Supply-side ecology of the brown mussel, *Perna perna*: an investigation of spatial and temporal variation in, and coupling between, gamete release and larval supply

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Abstract

Sampling of recruitment-associated variables of *Perna perna* was done approximately monthly for 14 months at intertidal locations 500 m apart, nested within sites 25 km apart. Paired with intertidal locations were nearshore locations, 600 m to sea. Sampling assessed spawning, densities of larvae in the water column and densities of late plantigrades and juveniles on the shore. Major events in each variable were synchronous over larger scales (10s of kilometres) while subsidiary events were synchronised at smaller scales, varying within sites (100s of metres) or even within locations (metres). This suggests that the processes driving major events operated over large scales while processes operating at much more local scales drove less intense, more localised events. A major spawning event occurred at all locations in May–June 1998. Weaker spawning events occurred at different times in different locations. Larvae were found on 80% of sampling occasions, densities peaking in January–March 1998 and 1999 at all locations. Plantigrades and juveniles showed less clear patterns, with considerable residual variation. There was no sign of strong coupling among variables with few significant direct or cross correlations. The major sources of variability shifted from time to space as one progressed from spawning, to plantigrade density to juvenile density. For spawning, time was the most important source (58%) of heterogeneity and space accounted for little (8%) of the total variance. For larvae and late plantigrades, time was still the most important source of variability (41% and 33%, respectively), but space was a much more substantial component. For juveniles, small-scale (residual) spatial variability dominated total variability (75%). This strongly suggests the importance of hydrography and its effects on variation in delivery of larvae to the intertidal from offshore. These findings also indicate greater spatial heterogeneity as recruits age, reflecting small-scale variations in larval delivery and the increasing importance of post-settlement mortality.

Introduction

Mussels are a ubiquitous feature of rocky shores in temperate regions. They have economic importance to commercial and/or artisanal subsistence fisheries and ecological importance as dominant rocky shore species. A wealth of literature exists on the ecology of mussels, especially *Mytilus spp*. (Bayne *1976*; Suchaneck *1985*; Gosling *1992*), and there is increasing interest in the supply of recruits into populations, so-called supply-side ecology (Hunt and Scheibling*1996*; Young et al. *1996*; Beukema et al. *2001*). Supply-side ecology is an important aspect of the processes governing populations of many marine organisms (Lewin *1986*; Roughgarden et al. *1987*; Underwood and Fairweather *1989*) and data on larval release and abundance, dispersal, settlement and recruitment are fundamental to understanding population dynamics and the development of appropriate management policies (Fairweather *1991*; Lipcius and Stockhausen *2002*). Early studies on *Mytilus edulis* suggested synchronous spawning, followed by a 2- to 4-week larval period in the water column, with primary settlement onto filamentous algae and secondary settlement, after a second mobile phase, onto adult mussel beds (Thorson *1950*; Bayne *1964*). Buchanan and Babcock (*1996*) found this in *Perna canaliculus*, but as more mussel species have been studied, and the same species have been studied in different geographical regions, it has become clear that synchronous spawning and primary and secondary settlement are not universal features of mussel populations (Petersen *1984*; McGrath et al. *1988*; Lasiak and Barnard *1995*).

Roughgarden et al. (*1987*) have noted that, in terms of population structure and larval supply, all systems are open at some scale. Mussels, along with most other marine invertebrates with a planktonic larval stage, have been considered to have relatively open populations because of their potential for long distance dispersal as larvae (Thorson *1950*; Cameron *1986*). However, scales of dispersal and thus the relative "openness" of the system vary, depending largely on the prevailing water currents and their variation at different times of the year (Scheltema *1986*; Young et al. *1996*; McQuaid and Phillips *2000*). In addition, larvae need not behave as passive particles and, in certain circumstances, larval behaviour can affect scales of dispersal and settlement success (Dobretsov and Miron *2001*; Kingsford et al. *2002*). Hydrodynamics and topography have also been advocated as principal determinants of spatial heterogeneity in settlement, recruitment and ultimately adult density of sessile marine invertebrates from within-shore scales of cm to geographic scales of 100s of km (Shanks and Wright *1987*; Shepherd et al. *1992*; Harii and Kayanne *2003*).

Spawning, settlement and recruitment of the intertidal mussel *P. perna* in South Africa have been examined in relative detail over small areas (Lasiak and Barnard *1995*; Lawrie and McQuaid *2001*), and in less detail at biogeographic scales (Harris et al. *1998*). Overall, these studies indicate extreme variation in the frequency and intensity of spawning, settlement and recruitment both around the coast and within shores. There is also a high degree of variation from month to month and from year to year. However, these studies of *Perna* often differ in the scales of time and space that are examined and generally deal with the various supply processes in isolation from one another. In addition, only one study (McQuaid and Phillips *2000*) has attempted to examine larval density of *Perna* in the water column. We are not aware of studies that have examined all these supply variables in unison, sampling over the same temporal and spatial scales. Furthermore, most previous studies have not dealt explicitly with scales of variation in these processes.

The present study monitored spawning, larval density and recruitment along a section of coastline on the southern coast of South Africa over a period of 14 months. The study had three main aims: (1) to identify the spatial scales of greatest variation in spawning, larval density and recruitment of *P. perna*, (2) to identify intra-annual trends in the timing of periods of peak activity of each of these variables, and (3) to examine whether these variables were coupled to one another in time and space and, if so, at what scales.

Methods and materials

Between January 1998 and April 1999 we monitored female condition as an indication of spawning, larval density in the nearshore water column and recruitment to established mussel beds on the southern coast of South Africa. Two exposed rocky shore sites, Port Alfred and Dias Cross, were used. Each site was 1 km long and they were 25 km apart. Two samples of mussel beds were taken using 10×10-cm quadrats from areas of 100% cover within each site at three low shore, intertidal locations of 1×5 m. Samples were taken approximately monthly on 14 occasions. Intertidal locations were of similar height, aspect and exposure and were separated by approximately 500 m. Samples were taken at each site on the same day or over a 2-day period. The density of larvae in the water column was assessed by bottom to surface vertical hauls of an 80- μm mesh net with a 30×30-cm mouth, hauled at 0.5 ms^{-1}. Sampling was approximately monthly, with sampling intensity increased to either weekly or fortnightly during periods of anticipated spawning or recruitment (*n*=19). Hauls were taken at three locations along fixed transects in the nearshore water column, behind the surf zone and running parallel to the shoreline. Nearshore locations were 300 m apart and each location included a pair of sampling stations separated by approximately 100 m (Fig. 1). On several occasions one or two additional parallel transects lying further seawards or landwards were also sampled to evaluate variation in larval number with distance from the shore.
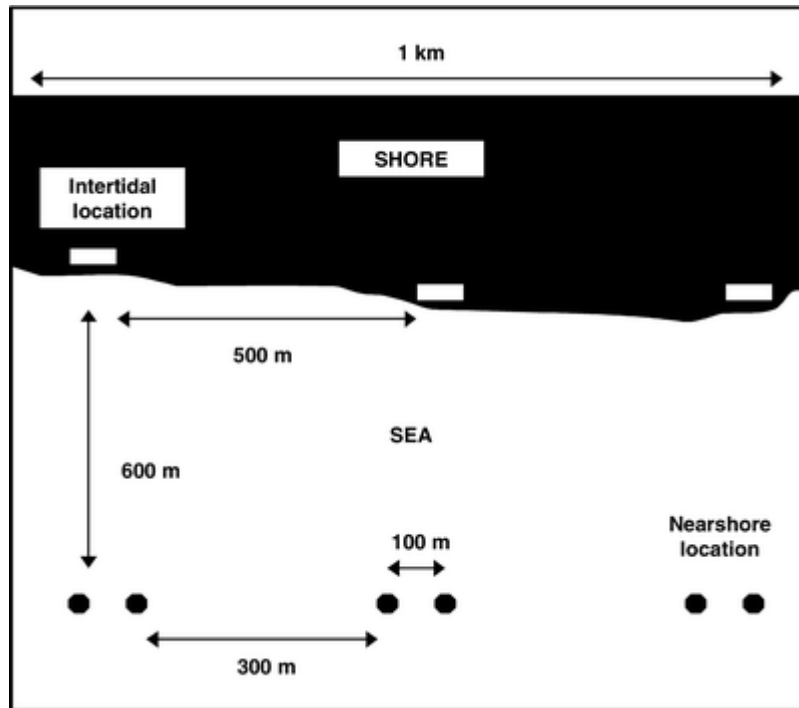
Fig. 1 Schematic representation of the intertidal and nearshore locations for one site

Adults of >25 mm length were separated from the shore samples and the individual dry flesh weight and shell length of each adult female recorded. There is strong evidence that length–weight relationships of *P. perna* accurately reflect reproductive state as evaluated by histological sections (unpublished data) and that this frequency of sampling is adequate to capture most spawning events (Lasiak *1986*). Recruits were separated into late plantigrades of <3.5 mm and juveniles of 3.5–10 mm, and their numbers recorded for each sample. This distinction between late plantigrades and juveniles was based on observations that individuals <3.5 mm can appear from the water column directly onto settler collectors on the shore (unpublished data). The density of *Perna* larvae per m^3 was calculated from the depth of each haul. Veliger and pediveliger larvae were found, ranging from 150 μm to 600 μm in size. D larvae (<150 μm) were also found, sometimes in high numbers. Plantigrade post-larvae, ranging from 500 μm to 1 mm, were occasionally found in plankton samples in very low numbers, but were not included in analyses.

Scales of greatest variation for each of the variables were assessed using nested ANOVA with all factors being random. This analysis indicates whether significant variability occurs among scales of time and space. Location was nested within site, with both of these factors crossed by occasion. For female condition, a nested ANCOVA was used, with dry flesh weight as the dependent variable and shell length as the covariate. For analyses of samples from the shore, a value of 12 degrees of freedom was used at the location level as one pair of samples was lost on one occasion. Variance components provided an indication of which scales/factors explained the greatest proportion of the variability observed and were calculated as: $\frac{MS\,between - MS\,within}{n\,within}$ for each level of the analyses.

Bartlett's test for homogeneity of variances and Shapiro's test for normality of the data were performed in all cases and ln (x+1) transformations used when appropriate. Peak periods for each of the variables were estimated by graphical examination of the time series data. Direct correlations between variables measured on the same occasions and cross-correlations, using lagged correlations between variables measured on sequential occasions, were carried out to provide indications of coupling.

Results

Scales of variation

Sampling occasion had a significant effect on all the measured parameters, but their spatial scales of variability differed. Female condition varied significantly both between sites (25 km) and among intertidal locations (500 m) within sites. Condition also varied among occasions, with significant interactions between both site and occasion, and intertidal location and occasion (Fig. 2, Table 1). Variance components indicated temporal variation as the major component of total variance (0.64, 58%). Density of *Perna* larvae in the water column also varied significantly between sites and among sampling occasions, again with a significant interaction (Fig. 3, Table 2). However no significant variation was found among nearshore locations within sites. Again, occasion was a major contributor to variance, as was the interaction between site and sampling occasion; each had a value of 0.95 and explained 33% of the total variance for larvae. There was also a high degree of residual variation (0.74, 26%) suggesting that smaller scale variation within locations may also be important. ANOVA analyses between parallel transects sampled either shorewards or seawards of the main sampling transects at the two sites, found no significant variation in the density of *Perna* larvae in the water column among transects on any occasion ($P>0.05$).
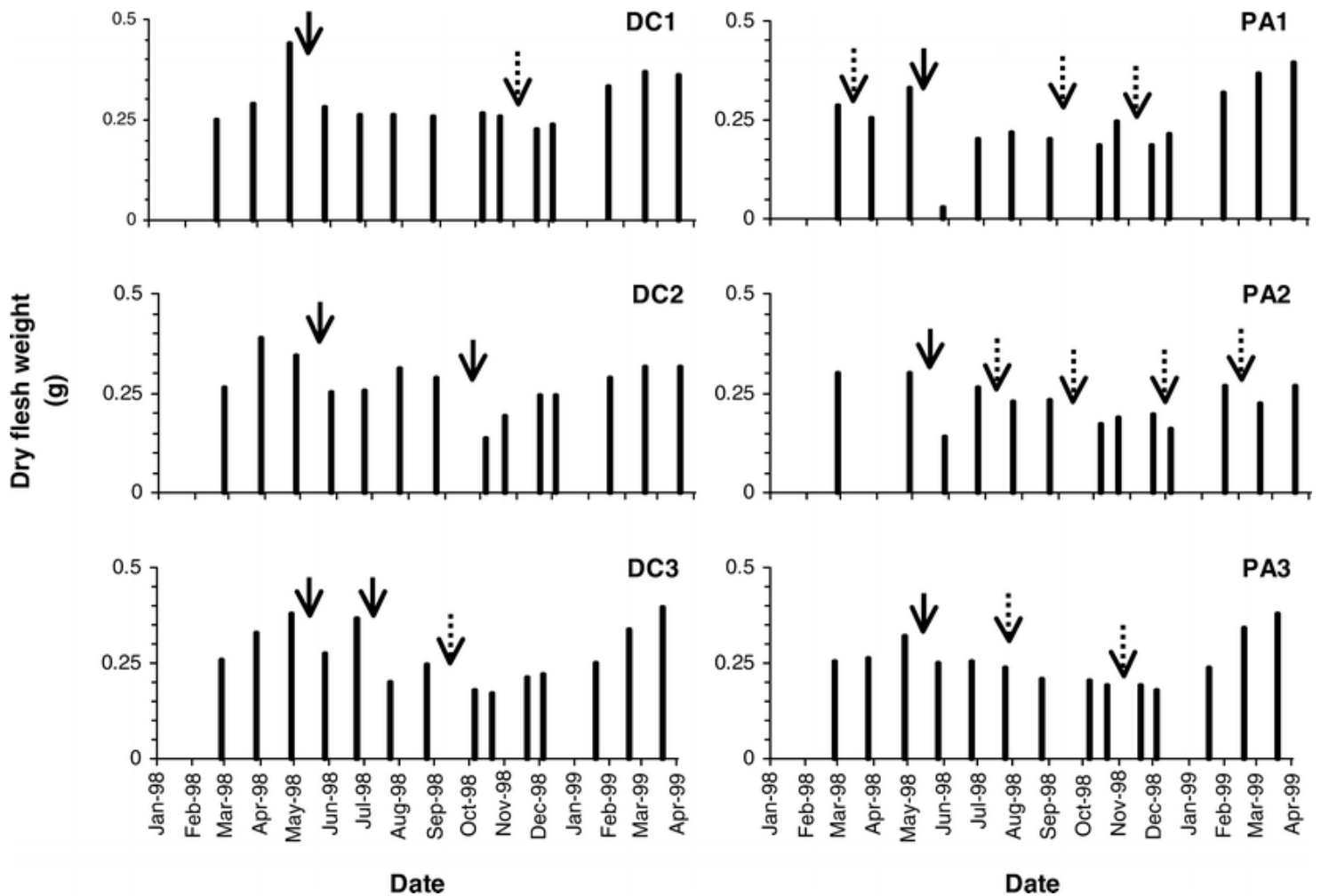

Fig. 2 Temporal variation in the flesh weight of a standard 45 mm female at each intertidal location. DC = Dias cross, PA = Port Alfred. Sudden drops in flesh weight denote probable spawning periods. *Full arrows* indicate major spawning events and *dashed arrows* indicate subsidiary spawning events

Table 1 Scales of variation in female condition from ANCOVA analysis, showing variance components and percentage variance explained at each scale and the effect of the covariate shell length

Source	df	Mean square	F	P	Variance component	Percent variance
Site	1	5.33	55.5	<0.0001	0.05	4.5
Location	4	1.29	13.4	<0.0001	0.04	3.5
Occasion	12	7.8	81.3	<0.0001	0.64	58
Site × occasion	12	0.69	7.2	<0.0001	0.099	9
Location × occasion	48	0.46	4.8	<0.0001	0.18	16
Residual	2359	0.096			0.096	9
Shell length	1	796	8291	<0.00001		
Residual	2359	226				

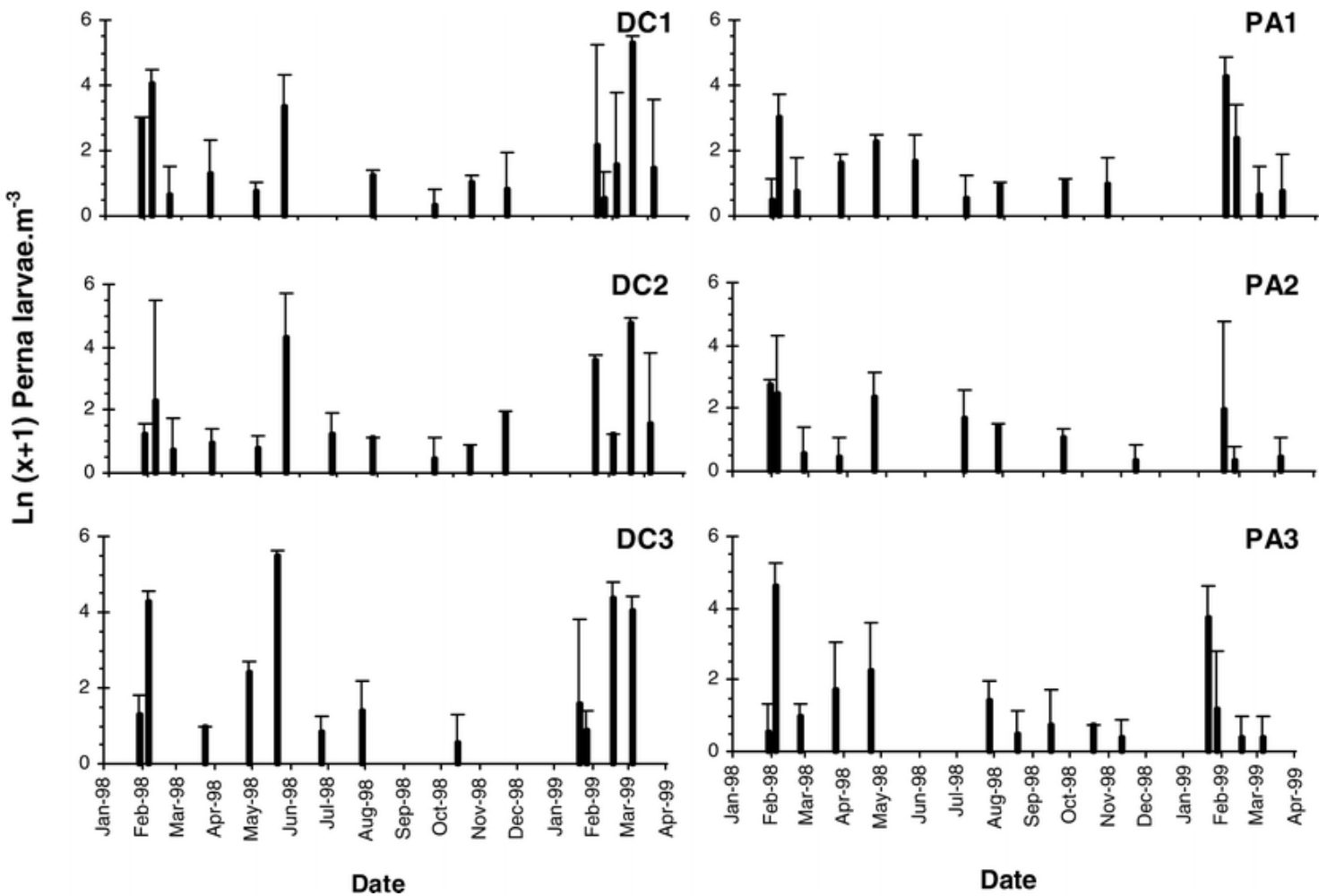NS indicates not significant.

Fig. 3 Temporal variation in the density of mussel larvae in the water column [ln $(x+1)$ transformed] at each nearshore location. Values are means and *error bars* are standard deviations

Table 2 Scales of variation in larval density in the water column [transformed ln $(x+1)$] from ANOVA analysis, showing variance components and percentage variance at each scale. *NS* indicates not significant

Source	df	Mean square	F	P	Variance component	Percent variance
Site	1	11.79	15.88	<0.0002	0.094	3.3
Location	4	0.44	0.59	NS	0	0
Occasion	18	12.14	16.35	<0.0001	0.95	33
Site × occasion	18	6.48	8.73	<0.0001	0.95	33
Location × occasion	72	1.01	1.36	NS	0.135	4.7
Residual	114	0.74			0.74	26

Late plantigrades and juveniles varied significantly within and between sites and also among occasions (Figs. 4, 5). Only one significant interaction, between site and occasion, occurred for late plantigrades, and there were no significant interactions for juveniles. For plantigrades (Fig. 4), temporal variation was still the main variance component (15.3, 41%), but again there were high values of residual variation (9, 24%). This was even more notable for juveniles; for them the residual was the main source of variation (66, 75%; Table 4), indicating an increasing influence of small-scale spatial heterogeneity moving from recently settled plantigrades to older juveniles.
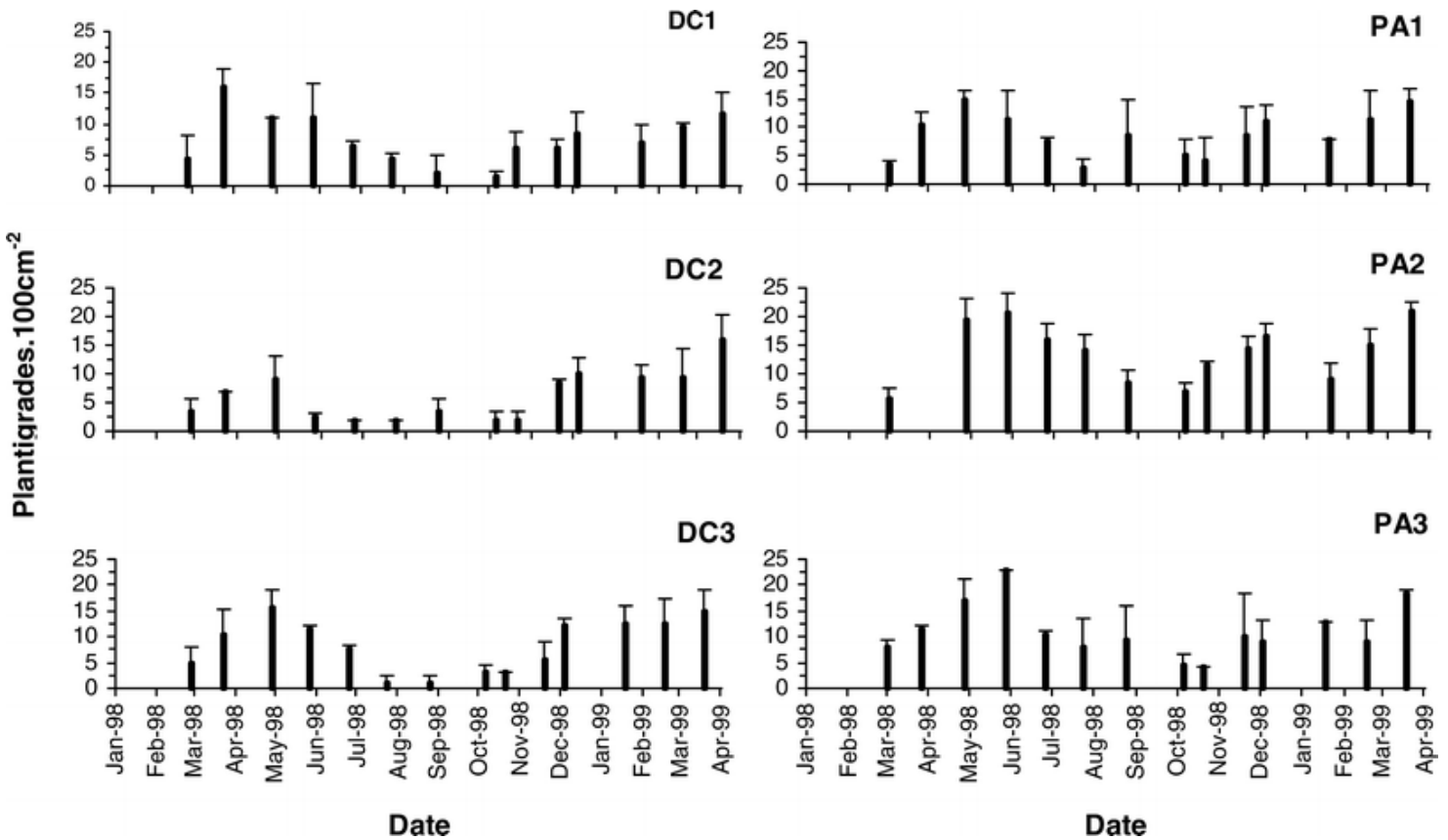

Fig. 4 Temporal variation in the density of late plantigrade mussels (<3.5 mm) at each intertidal location. Values are means and *error bars* standard deviations
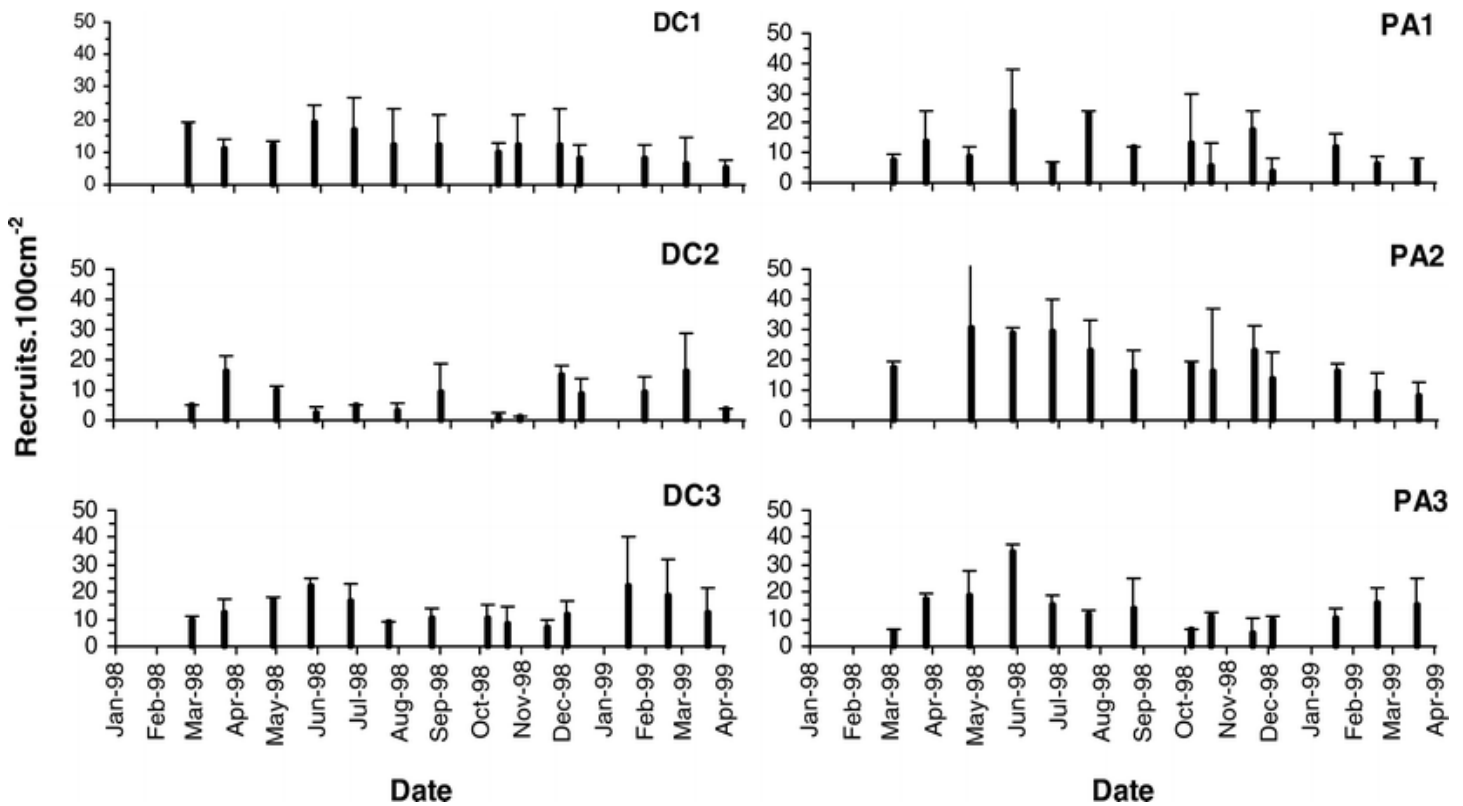
Fig. 5 Temporal variation in the density of juvenile mussels (3.5–10 mm) at each intertidal location. Values are means and *error bars* standard deviations

Temporal trends

The dry flesh weight of a hypothetical standard female of 45 cm was interpolated by regression for each sampling occasion. Fig. 2 shows temporal variation in this value at each of the six sampling locations. Potential spawning periods are indicated as "abrupt" drops in weight, i.e. a loss of >30% of estimated body weight between consecutive monthly samples. There was some degree of consistency in the timing of major spawning events among locations. This suggests a level of synchrony both within and between shores in the main spawning events. For example, large drops in weight occurred at all locations between May and June 1998. This is in accordance with histological data from the region (Lasiak 1986). However, some degree of synchrony in spawning is required for this method to hold. Less marked decreases in weight and decreases that occurred over longer time periods suggest less intense, or less synchronised, subsidiary spawning periods. These were frequently specific to a single location, and suggest a degree of asynchrony within locations, within sites and between sites.

Two striking features of the variation in the density of larvae in the water column are immediately apparent (Fig. 3). Firstly, two or three periods of extremely high larval density, with up to 400 *Perna* larvae per m^3, occurred at all nearshore locations around January–February 1998 and January–March 1999 and also at Dias Cross around May–June 1998. Secondly, *Perna* larvae were present in the water column at each site on 80% of the sampling occasions. Therefore, larvae were available, at least in low numbers, for most of the year.

Temporal trends in density of late plantigrades were relatively consistent within sites (Fig. 4), but there were clear differences between sites. Two peak periods occurred at Dias Cross (March–June 1998 and December 1998–April 1999) and similarly two main peaks occurred at Port Alfred (March–July 1998 and January–April 1999).

However, at Port Alfred, less distinct subsidiary peaks also occurred (September 1998, November–December 1998) at one or more intertidal locations. The greater degree of residual variation for juveniles is apparent in Fig. 5 and peaks are less clearly defined. High residual variation may explain the lack of significant interactions between temporal and spatial factors.

Coupling

There was some degree of synchrony within variables and some degree of overlap in timing among variables but neither was consistent (Figs. 2, 3, 4, 5). Direct and cross correlations carried out between variables for each site separately reflected this, with little evidence of overall coupling. Only two direct correlations were significant: female condition with plantigrades (r=0.801 P<0.001); and larval density with plantigrades (r=0.669 P<0.05), both at Dias Cross, reflecting peaks in these variables during March–June 1998.

Discussion

Measuring spawning, larval density and recruitment over the same spatial and temporal scales, allows us to assess the scales at which significant variation occurs in each factor. Within the limits of this study we can also assess the degree of coupling among these factors, and the scales at which coupling occurs.

Scales of variation

All four variables measured differed significantly between sites, at least at some times of the year. However, female condition and recruitment, unlike larval density in the water column, also varied significantly among locations within sites. Furthermore the significant interaction between location and occasion for female condition indicates that spawning patterns at one location may bear little resemblance to those at other locations. Recruitment of plantigrades, on the other hand, showed a clear temporal trend within sites, but differences in absolute density of plantigrades among the locations.

Similar patterns of spatial and temporal variation in recruitment and female condition have been recorded for mussels in South Africa (Lasiak _1986_; Harris et al. _1998_) and the data and review of Van Erkom Schurink and Griffiths (_1990_) suggest a biogeographic trend of extended spawning on the east coast, shifting towards two to three shorter spawning periods farther west. However, our results indicate the same degree of variation within and between two shores separated by only 25 km.

For female condition, the residual variation was relatively small, explaining only 9% of total variation (Table 1), while temporal variation and the interaction between intertidal location and occasion made up the majority of total variance, explaining 58% and 16%, respectively. Nevertheless, residual variation was important, making a greater contribution than either site or intertidal location alone.

For larvae, we found no significant variation at the location scale, but residual variation made up over one quarter of total variation (Table 2), indicating a degree of patchiness similar to that recorded by McQuaid and Phillips (_2000_) who sampled nearshore grids of stations on several days, repeating sampling within each day, and finding highly patchy distribution of _Perna_ larvae at scales of 10s to 100s of metres.

Relatively high residual variation was also apparent for the two classes of recruits. For late plantigrades, temporal variation was the most important component of variance (41%), but residual variation made a greater contribution to total variance than site (24% and 17.5%, respectively; Table 3). Residual variation for juveniles was even greater; it made up 75% of the total variance and far outweighed the contributions of the spatial and temporal factors of the analysis (Table 4). Thus, small-scale heterogeneity at scales of metres or less, increased from late plantigrades to juveniles. This reflects the compounding of variability in both settlement and post-settlement mortality. Mortality following settlement will vary within a shore due to small-scale variation in factors such as

predation, competition, and abiotic stress, and so is linked to small-scale variation in topography, hydrodynamics, algal cover, etc. (Rodriguez et al. *1993*; Gosselin and Qian *1997*). There may also be differences in individual behaviour, such as active secondary settlement.

Table 3 Scales of variation in late plantigrade density on the shore from ANOVA analysis, showing variance components and percentage variance at each scale. *NS* indicates not significant

Source	df	Mean square	F	P	Variance component	Percent variance
Site	1	652	70	<0.0001	6.6	17.5
Location	4	99	11	<0.0001	3.2	8.5
Occasion	12	193	21	<0.0001	15.3	41
Site × occasion	12	21	2	<0.025	2	5
Location × occasion	48	12	1.3	NS	1.5	4
Residual	78	9			9	24

Table 4 Scales of variation in juvenile density on the shore from ANOVA analysis, showing variance components and percentage variance at each scale. *NS* indicates not significant

Source	df	Mean square	F	P	Variance component	Percent variance
Site	1	596	9.06	<0.005	2.7	3
Location	4	368	5.59	<0.0005	10.8	12
Occasion	12	157	2.38	<0.025	7.5	8.5
Site × occasion	12	73	1.11	NS	0.6	1
Location × occasion	48	12	1.3	NS	1.5	4
Residual	78	66			66	75

Thus, there was an overall shift in the balance between time and spatial heterogeneity as sources of variation moved from spawning to recruitment. Sampling occasion was highly important to spawning, while spatial variation was less so. The reverse was true for juvenile density. For juveniles, residual variation, occurring at scales smaller than those measured, was by far the greatest source of variability. Late plantigrade and larval density showed intermediate values, though direct comparisons cannot be made for larvae, as they were sampled differently.

Temporal trends

Sampling at intervals of 1–4 weeks might have missed events happening on shorter time scales, such as peaks in larval density. Nevertheless, we believe that the sampling frequency was intense enough to detect major trends in all the variables measured. In our study, the major spawning period roughly coincided at all locations. The same was true for most periods of high larval density and the times of highest recruitment. This would suggest synchrony within variables at scales of 25 km or more. This could be explained by the cues or forcing processes for spawning and settlement being directly related to climatic conditions, such as temperature and wind, or indirectly related, for example via the occurrence of phytoplankton blooms (Starr et al. *1990*, *1991*). However, significant variation was also shown within and between shores, indicating that subsidiary spawning events, and periods of high local larval density or recruitment occur at smaller scales. We interpret subsidiary events as

reflecting smaller scale, localised variation in the same cues, or as reflecting ancillary cues. For example, localised spawning could be elicited by localised concentrations of phytoplankton driven by smaller-scale effects such as hydrodynamic entrapment of phytoplankton (Murdoch *1989*; Fogg *1991*).

Although recruits were found year-round, periods of higher recruitment occurred in austral summer/autumn and in winter (March and July 1998; between December 1998 and April 1999). This accords with earlier work (Beckley *1979*; Lasiak and Barnard *1995*) and broad similarities in timing among these studies suggest coherence at geographical scales. This probably reflects semi-predictable external forcing processes such as air temperature or seasonal wind patterns (Phillips *1994*).

Coupling

If the supply-side variables measured were coupled to one another at the scales examined, then peaks in spawning would be expected to be followed by peaks in larval density with subsequent peaks in settlement/recruitment. On the whole this was not the case. At Dias Cross, peaks in all the variables occurred in May–June 1998. This could reflect coupling of these processes at this site, with settlement occurring within 1 month of spawning. Bayne (*1965*) proposed that *M. edulis* larvae spend between 2 and 4 weeks in the water column, so that this is possible, but it seems unlikely as plantigrade density on the shore started to increase before the density of larvae in the water column (Figs. 3, 4). Phillips (*1994*) did find a significant correlation between the gamete output and the intensity of the following settlement peak for *Perna*, but there was no consistent time lag between spawning and settlement, so again there is no good evidence of strong coupling.

Uncoupling may occur between spawning and larval density and between larval density and settlement/recruitment due to a variety of factors. The former may be explained by fertilisation failure, larval mortality and/or dispersal over a greater range than considered in the study. Dispersal of larvae over scales larger than we measured implies that their availability may be determined by spawning success outside the study area, and by larval transport. Both reproductive success and transport are likely to be highly variable among years, so that conclusions drawn from a single study year should be cautiously interpreted. Uncoupling of larval density and settlement/recruitment may also be explained by dispersal distance. Other explanations include post-settlement mortality, hydrodynamic effects on larval delivery and/or the duration of the larval period in the water column. Some evidence is available to support each of these hypotheses (Shanks and Wright *1987*; Hurlbut *1991*; Gosselin and Quian *1997*), but uncoupling due primarily to hydrodynamic dispersal of larvae is the most likely explanation. This would include highly local effects on larval delivery, and we have evidence that sites separated by 100s of metres can be consistently ranked on the basis of daily settlement rates (unpublished data). Jeffery (*2003*) found that post-settlement mortality was not the main determinant of distribution or abundance of juvenile barnacles, and that adults retain the spatial patterns shown by juveniles. Nevertheless, post-settlement mortality or secondary dispersal may further confound relationships between larval density and recruitment and are themselves related to abiotic factors such as topography and hydrodynamics. In the case of *P. perna*, distribution patterns within the same zone on a shore change as plantigrades grow into larger recruits (Erlandsson and McQuaid *2004*).

The fact that major peaks in larval density (January 1999) were not preceded by major spawning events in November or December 1998 highlights the openness of these populations at the scale of this study. We are left with two non-exclusive explanations for the uncoupling of these supply-side processes. Nearshore larvae do not originate from these populations; or physical forces, rather than spawning intensity, dictate nearshore larval density. Recent studies support the latter hypothesis (Porri, McQuaid and Radloff, unpublished data). In either event, correlations between spawning intensity and settlement rates are either coincidental, or reflect covariation of spawning output and settlement as independent responses to variation in adult densities and/or other factors.

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