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Habitat-associated variability in survival and growth of three species of microgastropods

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Three species of microgastropods, *Eatoniella atropurpurea*, *Eatonina rubrilabiata* and *Amphithalamus incidata*, are common in various habitats at mid to low levels on intertidal shores in New South Wales, Australia. These habitats include patches of sediment, pebbles and algal turf. These species are very patchy, varying in abundance within and among habitats at scales of centimetres to many metres. This study describes laboratory experiments which tested hypotheses about differences in mortality and growth rates for each species in three different habitats: sediment, pebbles and coralline turf. There was greater mortality in coralline turf without sediment for *E. rubrilabiata* and *A. incidata*, whereas *Eatoniella atropurpurea* showed a greater mortality in sediment. Moreover, *Eatonina rubrilabiata* had a faster rate of growth in sediment, whereas *Eatoniella atropurpurea* grew more rapidly in coralline turf. The different rates of mortality and growth for these species in different habitats provide mechanisms which may partially explain the patterns of abundance in the field.

INTRODUCTION

The structure of intertidal assemblages results from many interacting processes, including disturbances (e.g. Sousa, 1980; Littler et al., 1983; Chapman & Underwood, 1998), predation or competition (e.g. Dayton, 1971; Fairweather & Underwood, 1991) and settlement and/or recruitment (e.g. Dayton, 1975; Underwood & Fairweather, 1989). Understanding the structure and dynamics of these assemblages is, however, not possible without knowledge of the ecology of the component species (Hutchinson, 1961; Dayton, 1971). Studies of reproduction, recruitment, growth and mortality have provided great insight into many interactions that occur within and among the various trophic levels in assemblages (Boulding & Van Alstyne, 1993; Otway, 1994). In addition, studies of behavioural responses of individuals to other individuals or habitats provide an understanding of patterns of distribution of organisms and structure of intertidal assemblages (Creese, 1982; Chapman & Underwood, 1994).

Research in New South Wales, Australia, has focused on various aspects of ecology of large prosobranchs such as distribution of species (e.g. O'Gower & Meyer, 1971), reproduction (e.g. Underwood, 1974), growth and mortality (e.g. Fletcher, 1984; Underwood, 1984a) or behaviour (e.g. Chapman & Underwood, 1994). The same degree of ecological understanding is not available for microgastropods (i.e. gastropods with adult size approximately <2 mm), even though they are abundant and widespread on intertidal shores (Wigham, 1975; Southgate, 1982; Borja, 1987; Grahame & Hanna, 1989). This is particularly true for intertidal shores in Australia (Olabarria & Chapman, 2001), where most research has been taxonomic or anatomical (Beesley et al., 1998).

Although field experiments in intertidal habitats are increasingly important, most have focused on the largest components of the fauna (see review Underwood et al., 1983). Because many small species live in cryptic habitats (e.g. algal mats), the logistics of doing experiments which require growth measures, survival or behaviour of individual animals, are very difficult in the field. Despite limitations (Chapman, 2000), laboratory experiments have therefore often been used to imply processes that determine patterns of abundance in the field (e.g. Fenchel, 1976; Underwood & McFadyen, 1983; Levinton et al., 1985).

Three common microgastropods on intertidal shores of New South Wales are *Eatoniella atropurpurea* (Frauenfeld, 1867), *Eatonina rubrilabiata* Ponder & Yoo, 1980 and *Amphithalamus incidata* (Frauenfeld, 1867). Populations of these species are found at mid- to low-shore levels in different habitats, such as sediment, on pebbles or in algal turf. All three species are particularly abundant in coralline turf (i.e. algal beds composed primarily of *Corallina officinalis* Linnaeus, often containing patches of sediment), although the latter two are also quite abundant in patches of sediment. All three species vary in abundance among patches of habitats at very small spatial scales (Olabarria & Chapman, 2001). In addition, adults of the three species rapidly colonize new boulders in boulder fields (M.G.C., unpublished data).

A number of different general models can explain these different patterns of distribution, for example, different rates of recruitment or different survivorship among habitats. We tested the models that: (i) all species are more abundant in algal turf than in sediment because they survive better in the same habtat; (ii) *E. rubrilabiata* and *A. incidata* may survive better in sediment than does *Eatoniella atropurpurea*, hence their relative greater abundance in this habitat in comparison to this latter one; and (iii) all three species may show different rates of survival in different habitats because they grow faster in some habitats than in others. This study describes laboratory experiments to test hypotheses from these models. Specific predictions are made (see Material and Methods) about survivorship and rate of growth of each species in different habitats (i.e. pebbles, sediment and coralline turf).

MATERIALS AND METHODS

Collection of samples

Samples of *Eatoniella atropurpurea*, *Amphithalamus incidata* and *Eatonina rubrilabiata* were collected from algal turf at the mid-shore level on one shore (described in Olabarria & Chapman, 2001) in the Cape Banks Scientific Marine Research Area, New South Wales in January 2000 and May 2000.

In the first experiment, samples of rock chips (~1–2 cm deep, 5 cm diameter) with turf were collected by chiselling from a patch of mid-shore coralline turf. Sediment and pebbles of similar size to the rock chips with a fine cover of filamentous algae were collected from nearby sites at the same level on the shore. All samples were taken to the laboratory, examined under a microscope and all visible organisms removed. Each sample, a chip of rock with coralline algae, a pebble or approximately 2 cm of sediment, was then placed in a transparent pot (6.5 cm diameter, 8 cm high). These were then covered with a 200-μm mesh, and maintained with a continuous flow of seawater.

In the second experiment, the coralline turf was collected using a 6-cm diameter corer. For treatments in which turf without sediment was needed, the sediment was washed out of the turf using running seawater. Both the algae and the sediment were defaunated, removing all visible organisms under a microscope, before being placed into the transparent pots.

Experiment 1

This experiment evaluated whether these species would survive and grow under laboratory conditions and tested the hypothesis that each species would show greater survival and faster growth on the chips of rock covered with coralline algae than on the other two habitats.

Eight animals (four adults and four juveniles where possible; in most of the pots) of each species were placed in each pot; N=10 pots for each species on each substratum. The pots were placed in five tanks, with two replicates of each treatment for each species in each tank. The experiment was done under 12 h L:12 h D. The duration of the experiment was chosen to be 28 days based on previous studies of growth rates of small gastropods carried out in the laboratory, which showed measurable growth after a few weeks (Underwood & McFadyen, 1983; Boulding & Van Alstyne, 1993).

At the end of the experiment, the length of each shell was measured from the apex to the lower lip on the opercular side, using a binocular microscope fitted with an eyepiece micrometer (measurement error 0.001 mm). The rate of growth of each mollusc was calculated as:

$$R = \ln (L_t/L_0)/t \qquad (1)$$

where R is the instantaneous rate of growth per unit length, L_t and L_0 are shell lengths at times t and 0, respectively. This model assumes exponential growth and is preferred to alternatives because it allows accurate comparison of individuals of slightly different initial sizes (Denley & Underwood, 1979). Individual snails were not marked and, therefore, all calculations (values of L_0) were based on the mean size of animals for each pot.

Data of mortality and rates of growth were analysed using analysis of variance.

Experiment 2

Using the data obtained from experiment 1 *A. incidata* and *Eatonina rubrilabiata* survived better in sediment, although in the field they are more abundant in coralline turf (Olabarria & Chapman, 2001) and the observations that (i) much of the coralline turf in the field contains sediment (personal observation); and (ii) *Eatoniella atropurpurea* was mainly found in coralline turf, a second experiment was done. This tested the predictions that: (i) *A. incidata* and *Eatonina rubrilabiata* would have greater survival and a faster rate of growth in sediment, whether or not this occurred with coralline algae; and (ii) *Eatoniella atropurpurea* would have greater survival and rates of growth in coralline algae, whether sediment was present in the algae or not.

This experiment used three different habitats: (i) sediment that had been removed from coralline turf; (ii) coralline turf with associated sediment; and (iii) coralline turf from which the sediment had been removed. The turf was collected using cores (see earlier), taken to the laboratory and then washed with seawater under high pressure to eliminate most of the organisms. This also removed the sediment from the cores. The sediment was sieved through 60-μm mesh and examined under a microscope to remove all visible organisms. Subsequently, the cores were treated in one of three different ways, depending on the type of substratum needed: (i) the sediment was defaunated, the algae scraped from the surface of the core and the sediment was placed on the core; (ii) the algae and sediment were defaunated and the sediment was put back into the coralline algae on the core; (iii) the sediment was eliminated and coralline algae was defaunated.

The samples were then put into separate pots (N=10) and maintained with a continuous flow of seawater. In this experiment, the animals (eight per replicate) were individually marked using permanent markers. Once the shell was dry, a colour code of up to four dots of permanent marker were carefully applied to each shell under a dissecting microscope. Six colours were used to mark the snails: blue, red, yellow, green, pink and orange. Snails were immersed in seawater as soon as the paint was dry and any that did not emerge within two min were discarded.

Because of the large mortality in experiment 1, the pots were assigned at random in the experimental area and re-randomized into different positions once a week to minimize any potential effects of position on survival.

Rates of growth and mortality after 35 days (see above, experiment 1) were analysed using analysis of variance.

RESULTS

Experiment 1

There were significant differences in mortality after 28 days among the different habitats (Table 1). Each species

Table 1. *Analysis of mortality of* Amphithalamus incidata *and* Eatonina rubrilabiata *in three different habitats (N=10). Species (two levels) and habitat (three levels) are fixed factors; tank (five levels) is a random factor. Variances were homogeneous (Cochran's test,* P>*0.05). Student–Newman–Keuls tests were used to identify significant differences among means (see text).*

Source	df	MS	*F*-ratio	*P*
Sp	1	0.15	0.02	0.907
T	4	2.98	0.76	0.562
Hb	2	40.72	10.32	0.006**
Sp×T	4	9.82	2.49	0.064
Sp×Hb	2	1.25	0.14	0.870
T×Hb	8	3.95	1.00	0.457
Sp×T×Hb	8	8.85	2.24	0.062
Residual	30	3.95		

Hb, habitat; Sp, species; T, tank; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

Table 2. *Analysis of rates of growth of* Amphithalamus incidata *and* Eatonina rubrilabiata *in three different habitats (rate of growth is in mm* 10^3*). Because there was large mortality in many pots, rates of growth were from those pots with >50% survival (N=2). Tank (two levels) is a random factor nested in species (two levels, fixed) and habitat (three levels, fixed). Variances were homogeneous (Cochran's test,* P>*0.05). Student–Newman–Keuls tests were used to identify significant differences among means (see text).*

Source	df	MS	*F*-ratio	*P*
Sp	1	24.00	8.47	0.021*
Hb	2	1.04	0.37	0.082
T (Sp×Hb)	6	2.83	0.35	0.546
Sp×Hb	2	3.88	1.37	0.075
Residual	12	8.08		

Hb, habitat; Sp, species; T, tank; *, $P<0.05$, **, $P<0.01$, ***, $P<0.001$.

showed smaller mortality in sediment than in coralline turf or on pebbles (Student–Newman–Keuls (SNK) tests, $P<0.05$; Figure 1A). Each species also showed slightly smaller average mortality on pebbles although the differences were not significant (Figure 1A).

There were significant differences in rates of growth among species (Table 2), but not among the different habitats. *Eatonina rubrilabiata* grew faster than *Amphithalamus incidata* (Figure 1B). The two species grew slightly faster in sediment than in coralline turf or on pebbles although the differences were not significant.

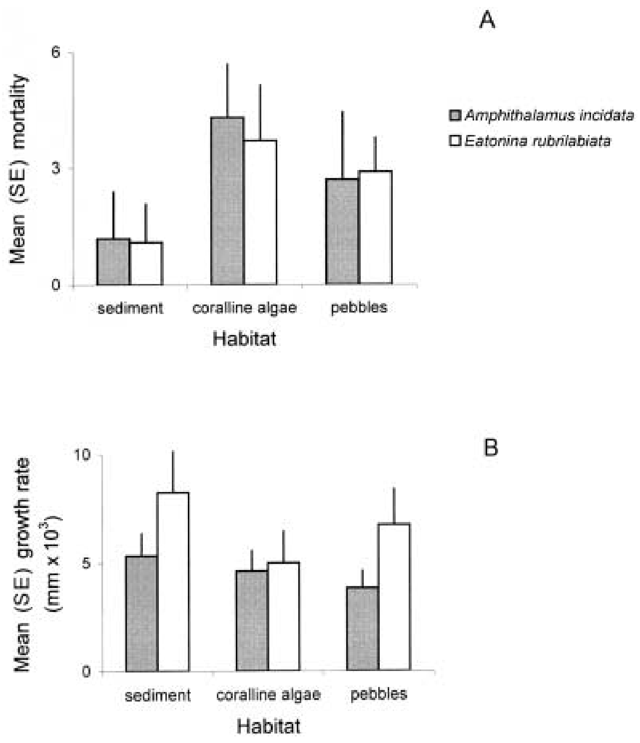

Figure 1. Results from experiment 1. (A) Mean mortality of *Eatonina rubrilabiata* and *Amphithalamus incidata* in three different habitats (N=10); (B) mean rate of growth of *E. rubrilabiata* and *A. incidata* in (N=6).

Experiment 2

Eatonina rubrilabiata and *A. incidata* had significantly smaller mortality in sediment and coralline algae plus sediment, than in coralline algae by itself (SNK tests, $P<0.05$; Figure 2A; see interaction in Table 3). *Eatoniella atropurpurea*, in contrast, showed significantly smaller

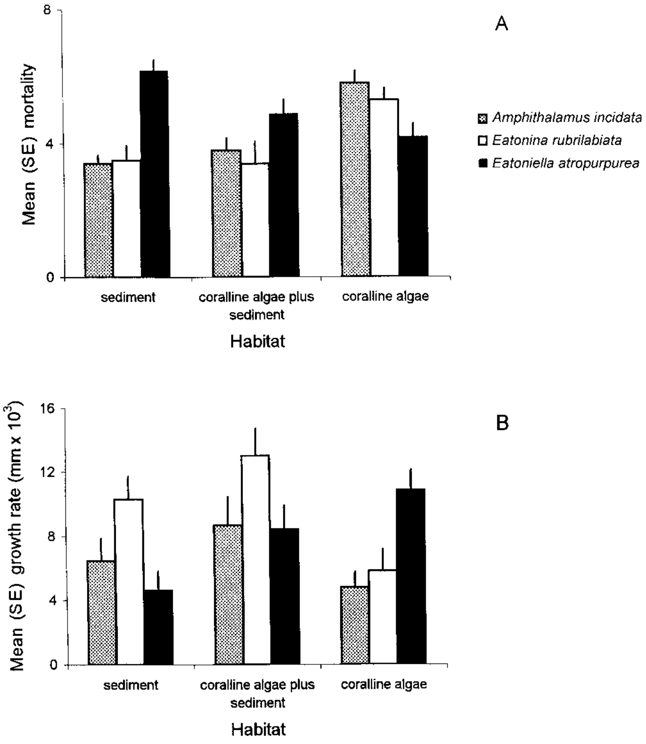

Figure 2. Results from experiment 2. (A) Mean mortality of *Amphithalamus incidata*, *Eatonina rubrilabiata* and *Eatoniella atropurpurea* in three different habitats (N=10); (B) mean rate of growth of *A. incidata*, *Eatonina rubrilabiata* and *Eatoniella atropurpurea* in three different habitats (N=18).

Table 3. *Analysis of mortality of* Amphithalamus incidata, Eatonina rubrilabiata *and* Eatoniella atropurpurea *in three different habitats (N=10). Species (three levels) and habitat (three levels) are fixed factors. Variances were homogeneous (Cochran's test,* $P>0.05$*). Student–Newman–Keuls tests were used to identify significant differences among means (see text).*

Source	df	MS	*F*-ratio	*P*
Sp	2	8.63	4.70	0.012*
Hb	2	8.93	4.87	0.011*
Sp×Hb	4	14.67	7.99	0.000***
Residual	81	1.84		

Hb, habitat; Sp, species; *, $P<0.05$, **, $P<0.01$, ***, $P<0.001$.

mortality in coralline algae, with or without sediment, than in sediment alone (SNK tests, $P<0.05$; Figure 2B). In addition, differences in rates of mortality among the three species depended on the habitat (Figure 2A). For example, *A. incidata* and *Eatonina rubrilabiata* had the greatest mortality in coralline algae by itself, whereas *Eatoniella atropurpurea* survived best in coralline algae.

The initial size of these animals did not vary significantly among treatments for each species, i.e. there was no interaction ($F_{4,\,81}$=0.43, $P>0.05$). Because the rates of growth of individuals did not differ significantly among pots in each treatment ($F_{81,\,630}$=1.05, $P>0.05$) and to balance the data (the minimal number of individuals which survived in one of the habitats was 18), 18 randomly-selected individuals of each species from each substratum were used to test the hypothesis of differences in rates of growth among habitats for each species.

Rates of growth varied interactively between species and habitat (Table 4). *Amphithalamus incidata* grew at similar rates among the different habitats (SNK tests, $P<0.05$; Figure 2B). *Eatonina rubrilabiata*, in contrast, grew significantly faster in sediment, with or without coralline algae, than in algae alone (SNK tests, $P<0.05$) and *Eatoniella atropurpurea* grew faster in coralline algae, with or without sediment than in sediment alone (SNK tests, $P<0.05$).

Table 4. *Analysis of rates of growth of* Amphithalamus incidata, Eatonina rubrilabiata *and* Eatoniella atropurpurea *in three different habitats (N=18) (rate of growth is in mm 10^3). Species (three levels) and habitat (three levels) are fixed factors; pot was not a significant factor (see text) and was consequently eliminated from this analysis. Variances were homogeneous (Cochran's test,* $P>0.05$*). Student–Newman–Keuls tests were used to identify significant differences among means (see text).*

Source	df	MS	*F*-ratio	*P*
Sp	2	127.94	3.38	0.036*
Hb	2	151.39	4.00	0.020*
Sp×Hb	4	166.52	4.40	0.002**
Residual	153	37.82		

Hb, habitat; Sp, species; *, $P<0.05$, **, $P<0.01$, ***, $P<0.001$.

DISCUSSION

These experiments clearly showed differences in mortality and rates of growth among the different types of habitat for the three species. *Eatonina rubrilabiata* and *Amphithalamus incidata* survived better in sediment than in algal turf without sediment or on pebbles coated with a fine cover of filamentous algae, whether the sediment was with or without algae. *Eatoniella atropurpurea*, in contrast, showed greater mortality in sediment, surviving better in coralline turf, whether sediment was present in the turf or not. Furthermore, *Eatonina rubrilabiata* grew faster in sediment, whereas *Eatoniella atropurpurea* grew faster in coralline algae. *Amphithalamus incidata*, in contrast, grew at similar rates on all three habitats. In general, all species showed greater rates of survival in those habitats where they showed greater rates of growth. These results contrast with their distribution among habitats in the field, where all three species are more common in algal turf than in sediment (Olabarria & Chapman, 2001).

The availability of food is one of the most important factors affecting the rates of growth and survival of different species of gastropods (Sutherland, 1970; Creese, 1981; Underwood, 1984a). Therefore, the patterns of survival and growth of *Eatonina rubrilabiata*, *A. incidata* and *Eatoniella atropurpurea* in different habitats could be explained in terms of availability of food. Although there are no quantitative data on feeding in these species, all three species are assumed to be microphagous feeders, feeding on diatoms, micro-algae and detritus (Beesley et al., 1998). Whether they do eat the same range of food is not, however, known.

Although the three species have taeniglossan radulae, there are small differences in the structure of these which could be related to different types of feeding. Thus, the rachidian tooth of *E. atropurpurea* is large and square, with three cusps with strong basal processes and lateral and marginal teeth with few cusps. In addition, this species has jaws with chitinous rods (Beesley et al., 1998). *Eatonina rubrilabiata* and *A. incidata* have radulae with smaller central teeth with small obsolete cusps and lateral and marginal teeth with more cusps. Snails with pluricuspid teeth such as these are more likely to be grazers of micro-algae and filamentous algae, whereas herbivores with fewer cusps and robust teeth are more likely to consume tougher algae, including articulated corallines (Steneck & Watling, 1982). Thus, *Eatoniella atropurpurea* could use its radula to scrape microalgae and feed on the branches of the coralline turf, thus explaining its greater rates of survival and growth when maintained in algae. *Amphithalamus incidata* and *Eatonina rubrilabitata* could use their radulae to feed on detritus and diatoms in the sediment, thereby explaining their greater rates of survival and growth in this habitat.

Coralline turf and other complex biogenic structures can be a trap for sediment and food (Taylor & Littler, 1982; Grahame & Hanna, 1989; Akioka et al., 1999). Therefore, microgastropods feeding on micro-algae associated with sediments may obtain adequate food from the sediment in coralline turf. On the relatively exposed shore used in this study, the sediment is rather coarse-grained and loosely packed. This may make it susceptible to disturbances from movement of water, which can limit production of micro-algae (Riznyk et al., 1978; Varela & Penas, 1985). Grain-size can be a limiting factor for primary production because of the strong attachment of the microphytobenthos to coarse sediment (Barranguet et al., 1998). Factors such as these may prevent micro-algal grazers from occupying patches of sediment in the field. In these laboratory experiments, the sediment was not disturbed and there was continuous gentle flow of water providing nutrients and adequate light, any of which may have increased productivity, or provided greater opportunity to feed.

Coralline turf can also provide different microhabitats because it is an heterogeneous substratum, which may offer refuge from predation (Hassell & May, 1973; Murdoch, 1977; Edgar et al., 1994). Heterogeneous habitats can, in contrast, provide shelter for predators, thus increasing rates of predation around the source of heterogeneity (Fairweather, 1988; Underwood, 1999). Coull & Wells (1983), in field and laboratory experiments, showed complex habitats offered a significant refuge for meiofauna from predation by fish. Therefore, algal turf may be an important refuge from predation for the microgastropods in this study, but, as yet, any predators of these species have not been identified.

Processes that can influence the distribution of invertebrates, such as predation (Fairweather & Underwood, 1991; Osman & Whitlatch, 1996), competition (Underwood, 1984b; Fletcher & Underwood, 1987), morphology, life history (Boulding & Van Alstyne, 1993), behaviour (Chapman & Underwood, 1994) are very complex and interactive (e.g. Menge, 1992, 1997). Most advances in understanding of these complex interactions have been obtained from experimental studies of relatively large animals (but see Creese, 1981; Fairweather et al., 1984; Boulding & Van Alstyne, 1993). It is reasonable to assume that similar processes operate to determine the distribution of small species, although the scales over which they operate are likely to be smaller (Lawton, 1990; Cotgreave, 1993). Therefore, more understanding of the ecology of these species will also depend on our ability to use manipulative experiments to test specific hypotheses (Underwood, 1990). Although field experiments provide more reliable information about ecological processes (Crowe & Underwood, 1998), they may not be feasible for tests of many hypotheses when the animals are small and live in cryptic habitats. In this case, laboratory experiments may be the only practical approach, although a combination of laboratory and field experiments would be more desirable (Chapman, 2000).

The present study has provided data about mortality and growth of three common microgastropods, which can be used with previous data on patterns of distribution in the field (Olabarria & Chapman, 2001) to develop further models on the processes that most affect these species. It has also been demonstrated that these species survive and grow in laboratory conditions and that individuals can be marked and tracked through time in different types of habitat. Nevertheless, in the field these parameters are likely influenced by many interacting variables. Further tests of natural spatio–temporal change in their populations, together with ongoing laboratory tests of hypotheses of habitat-choice and competition, will contribute important information to the ecology of these common, but poorly understood, gastropods.

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