

Inconsistency in short-term temporal variability of microgastropods within and between two different intertidal habitats

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Abstract

Small-scale temporal variation in abundances of fauna in marine soft sediments has long been recognised. Many studies on rocky intertidal shores have, however, focused on larger fauna in single habitats and have primarily examined relatively long time-scales. The implications of small-scale variability are frequently not adequately addressed in the studies of changes in fauna over longer time-scales. Without knowledge of the magnitude of variation at smaller scales, comparisons across longer time-scales may be confounded. In this study, the temporal variability of a number of co-existing species of microgastropods in patches of two different intertidal habitats (coralline turf and sediment) in Botany Bay, New South Wales, Australia, was measured using a nested, hierarchical sampling design incorporating temporal scales of weeks, 1 and 3 months. In addition to habitats, there were also spatial scales of metres between plots and 100s of metres between the locations. There was generally a lack of consistency in the trends of variance for the three temporal scales at the smallest spatial scale of plots. In addition, the different species, including those that were closely related, showed different patterns of variation, depending on the habitat and site. These data show the importance of incorporating adequate scales of sampling in different habitats when analysing the distribution and abundance of microbenthos in intertidal habitats. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Ecological systems are naturally heterogeneous and there is a growing evidence that the processes which generate natural variability operate over different scales of time and space (e.g. Dayton and Tegner, 1984; Levin, 1988; Wiens, 1989; Thrush, 1991; Menge et al., 1997). Understanding these scales is a fundamental conceptual problem in ecology, if not in all science (Levin, 1992). Quantification of patterns at one or several spatial and/or temporal scales is often an important starting point of the scientific process from which other models and hypotheses arise (Underwood, 1991; Levin, 1992; Underwood et al., 2000).

In studies of intertidal habitats, there have been several approaches to considering hierarchies of spatial scales of abundances of organisms (e.g. Underwood and Petraitis, 1993; Underwood and Chapman, 1996, 1998a; Menconi et al., 1999). Temporal variability has, however, generally been less well studied using a number of different temporal scales. Nevertheless, variation in abundances and distributions can change markedly over periods of days, months, decades, etc. (Dayton, 1971; Underwood et al., 1983; Caffey, 1985; Menge et al., 1985; Barry and Dayton, 1991; Morrissey et al., 1992; Åberg and Pavia, 1997). Changes can be due to biological processes, such as predation, competition or recruitment (Loosanoff, 1964; Connell and Keough, 1985), natural disturbances, such as storms and floods (Underwood, 1999) or physical factors (e.g. tidal inundation, exposure time, currents, bottom topography, etc.) (Bell et al., 1997). The relationships between temporal variation in abiotic variables and biological patterns and processes in aquatic assemblages are still poorly known, particularly the importance of small-scale variation in such measures. Nevertheless, there is increasing evidence that the spatial scale of patterns of abundance and the temporal scales of processes that cause them to vary and interact in complex ways, change from one spatial or temporal scale to another (e.g. Morrissey et al., 1992).

Most temporal studies in intertidal habitats have focussed on large temporal scales (seasons and/or years) within one particular type of habitat (e.g. Metaxas and Scheibling, 1994; Farnsworth and Ellison, 1996; Underwood and Chapman, 1998a,b; Menconi et al., 1999). Small-scale temporal variation has the potential to confound larger-scale comparisons if smaller scales are not included in the longer study (Underwood, 1991). Statistically significant differences among means measured among seasons, which are often interpreted to reflect a seasonal cycle or pattern of difference, could be due to shorter-term variation, say from day to day, week to week or month to month within each season, unless other temporal scales are incorporated into the sampling design (Underwood, 1991; Morrissey et al., 1992). Multiple scales of variation can be measured using a hierarchical sampling design and nested analysis of variance (Underwood, 1997) which provide estimates of the contribution of each scale to the total variation among the samples (Morrissey et al., 1992).

Many studies on temporal variation have been focused on the larger components of the fauna in intertidal and subtidal habitats (e.g. Gray, 1991; Quijón and Jaramillo, 1993; Benedetti-Cecchi et al., 1996; Smith and Otway, 1997; Apolinário, 1998; Underwood and Chapman, 1998a). Microgastropods (gastropods with adults smaller than 2 mm), which are a large component of intertidal fauna, form an ideal assemblage to test many models

about ecological processes and responses to environmental change (Olabarria and Chapman, 2001) because they are diverse, abundant and occur in many different habitats (Poulicek, 1988; Borja, 1988; Fernández et al., 1988). Nevertheless, there is no quantitative information on variation in the numbers of these snails at different temporal scales. This information is important for understanding natural variation in and changes to biodiversity in addition to evaluating the value of this assemblage for measuring environmental impacts in different intertidal habitats.

Many investigations into relationships between the structure of assemblages and environmental heterogeneity have put species into groups according to anatomical characteristics, trophic preferences or other ecological attributes. This “functional group” approach has been a useful tool in diverse studies of terrestrial assemblages (e.g. Bouchard et al., 1987; Wilson and Roxburgh, 1994), freshwater assemblages (e.g. Poff and Allan, 1995) and assemblages of marine algae and invertebrates (e.g. Littler and Littler, 1980; Steneck and Dethier, 1994). Each species in an apparent “functional group” may, however, respond to spatial and temporal environmental heterogeneity in a different way (Farnsworth and Ellison, 1996). For example, closely-related species of microgastropods of families that apparently feed in a similar way on similar resources (and, thus, may form a “functional group”) showed different patterns of distribution and abundance within and among intertidal habitats at small spatial scales (Olabarria and Chapman, 2001). It is therefore necessary to analyse individual species in studies about the spatial variability of this assemblage.

This paper describes patterns of variability of 10 species of microgastropods measured at a hierarchy of temporal scales in two different intertidal habitats (sediment and coralline algal turf) and determines the extent to which small-scale temporal variation may confound measures of seasonal patterns in abundance of these species. Particularly, we aimed to test the models that: (1) as has been described for other species (Morrissey et al., 1992), most of the temporal variation in abundance of these microgastropods within each habitat is at small scales (weeks); (2) closely related species show similar patterns of variation; (3) patterns of variation differ consistently across different habitats.

2. Methods

2.1. Sampling design

The samples were collected on an intertidal shore in the Cape Banks Scientific Marine Research Area on the northern headland of Botany Bay, New South Wales, Australia (sites described in Olabarria and Chapman, 2001). Two sheltered mid-shore habitats were chosen: coralline turf on intertidal rock platforms and patches of sandy sediment among intertidal boulders adjacent to the platforms. The turf was composed of tightly-packed upright branches of coralline algae, primarily *Corallina officinalis* Linnaeus, forming a stiff matrix which held quantities of sediment. Some patches of turf also included other taxa of articulated coralline algae (e.g. *Jania* spp., *Amphiroa* spp.).

The sampling design incorporated two spatial scales: two plots (2 × 2 m) 10 m apart, nested within each location. Locations were about 300 m apart. A previous study

demonstrated patchiness in the distribution of these species of microgastropods in Botany Bay at different scales, depending on the habitat (Olabarria and Chapman, 2001). The use of replicate plots and locations in this study was therefore intended to measure temporal–spatial interactions and, thus, to test for the generality of any temporal variation.

Each plot was sampled on each of two consecutive weeks in each of two consecutive months in each of two consecutive “seasons,” i.e. three-month intervals (March–April and June–July 2000). Three replicate cores (Olabarria and Chapman, 2001) were collected randomly from each plot on each occasion.

2.2. Sampling methods

Samples were collected using a 10 cm-diameter plastic corer. The corer was pushed into the sediment to a depth of 5 cm. In the coralline turf, the corer was pushed into the turf and the algae and sediment inside the corer were scraped off at the level of the rock. On average, the turf was approximately 5 cm thick. A corer of 10 cm in diameter was used because previous studies of the fauna in the coralline turf in this area showed that the precision of the estimates of abundance obtained with this size of core was acceptable (S.E. $\bar{X} < 0.06$; Kelaher, personal communication). The positions of replicate cores in each plot were recorded on each sampling occasion and spaced to maximise the collection of independent data at each time of sampling.

Samples were fixed in 7% formalin in seawater and sieved through a 63- μ m mesh. Ten species of microgastropods were selected for the analysis because a previous study showed that they occurred in the two habitats, were relatively abundant in at least one of these habitats and included representatives of a range of families (Table 1). Despite their large abundances in some habitats, there is little information about the basic ecology of these species (Beesley et al., 1998).

2.3. Analyses of data

Only one species was abundant enough in each habitat for statistical analysis of variation across all spatial and temporal scales examined. Therefore, for each habitat separately, the spatio-temporal variation was examined for those species found in more

Table 1
The taxonomic relationships of the species of microgastropods selected for this study

Superfamily	Family	Species
Cingulopsoidea	Eatonellidae	<i>Eatoniella atropurpurea</i> (Frauenfeld, 1867)
		<i>Crassitoniella flammea</i> (Frauenfeld, 1867)
	Cingulopsidae	<i>Eatonina rubrilabiata</i> (Ponder and Yoo, 1980)
		<i>Pseudopisinna gregaria gregaria</i> (Laseron, 1950)
Rissooidea	Anabathridae	<i>Amphithalamus incidata</i> (Frauenfeld, 1867)
		<i>Scrobs luteofuscus</i> (May, 1919)
		<i>Scrobs elongatus</i> (Powell, 1927)
		<i>Pisinna olivacea</i> (Frauenfeld, 1867)
Rissoelloidea	Rissoellidae	<i>Rissoella confusa robertsoni</i> (Ponder and Yoo, 1977)
Omalogyroidea	Omalogyridae	<i>Omalogyra liliputia</i> (Laseron, 1954)

than 75% of the cores in that habitat (over all times of sampling). For each of these analyses, the spatial sources of variation were locations and plots nested in the location. The temporal sources of variation were weeks nested in months, months nested in the two 3-month periods and 3 months. All of these were random factors. Data were not transformed whether or not variances were heterogeneous because (1) the analysis of variance is robust to heterogeneous variances when there are many independent estimates of variance (Underwood, 1997), (2) there were generally no simple relationships between the means and either the variances or standard deviations and (3) it was desirable to analyse all species in a similar scale to facilitate comparisons across the species.

Because many species showed significant spatio-temporal interaction at the scale of plots (i.e. the different plots showed significantly different temporal trends), the compo-

Table 2

Variance estimates derived from the analyses of variance for selected taxa from the different plots at each location at each habitat

		L1C		L1S		L2C		L2S	
		P1	P2	P5	P6	P3	P4	P7	P8
<i>E. atropurpurea</i>	3M	0.00	8601.94			102 641.79	92 691.51		
	1M	98 286.26	12 774.64			0.00	9733.17		
	W	28 056.72	32 471.79			0.00	20 848.04		
<i>C. flammea</i>	3M	24.33	1.72			0.00	5.40		
	1M	11.22	0.00			0.00	0.00		
	W	196.92	0.00			0.53	0.00		
<i>E. rubrilabiata</i>	3M	0.00	0.00			106.66	75.39		
	1M	0.00	54.33			0.00	80.00		
	W	633.94	0.00			21.09	61.37		
<i>P. gregaria gregaria</i>	3M	0.00	1496.10			0.00	26.51		
	1M	0.00	0.00			0.00	0.00		
	W	506.56	2254.93			138.16	0.00		
<i>A. incidata</i>	3M	3461.30	674.64	0.00	15.98	52.14	2573.00	3.33	0.23
	1M	0.00	0.00	0.00	0.00	289.80	15.44	0.93	0.00
	W	2715.97	241.36	2.19	0.00	0.00	83.51	0.18	1.46
<i>S. luteofuscus</i>	3M			0.00	0.00	0.00	0.00	2.63	0.09
	1M			0.67	0.60	7.06	2.42	0.40	0.00
	W			1.26	0.00	0.14	0.00	0.00	1.79
<i>S. elongatus</i>	3M	0.00	0.00	0.00	0.00	0.00	0.00		
	1M	0.00	0.00	0.00	0.00	0.00	0.04		
	W	50.56	2.09	0.00	1.91	0.00	0.00		
<i>P. olivacea</i>	3M	0.18	0.00			0.44	0.00		
	1M	0.00	0.00			0.08	0.95		
	W	0.99	4.61			0.00	5.85		
<i>R. confusa robertsoni</i>	3M	8.44	0.00			0.15	6.40		
	1M	0.00	0.42			0.00	0.00		
	W	5.26	0.00			1.83	2.31		
<i>O. liliputia</i>	3M	0.00	0.00		0.32	0.00	2.37		
	1M	6.81	0.17		0.00	0.00	0.00		
	W	16.71	0.00		0.16	0.00	13.70		

Only variance estimates for species in at least 25% of the samples. 3M, 1M, W: 3-month interval, 1 month, week; L1, L2: Location 1, Location 2; S: sediment; C: coralline turf; P1–P8: Plots 1–8.

nents of variation for each temporal scale (weeks, months and 3 months) were measured for each plot separately. Components of variation for each of the three temporal scales investigated (i.e. weeks, 1 and 3 months) were independently calculated from the mean square estimates for each habitat, each species and each plot. Where a component of variation was estimated to be negative, it was removed from the model and the mean square estimates were recalculated for the remaining factors (Thompson and Moore, 1963).

The rank order of temporal components of variance (smallest to largest) for each species, location and habitat was then recorded. If any component showed a particular tendency to be larger, that component would repeatedly have a larger rank than the other components. These ranks were then analysed across each species, location and habitat using the Anderson (1959) test to test the hypothesis that the variation at the scales of weeks consistently ranked larger. When two or more components of variation for temporal scales were equal, ranks were attributed randomly.

3. Results

3.1. Spatio-temporal variability in abundances

Although all species appeared in both habitats, most of them, except *Amphithalamus incidata* and *Scrobs luteofuscus*, were too rare and patchy in the sediment to be analysed

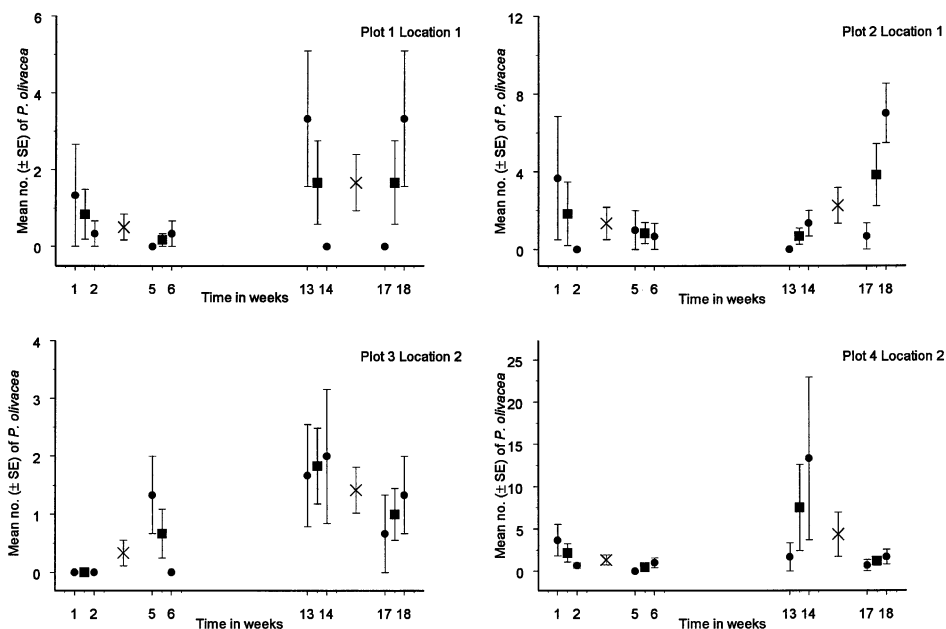


Fig. 1. Mean number (± S.E.) of individuals of *P. olivacea* in the coralline turf at Locations 1 and 2 for each two consecutive weeks (●), two consecutive months (■) and two consecutive 3-monthly intervals (×) ($n=3$).

further. Considering only species which occurred in more than 75% of the samples, the data could be analysed for nine species in the algal turf at each location and for two in the sediment in each location (Table 2).

Because all factors were random, there were no tests in the original analyses for the terms Locations, 3 months, 1 month(3 months), Locations $\times$ 3 months, nor Locations $\times$ 1 month(3 months) and many terms in the analyses had relatively few degrees of freedom (i.e. F ratios were calculated using interaction terms). Therefore, mean square estimates were pooled (or eliminated) at $P > 0.25$ according to Underwood (1997) to provide tests (or more powerful tests) where appropriate.

Only one species, *Pisinna olivacea* in the coralline turf showed no significant variation at any temporal or spatial scale (all F ratios $P > 0.05$ after pooling; Fig. 1). One species, *S. elongatus*, showed significant variation at the scale of plots ($F_{2,18} = 5.31$, $P < 0.05$), but there were no significant temporal trends at any scale. There were consistently more snails in Location 1 than in Location 2, particularly in one of the plots (Fig. 2). Two species showed temporal variation that was similar among all plots and locations. Numbers of *Omalogyra liliputia* varied significantly from week to week ($F_{4,4} = 33.31$, $P < 0.01$; Fig. 3) and *S. luteofuscus* (in the sediment) varied from month to month ($F_{2,64} = 4.02$, $P < 0.05$).

All other comparisons showed significant interactions among mean numbers in space and time. Except for *Rissoella confusa robertsoni* ($L \times W(1M(3M))$, $F_{4,76} = 2.58$, $P < 0.05$) which showed significant temporal interaction between locations, all other species showed

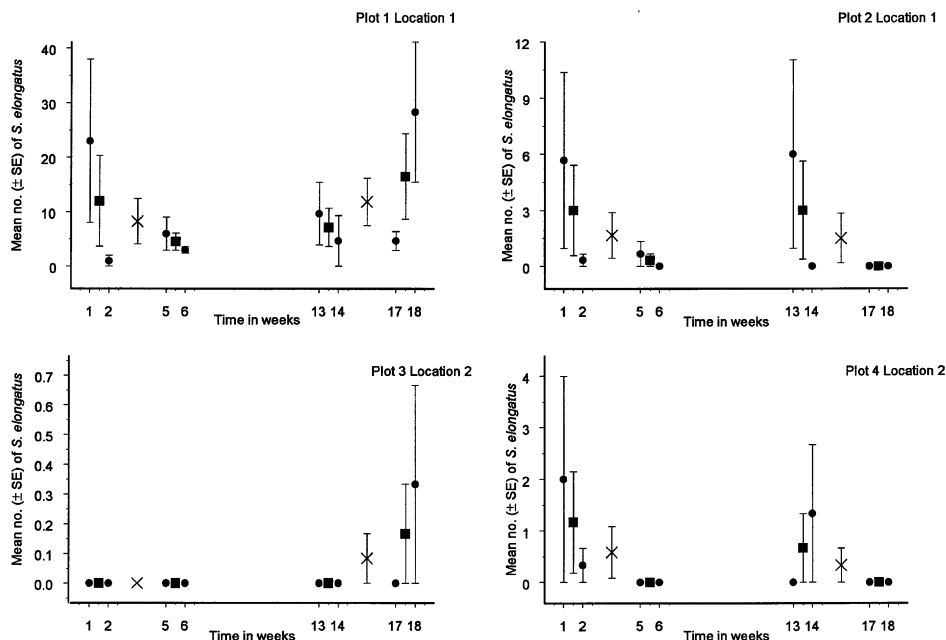


Fig. 2. Mean number ($\pm$ S.E.) of individuals of *S. elongatus* in the coralline turf at Locations 1 and 2 for each two consecutive weeks ($\bullet$), two consecutive months ($\blacksquare$) and two consecutive 3-monthly intervals ($\times$) ($n = 3$).

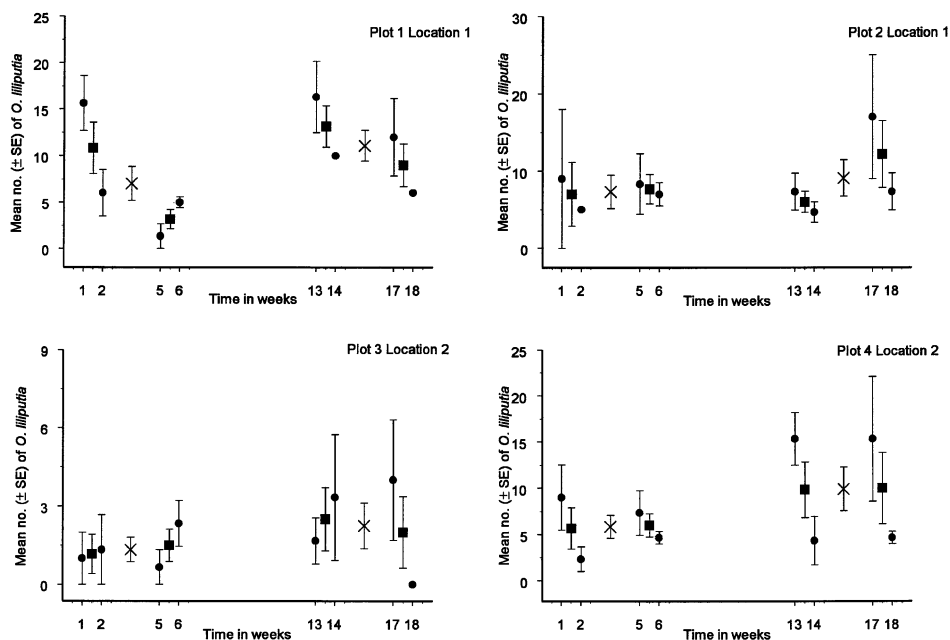


Fig. 3. Mean number ($\pm$ S.E.) of individuals of *O. liliputia* in the coralline turf at Locations 1 and 2 for each two consecutive weeks (●), two consecutive months (■) and two consecutive 3-monthly intervals (×) ($n=3$).

different patterns of change from plot to plot. *Eatonina rubrilabiata*, *Crassitoniella flammea* and *Eatoniella atropurpurea* showed significant interactions at the smallest scales ($P(L) \times W(1M(3M))$; $F_{8,64}=2.36$, $P<0.05$; $F_{8,64}=3.96$, $P<0.001$; $F_{8,64}=2.16$, $P<0.05$, respectively). It is clear that for *C. flammea*, this arose because of very large abundances in Plot 1, Location 1 compared to the other plots and a very large increase in abundance in this plot over only one weekly period, between Weeks 17 and 18 (Fig. 4). *E. rubrilabiata*, in contrast, showed relatively similar abundances in all plots and there was considerable weekly variation at a number of times this was measured. Patterns of change (increases or decreases) were not, however, in the same direction in the different plots (Fig. 5).

Finally, *Pseudopisinna gregaria gregaria* and *A. incidata* (in the coralline algae and in the sediment) showed changes over 3 months at the scale of plots ($P(L) \times 3M$; $F_{2,76}=5.19$, $P<0.01$; $F_{2,4}=11.12$, $P<0.05$; $F_{2,76}=4.04$, $P<0.05$, respectively; this is illustrated for *A. incidata* in the sediment in Fig. 6). *P. gregaria gregaria* and *A. incidata* in the sediment also showed a significant interaction between locations and weeks ($L \times W(1M(3M))$; $F_{4,76}=6.56$, $P<0.01$; $F_{4,76}=2.54$, $P<0.05$, respectively).

3.2. Components of temporal variation

Because for many species there were many significant differences among the plots, in addition to the significant time–plot and time–location interactions, it was clear that patterns of change in mean abundances of these species were not the same among the

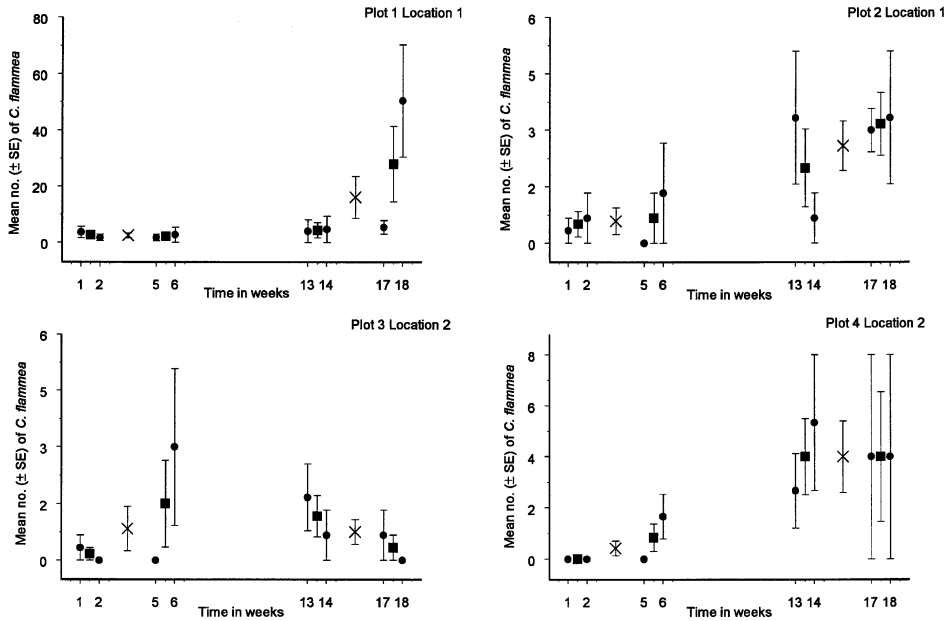


Fig. 4. Mean number ($\pm$ S.E.) of individuals of *C. flammea* in the coralline turf at Locations 1 and 2 for each two consecutive weeks (●), two consecutive months (■) and two consecutive 3-monthly intervals (×) ($n=3$).

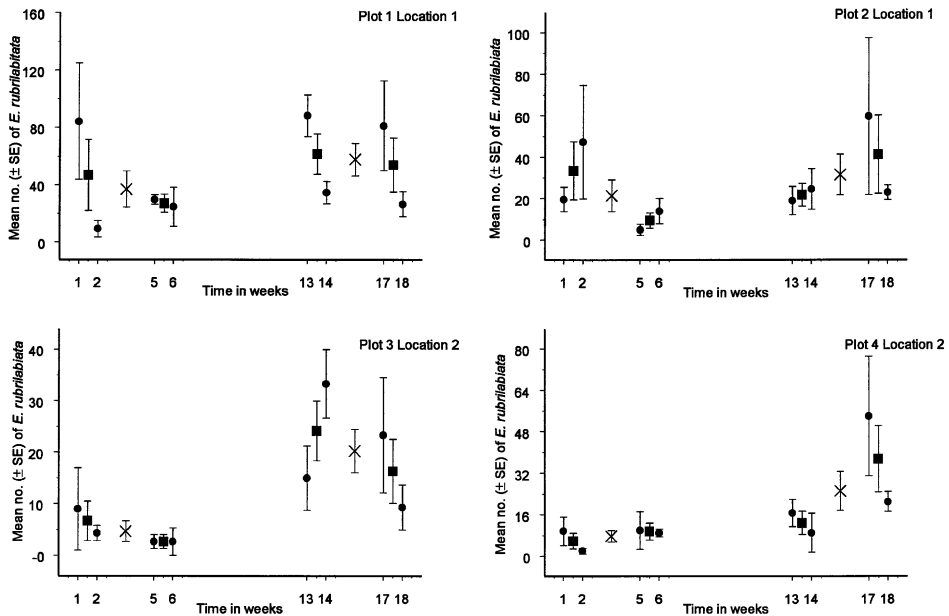


Fig. 5. Mean number ($\pm$ S.E.) of individuals of *E. rubriliabata* in coralline turf at Locations 1 and 2 for each two consecutive weeks (●), two consecutive months (■) and two consecutive 3-monthly intervals (×) ($n=3$).

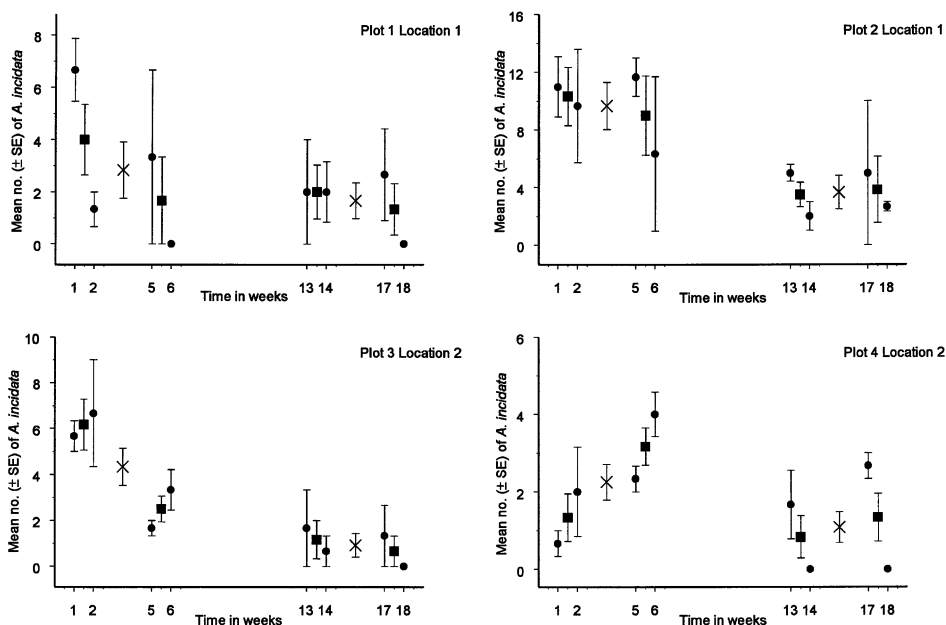


Fig. 6. Mean number ($\pm$ S.E.) of *A. incidata* in sediment at Locations 1 and 2 for each two consecutive weeks (●), two consecutive months (■) and two consecutive 3-monthly intervals (×) ($n=3$).

plots, even between the two plots in the same location. Thus, it was sensible to measure the contribution of each temporal scale to the total measures of variation for each plot separately (Table 2).

The first important result was that many of the components of variation calculated from the analyses of variance were negative. Thus, 17 of the 49 comparisons gave negative values for the variances between weeks, 28 gave negative values for the variances among months and 23 gave negative values for the variances between the 3-month periods. Therefore, for most analyses, the complete model for the analysis of variance for the three nested temporal scales was inappropriate and one or more of the scales had to be removed from the analyses and the temporal variances recalculated (the terms eliminated from the model are presented as zero variance in Table 2).

Second, for no species was there a consistent pattern of temporal variance among the different patches of habitat. Therefore, in one patch, *C. flammea* only showed positive variation at the scale of weeks. In two patches, there was positive variation at the scale of 3 months and in the third patch, variation was large at all temporal scales. Similarly, *P. gregaria gregaria* and *E. atropurpurea* showed relatively large measures of variation, but they too were variable among the patches. Other species, such as *S. luteofuscus* and *S. elongatus*, showed very small measures of variation at the different temporal scales.

No general trend in the temporal variation for any species was detected across the different plots (Anderson tests, $1 < Q^2 < 5.83$, $df=4$, all $P > 0.05$) or between locations (Anderson tests, $2.48 < Q^2 < 8.66$, $df=4$, all $P > 0.05$), nor between the algae and the sediment (for *A. incidata* and *S. luteofuscus*, Table 2). There were no patterns of greater

similarity in relative sizes of temporal variation between plots in the same location than among plots from different locations (Table 2), nor was there greater similarity among species of the same family than among species from different families (Table 1). For example, the two species of Eatoniellidae showed different patterns of temporal variation in the coralline turf, whereas *E. atropurpurea* and *E. rubrilabiata* had similar patterns of temporal variation.

Despite the spatio-temporal interactions, many species showed substantial differences in their abundances in the two different habitats. For example, in the coralline turf, *P. olivacea* was found in all weeks, but it showed a peak of abundance in Week 6. In contrast, in the sediment, this species only appeared during the first 3 weeks and the abundances were similar from week to week. Furthermore, in the coralline turf, all species were found at all times of sampling, while only *A. incidata* and *S. luteofuscus* were consistently found in the sediment throughout the whole period of sampling. Nevertheless, the other species were all found in the sediment at some times but in too few samples to allow analysis.

4. Discussion

Most analyses showed significant interactions between one or more temporal scales and the spatial scale of the plots. Therefore, the temporal patterns of variation in the abundances of these microgastropods were not the same between the plots of the same type of habitat that were spaced 10 m apart on the same shore. Neither were there any consistent patterns of change between locations that were 300 m apart, nor between two different types of intertidal habitat (coralline turf and sediment).

This inconsistency across the three temporal scales measured in this study shows the substantial spatio-temporal interaction in the abundances of these microgastropods.

There was not, as had been predicted, a general pattern of more temporal variability at the scale of weeks compared to 1 or 3 months. The components of variation, which measured the variance associated with each temporal scale independently, were not consistently larger at any of the three temporal scales. All species showed different magnitudes of variation at the different temporal scales from one plot to another. This contrasts with other studies of temporal variability in benthic assemblages, where small-scale variability is often larger than seasonal or yearly variability (e.g. Morrissey et al., 1992; Taylor, 1998; Underwood and Chapman, 1998a).

Within any plot, different species showed relatively different amounts of variation among the three temporal scales and again, in contrast to what was predicted, there was no close correlation between temporal patterns of abundance and taxonomic relationships of the different species. Therefore, although small microgastropods may be considered a “functional” group, temporal patterns of change, as were the spatial patterns of abundances (Olabarria and Chapman, 2001), are very different among species within this group.

Although patterns of variation differed among the plots, many of the components of variation from the analysis of variance model were estimated to be negative, particularly for the longer time-scales. This may occur because there is either positive correlation among times of sampling (underestimating error variances among samples) or negative

correlation within times (overestimating error variances within samples; Underwood, 1997). Samples were spaced in the field to get independent samples each time and there is no evidence from the patterns of changes (Figs. 1–6) that the data were non-independent at scales of weeks or months. In contrast, the magnitude and direction of change in any plot were unpredictable from week to week or month to month. It is, however likely that the model of the analysis of variance incorporating all three temporal scales was inappropriate for these species. For many species in many of the patches, there is little evidence of temporal variance compared to spatial variance (measured as residual variance). Therefore, the variation over a week was similar to that over 3 months, suggesting that either (1) long-term change in these populations needs more than 3 months to become apparent or (2) short-term changes occur more rapidly than over 1 week.

Despite asynchronous local fluctuations (i.e. interactions between plots and time), many species showed general differences in abundance between the two habitats. All species were more abundant and were found on each sampling occasion in the coralline turf. In the sediment, in contrast, microgastropods were only found in a few samples on few sampling occasions and were generally sparse in any sample. Therefore, for most species, it was not possible to compare temporal trends formally between the two habitats as had been planned. In addition, comparisons of temporal variability among populations with very different means tend to be confounded by variance to mean relationships, making such comparisons problematic (Gaston and McArdle, 1994). For those two species which were relatively abundant in each habitat, patterns of temporal variation were inconsistent from plot to plot in each of the two habitats. Therefore, although the sediment and coralline turf appear to provide different qualities of habitat as indicated by the very large average differences in abundance, this cannot be clearly related to the patterns of temporal change. In some habitats (Holling, 1988; Jokimäki et al., 2000), the positive correlation among the quality of habitat, abundances and patterns of temporal variability occurs because different processes act in different habitats. Alternatively, similar processes can operate at different rates in different habitats, creating different patterns of temporal variance (Steele, 1985). Whatever processes are causing changes in the abundances in these species need to be identified at the scale of small patches rather than broad categories of habitat.

Biotic processes, such as intra- or inter-specific competition (e.g., Underwood, 1984a; Fletcher and Underwood, 1987), predation (e.g. Choat and Kingett, 1982; Menge et al., 1985), availability of food (Underwood, 1984b), recruitment (e.g. Underwood and McFadyen, 1983; Dayton, 1984) and behaviour (e.g. Chapman and Underwood, 1994; Crowe, 1999; Norkko et al., 2001), have all been reported to have strong local influences on the patterns of abundance and distribution of marine benthic animals. Very little is known of the basic ecology of intertidal microgastropods on shores in Australia. Most of the species are direct developers (Beesley et al., 1998), which might suggest that different plots of habitat support relatively closed populations and therefore, these measures of temporal variation are estimates of variation of discrete populations (McArdle and Gaston, 1993).

Other similar organisms can, however, disperse as small adults or juveniles by drifting in the water column (e.g. Highsmith, 1985; Martel and Chia, 1991). There is also evidence that these species of small gastropods colonize patches of habitat as adults, presumably by

drifting (unpublished data). The hydrodynamic processes that might transport these species (e.g., current velocity, wind–wave activity, etc.) vary over scales of 10–100 m and over periods of days, weeks and months (Bell et al., 1997; Grant et al., 1997). If these species are transported among patches of habitat by physical processes, the populations are in fact open and temporal variances will include changes due to immigration/emigration, in addition to the processes of birth and death. Norkko et al. (2001) pointed out that dispersal may be more important than recruitment or mortality in the population dynamics of juvenile bivalves over small and mesospatial scales. Local interactions, such as predation or competition, might play an important role when dispersal rates are low, but are likely to be overwhelmed by immigration and emigration when there is great dispersal (Palmer et al., 1996).

Although these small gastropods might be subjected to passive transport and deposition like inanimate particles, as has been demonstrated for similar organisms (Turner et al., 1997), they might also actively select different patches of habitat, thereby altering patterns of colonization that might be created by physical processes only (e.g. Hannan, 1984; Butman, 1987; Snelgrove et al., 1993). If cues used for immigration are themselves patchy in time and space, this would add to the unpredictability of the patterns of abundance.

The results of this study illustrate the consequences for studies of temporal variation over larger scales when smaller temporal scales are not included (Morrisey et al., 1992). As an example, consider the changes in the abundance of *C. flammea* in Plot 1, Location 1 in the coralline turf (Fig. 4). One change in abundance over one of the four weekly periods examined (weeks 17–18) was so large that it caused a large measured variation at the scale of months and 3 months (Table 2). Yet, it was rapid change, i.e. a change at a small temporal scale. Second, it is clear that it cannot be assumed that temporal patterns observed at one place will be similar to those occurring at other places, even when the places are near each other. Care must be taken to ensure that relevant spatial and temporal scales are used to estimate density and its variance (Underwood, 1991).

Furthermore, if research is to assist in predicting, resolving or mitigating large-scale environmental problems, then the challenge of relating patterns and processes across space and time must be faced so that small-scale surveys and experiments can be related to conclusions at larger scales. Rates of reproduction, life cycles, scales of movement and differences in behaviour play important roles in how species respond to environmental heterogeneity at different spatio-temporal scales (Thrush et al., 1997). Before it is possible to develop sensible models that explain natural patterns of variation and change in species, it is necessary to have a good quantitative understanding of the scales at which patterns vary and, therefore, important processes are likely to operate.

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