanks, 2003](#)), it appears that settlement is likely to be a primary process in the shaping of these mussel communities. Therefore, all factors that have significant effects on the arrival of settlers will be important in developing an understanding of mussel population dynamics on this coast.

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