

Microhabitat Segregation of Co-Existing Gastropod Species

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Abstract. The formation of aggregations of four co-existing species of nerite gastropod was investigated on a tropical rocky shore in north Queensland, Australia. The results demonstrated that all species formed mono-specific aggregations, each of which had a strong fidelity for aggregating within a particular microhabitat type. Hence there was a distinct segregation of microhabitat usage among the four co-existing, ecologically similar species, and this segregation did not differ spatially or temporally. These results indicate that spatial and temporal fluctuations of abiotic conditions had little impact on the formation of aggregations, and that factors such as competition for microhabitats among species may play a greater role in the formation and maintenance of intertidal gastropod aggregations than previously thought.

INTRODUCTION

During periods of emersion, many intertidal rocky shore gastropods form multi-layered aggregations or clumps within particular microhabitats such as cracks/crevices in the rock surface. For species of the genus *Nerita* Linnaeus, 1758, there is considerable evidence (see Vermeij, 1973; Vannini & Chelazzi, 1978 and references therein; Garrity, 1984; Garrity & Levings, 1984) supporting the notion that aggregating behavior assists in alleviating the potentially lethal increases in temperature, and associated risks of desiccation, to which intertidal rocky shore gastropods are subject during low tides, particularly during summer.

The degree to which different species exhibit aggregation behaviors is dependent on local environmental conditions. For any one species, the prevalence of aggregations, and the intertidal distribution of those aggregations, will be dependent upon local patterns of water movement and availability of food (Rohde & Sandland, 1975; Vannini & Chelazzi, 1978; Branch, 1981); presence of conspecifics (Chapman, 1999; Davies & Bechwith, 1999); size of any individual animal within the population (Levings & Garrity, 1983; Chelazzi et al., 1984, 1985), and aspects of the habitat (Rohde & Sandland, 1975; Raffaelli & Hughes, 1978; Vannini & Chelazzi, 1978; Branch, 1981; Garrity & Levings, 1984; Chapman & Underwood, 1994; Crowe & Underwood, 1998). However, it remains to be seen whether aggregation behaviors are affected by seasonal fluctuations in abiotic conditions.

The formation of aggregations is facilitated by each species' ability to utilize direct visual cues (Vannini & Chelazzi, 1978; Chelazzi & Vannini, 1980) and by their ability to detect and follow substrate markings present in the mucus trails of conspecifics (Cook 1969, 1971; Chelazzi et al., 1983; Rafferty, 1983; Gilly & Swenson, 1978; Chapman, 1999; Davies & Bechwith, 1999). By having

a strong homing preference and following conspecific mucus trails, species do not occupy suitable sites at random but show a strong affinity for aggregating in particular microhabitats through time (Chelazzi et al., 1985). Although the formation of conspecific aggregations and their affinity for particular microhabitats has been recorded in *Nerita textilis* Gmelin, 1791 (Chelazzi et al., 1985 and references therein), the generality of this microhabitat loyalty across other species of *Nerita* is unknown.

Furthermore, it is also unknown whether the presence of more than one species of *Nerita* within a habitat affects the homing behavior of individual species and therefore influences the aggregation behavior of individuals within the population. Just as intraspecific competition affects the layering of individuals within monospecific aggregations (Garrity & Levings, 1984), so too could interspecific competition affect the behaviors of co-existing ecologically similar species. Each species may utilize unique aggregation cues and therefore form monospecific aggregations. Alternatively, aggregation cues may be the same among closely related species, which could result in a number of species aggregating together.

This study was carried out on a sheltered rocky shore in north Queensland where four nerite species co-exist in the mid and lower intertidal regions (unpublished data). The microhabitats in which these species aggregate during periods of emersion include the vertical surfaces of rocks, around the base of rocks, and within cracks and crevices on the rock surfaces. The specific aims of this study were to determine (1) whether aggregations within these microhabitats were mono-specific or if they consisted of a mixture of species; (2) whether any particular species was consistently found to occur in only one microhabitat type; (3) whether there was any difference in the structure of the aggregations formed in the low and mid-intertidal regions; and finally (4) whether there was

any temporal (between summer and winter) consistency in the observations made.

METHODS

Study Site

This study was carried out on a sheltered rocky shore in Townsville, north Queensland, Australia (19°11'S, 146°46'E). The intertidal topography of the shore varies considerably; large granite outcrops are prominent within the upper intertidal regions (above Mean High Water Neap, MHWN) but graduate into a boulder field below MHWN. Boulders vary in size from < 0.5 m up to approximately 2 m across the long axis.

The surfaces of boulders are fissured by cracks and crevices. For this study a crack was defined as a fissure in the rock surface which measured greater than 20 cm long, 5 cm wide, and 2 cm deep. A crevice was defined as a fissure in the rock surface which also measured greater than 20 cm long, but less than 5 cm wide and 0.5 cm–2 cm in depth. Although these microhabitats are quite similar, a distinction between them is necessary, as the differing depths and widths of each would result in different water retention capabilities within each microhabitat. Because decreasing the risk of desiccation is a strong force driving aggregation behaviors of tropical nerites (Vannini & Chelazzi, 1978 and references therein; Garrity, 1984; Garrity & Levings, 1984), the difference between these microhabitats may affect the frequency of use of either microhabitat by members of the nerite population inhabiting this shore.

Sampling Design

During periods of emersion, individuals of *Nerita chamaeleon* Linnaeus, 1758, *N. costata* Gmelin, 1791, *N. polita* Linnaeus, 1758, and *N. undata* Linnaeus, 1758, were typically observed forming multilayered aggregations in any of four microhabitats on the boulder surfaces: (1) cracks or (2) crevices present on the surfaces of the boulders, or on (3) the vertical surfaces, or (4) around bases of boulders at the rock-sand interface.

To examine whether or not the aggregations within any of these four microhabitats were mono-specific, 40 boulders greater than 1 m wide, and on which all four microhabitats were present, were identified from both the mid and lower intertidal regions. Twenty boulders from each intertidal area were then randomly selected from those 40. On each boulder I recorded the occurrence of species within one representative microhabitat of each of the four types. Hence, from both the mid and the lower intertidal regions I recorded the occurrence of species within 20 replicate cracks, 20 replicate crevices, 20 replicate vertical walls, and 20 replicate base areas.

In each microhabitat, samples were taken by laying a rectangular quadrat (10 cm wide × 20 cm long) over a

microhabitat and recording the abundances of species which occurred within the quadrat. The use of a quadrat provided consistency of sampling effort among each microhabitat on the same boulder, and among boulders.

To determine whether there was any temporal consistency in the observations, sampling was first conducted during the summer (January) and again repeated during the winter (June) of 1997. As such, a total of 20 replicates were sampled from each microhabitat type in each intertidal region (2 of) on two different sampling occasions.

Statistical Analysis

To determine if there was any intertidal or seasonal difference in the average number of species present in a microhabitat type, an Analysis of Variance (ANOVA) was used. An ANOVA was also used to determine if there were any significant differences in the mean numbers of each species occupying mid and low intertidal levels between summer and winter. To examine the spatial and temporal variability of the compositions sampled within each of the four microhabitats non-Metric Multidimensional Scaling (nMDS), K-Means clustering ($K = 4$) and SIMPER analysis (Clarke, 1993) were applied to the average number of each species occurring within each microhabitat for the two spatial and temporal scales. Identification of whether any species had an affinity for a microhabitat type or an intertidal level was also achieved using SIMPER. Analyses were applied to raw data, and the Bray Curtis distance measure was used to calculate the dissimilarity matrix for the nMDS.

RESULTS

There were no significant differences in the average number of species occurring in each of the four microhabitats between summer and winter or between the mid and lower intertidal levels (ANOVA, $n = 16$, $df = 1$, $P > 0.743$, $P > 0.948$, respectively). Each microhabitat was typically occupied by only one species regardless of season or intertidal level (Figure 1).

For each species (across all microhabitats) the average number of individuals sampled from the mid and lower intertidal regions did not differ significantly (ANOVA, $n = 40$, $df = 1$, $P > 0.3$, $P > 0.575$, $P > 0.784$, $P > 0.471$ for *N. chamaeleon*, *N. costata*, *N. polita*, and *N. undata*, respectively). However, there were significant differences in the average number of individuals sampled on each trip for all species except *N. undata*. Significantly more *N. chamaeleon*, *N. costata*, and *N. polita* were sampled during summer than during winter (ANOVA, $n = 40$, $df = 1$, $P < 0.001$, $P < 0.05$, $P < 0.05$, respectively; Figure 2).

The relative abundance of species present within each microhabitat was distinct from that of any other microhabitat. This is seen by the separation of the composition and abundance information into microhabitat-specific

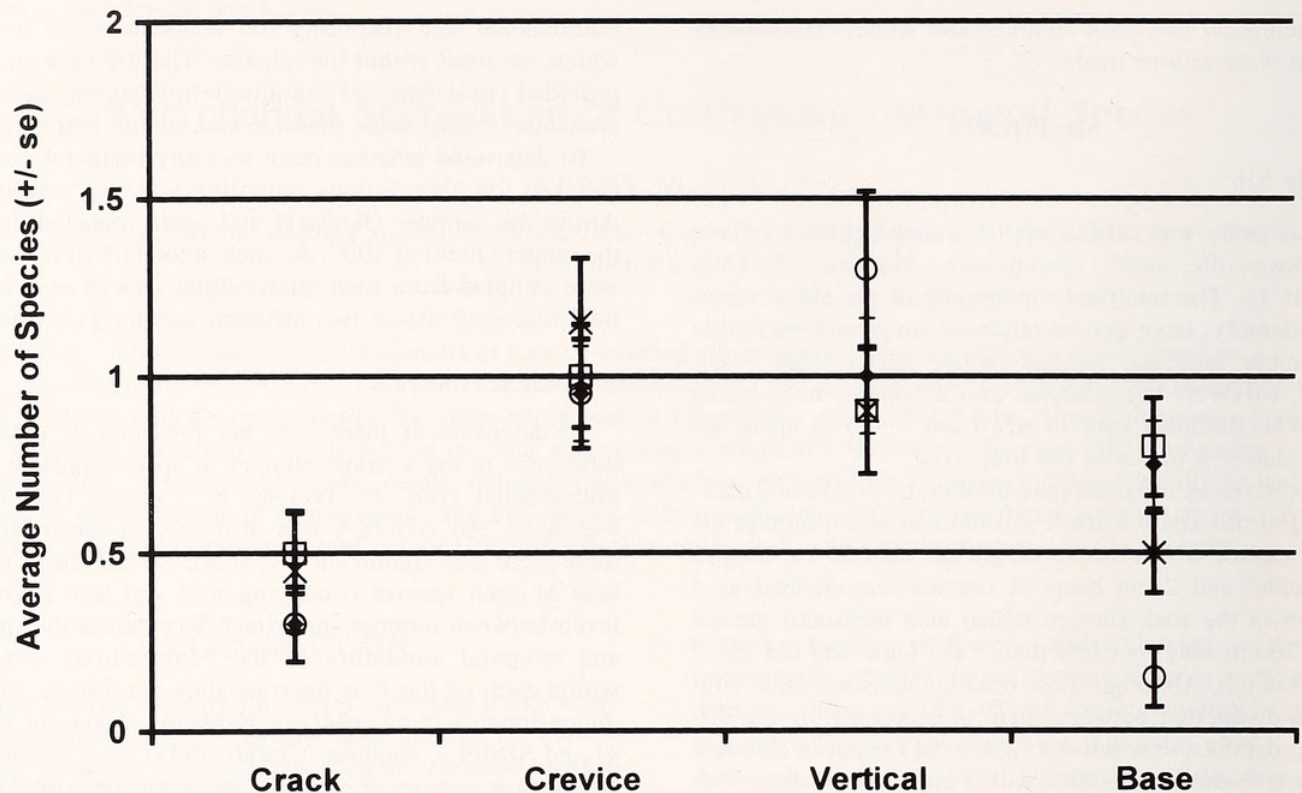


Figure 1. The average number of species occurring in each microhabitat (± 1 SE) in the mid and lower intertidal levels during summer and winter; (◆) mid intertidal level summer sample, (□) lower intertidal level summer sample, (*) mid intertidal level winter sample, (○) lower intertidal level winter sample.

clusters by the nMDS (Figure 3). However, within any one microhabitat the composition did not differ significantly between either intertidal level or season. The only exception was that the composition inhabiting cracks in the lower intertidal region during summer was most similar to that inhabiting crevices from both intertidal areas on both sampling occasions, as seen by the clustering of "sl crack" with all "crevice" samples on the ordination (Figure 3).

The relative contributions of each species, as determined by SIMPER analysis, to the structure of the ordination solution are shown in Table 1. This analysis indicates that *N. costata*, *N. polita*, and *N. undata* each had a strong affinity for a particular microhabitat. This is further supported by examining the relative contribution of each species to the total number of individuals found in each microhabitat (Figure 4). *Nerita costata* predominantly occupied the vertical surfaces of boulders, *N. polita* was typically found around the bases of boulders, and *N. undata* was mainly found in the crevices of boulder surfaces (Figure 4). Conversely, *Nerita chamaeleon* was present in consistent numbers in cracks and crevices, and was also found on the vertical walls, but not around the bases of boulders.

The affinity of each species for a different microhabitat regardless of season or intertidal level is responsible for the clear separation of the microhabitat types on the or-

dination (Figure 3). The clustering of "sl crack" with the "crevice" samples is due to the composition of cracks at this sampling time being most similar to the composition of crevices at any sampling time. During summer, both *N. chamaeleon* and *N. undata* were present in cracks in the lower intertidal region. However, in all other samples this microhabitat was typically only occupied by *N. chamaeleon*, whereas crevices were always occupied by both species. Although two species were found to occupy crevices, they did not cohabit in any one crevice, but each species formed mono-specific aggregations in separate crevices (Figure 1). No other spatial or temporal differences in the composition of each microhabitat were found. The dominance of each microhabitat by a particular species and the occurrence of *N. chamaeleon* in a number of microhabitats were consistent patterns between the two intertidal levels and between summer and winter.

DISCUSSION

The four species of nerite gastropods examined during this study each formed mono-specific aggregations on this shoreline. The formation of these mono-specific aggregations occurred in both the upper and lower intertidal regions and during both summer and winter. As such, this behavior was independent of any intertidal gradient and/or seasonal variability of abiotic conditions.

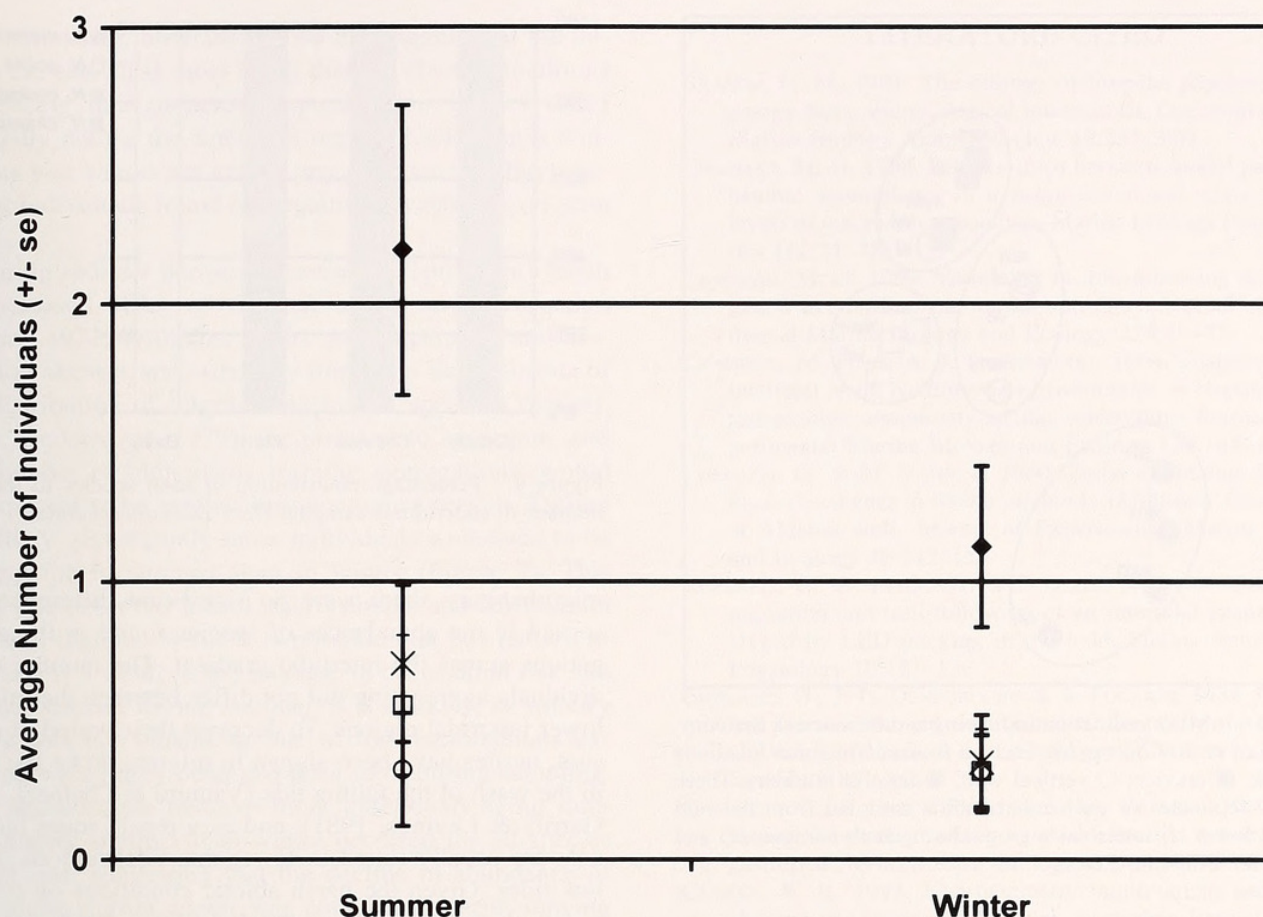


Figure 2. The average number of individuals (± 1 SE) of each species during summer and winter across all microhabitat types and both intertidal levels. (♦) *Nerita chamaeleon*, (□) *N. costata*, (*) *N. polita*, (○) *N. undata*.

Intertidal gastropods form aggregations to alleviate their exposure to potentially lethal abiotic stresses during periods of emersion (Moulton, 1962; Willoughby, 1973; Vermeij, 1973; Rohde & Sandland, 1975; Garrity & Levings, 1984). However, studies (e.g., Vannini & Chelazzi, 1978; Chelazzi et al., 1985) have not examined whether competition for aggregation sites between ecologically similar species affects the composition of aggregations. This study conclusively demonstrates that ecologically similar species do not aggregate together. Each of the four ecologically similar species studied here formed monospecific aggregations regardless of intertidal level or season. This suggests that while abiotic pressures may drive the need to form aggregations, biotic factors clearly play an important role in the formation of each species aggregation.

This suggestion is supported by the fact that three of the species studied preferentially aggregated in a particular type of microhabitat. *Nerita polita* occurred predominantly around the bases of boulders, *N. undata* was mainly found inhabiting shallow crevices in the boulder surfaces, whereas *N. costata* occurred only on the vertical surfaces of the boulders. Given the similarity between the crack and crevice microhabitats, it was not surprising that

N. undata occurred in both in some samples (summer, low intertidal). It was interesting to note that other species rarely occupied more than one microhabitat. *Nerita chamaeleon* was more of a generalist, aggregating in crevices and on vertical surfaces, but primarily within deep cracks in the rock surfaces. The loyalty of each species to these microhabitats was found within both the mid and lower intertidal regions and during both summer and winter periods.

Studies examining the formation of aggregations of intertidal gastropods have typically focused on the behavioral mechanisms individual species invoke to facilitate their aggregation ability (Garrity & Levings, 1984; Chelazzi et al., 1983, 1984, 1985; Crowe & Underwood, 1998). These studies have determined that species exhibit homing behaviors to favorable microhabitats by following substrate markers present in the mucus trails of conspecifics (Cook 1969, 1971; Chelazzi et al., 1983; Raftery, 1983; Gilly & Swenson, 1978; Chapman, 1998, 1999; Davies & Bechwith, 1999) and/or by detecting characteristics of the substratum (Vannini & Chelazzi, 1978; Garrity & Levings, 1984; Underwood & Chapman, 1990; Crowe & Underwood, 1998). However, these studies have not examined the specificity of different mech-

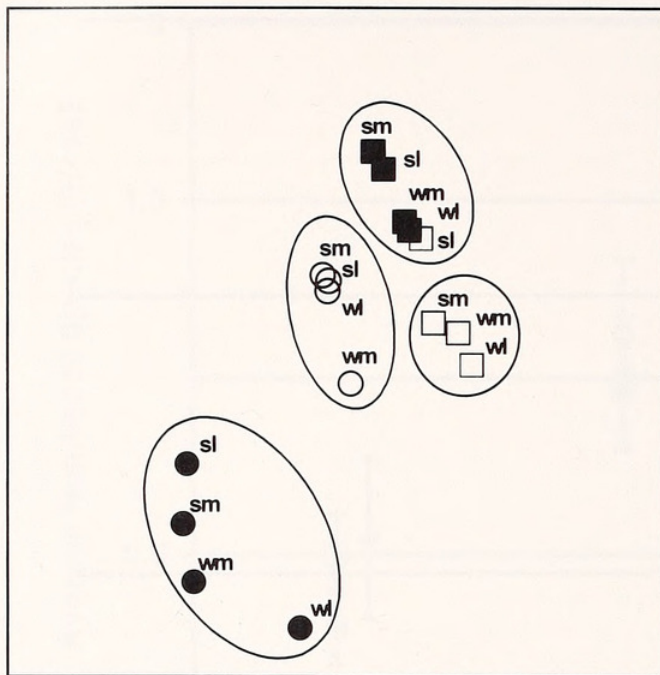


Figure 3. nMDS ordination indicating a difference in the composition of nerites occupying each of four microhabitat locations (□ crack, ■ crevice, ○ vertical wall, ● base of boulder). There were 20 replicates of each microhabitat sampled from the mid (m) and lower (l) intertidal regions during both summer (s) and winter (w). Stress = 0.04.

animals to particular species or genera nor have they determined if the presence or absence of competitive individuals affects aggregation behavior.

The formation of mono-specific aggregations within particular microhabitats regardless of any intertidal or seasonal variability of abiotic factors indicated that biotic factors may have a substantial influence on the formation and maintenance of aggregations for the species studied here. Furthermore, the results of this study, while not examining what process each species is using to form its aggregations, do clearly show that each species has a unique aggregation mechanism.

Given that space is one of the most limiting resources on rocky shores, particularly within the tropics (Lewis, 1964; Menge & Lubchenco, 1981; Garrity, 1984; Lubchenco et al., 1984), and that the four species examined here have similar ecological requirements, the fidelity of these species to particular microhabitats is most likely a response to competition, either current or historical, for aggregations sites. The aggregation cues each species utilizes may have evolved due to historical competitive pressures or may be an artifact of current competition for microhabitat space. The latter could be tested through a series of experimental manipulations whereby species are excluded from the habitat to determine if other species migrate into adjoining microhabitats.

In addition to the finding that there was no spatial variability in the preference of each species for particular

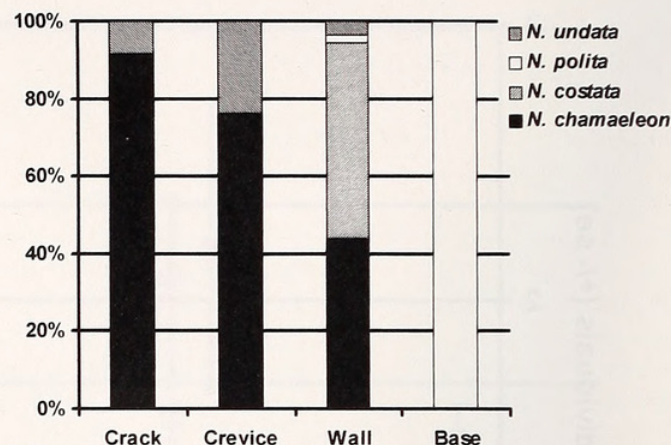


Figure 4. Percentage contribution of each species to the total number of individuals sampled from each microhabitat.

microhabitats, there were no significant differences observed in the abundances of species found in the aggregations across the intertidal gradient. The number of individuals aggregating did not differ between the mid and lower intertidal regions. To decrease their period of emersion, nerites have been shown to migrate down the shore in the wash of the falling tide (Vannini & Chelazzi, 1978; Garrity & Levings, 1981), and as a result, more individuals are usually found in lower intertidal regions during low tides. Given the harsh abiotic conditions on tropical rocky shores throughout the Indo-West Pacific (Lewis, 1964; Moore, 1972; Lubchenco et al., 1984), more individuals could be expected to occur at lower tidal levels. Conversely, the pressure to aggregate may decrease lower on the shore where conditions are less harsh; thus fewer individuals could be expected to occur in aggregations at lower tidal levels. As such, either an increasing or decreasing gradient of abundance could be expected. In this study no difference in the number of individuals aggregating across the intertidal gradient was detected. There are several possible explanations for this.

First, there may have been no difference in the abundance of individuals between the two areas because abiotic conditions differed little between the two areas. Alternatively, abundance may have differed between the intertidal regions, but the additional individuals were not in aggregations and were therefore not sampled during the

Table 1

Percentage contribution of each species of *Nerita* to the ordination solution as determined by SIMPER analysis.

	Crack	Crevice	Vertical	Base
<i>N. chamaeleon</i>	93	87	48	—
<i>N. costata</i>	—	—	45	—
<i>N. polita</i>	—	—	5	98
<i>N. undata</i>	—	12	2	—

study. However, observations do not suggest that the latter is the case. It is most likely that the abiotic conditions influencing this sheltered tropical shore do not differ markedly across the intertidal region. Under these conditions you would not expect any difference in the number of individuals found aggregating in each area, as seen here.

During summer periods, increases in temperature result in increased risks of thermal stress and desiccation (Moore, 1972; Williams, 1993). As temperature and desiccation stresses are extremely important determinants of the distribution of intertidal gastropod species (Vermeij, 1973; Underwood, 1979), the pressure to aggregate, and the number of individuals forming aggregations, would be expected to be greater during summer periods. During this study, significantly more individuals were seen to be aggregating in summer than in winter (Figure 2). This trend was observed for all microhabitats and across both intertidal regions. While it is possible that this pattern of behavior is a result of the increase in desiccation risk and thermal stresses during summer, it is unlikely, as solitary individuals not inhabiting one of the microhabitats examined were rarely observed prior to or during sampling.

In addition, the trend of more individuals being sampled during summer than winter occurred for all species except one, suggesting that the decline in abundance of individuals during winter was not due to species moving out of aggregations, but instead indicates an overall decline in the abundance of individuals occurring on the shore. This hypothesis is supported by the fact that a decline in abundance of all intertidal gastropod species inhabiting this area occurred during the winter sampling period (unpublished data).

In summary, the aggregations observed during this study generally comprised only one species. Furthermore, each species exhibited a strong fidelity to a single microhabitat type, and the microhabitat preference of each species did not vary over spatial or temporal scales. This is the first record of such a distinct segregation in the microhabitat usage between co-existing rocky shore gastropods in the tropics of the Indo-West Pacific. The consistency of these patterns suggests that biotic factors such as competition for microhabitats may play a greater role in the formation and maintenance of intertidal gastropod aggregations than they were previously thought to.

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