

A COMPARATIVE STUDY OF THE DEFENSE SYNDROMES OF SOME NEW ZEALAND MARINE CRUSTACEA

BY

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ABSTRACT

Five sympatric species of intertidal decapod crustaceans were studied in the field and laboratory with regard to the mechanisms used for predator defense. The species are sympatric and represent a gradient from high intertidal (*Cyclograpsus lavauxi*) to subtidal (*Notomithrax ursus*) with *Petrolisthes elongatus*, *Heterozius rotundifrons*, and *Halicarcinus innominatus* intermediate in tidal distribution. We tested the hypothesis that the diversity of defensive features would increase along a tidal gradient from high to low tide. All species were scored in the field for degree of background matching in color and tendency to autotomize appendages. In the laboratory individuals were scored with regard to delay to first movement following disturbance, maximum speed of movement, maximum extent of cheliped extension, and responses to conspecific alarm odors. Maximum sizes for individuals of the different species were obtained from the published literature. The five species varied significantly in the scores recorded for all of the different defensive features. *Halicarcinus innominatus* matched its background significantly better, *Petrolisthes elongatus* autotomized the most readily, *Heterozius rotundifrons* showed the longest periods of immobility following disturbance, *Cyclograpsus lavauxi* could move the fastest, and *Notomithrax ursus* reached the largest size. However, all species utilized multiple mechanisms related to predator avoidance. Summation of the rank scores for the seven different features revealed that the magnitude of the overall diversity of defensive features (1) did not vary along the tidal gradient and (2) showed surprisingly little variation among the different species.

RÉSUMÉ

Cinq espèces sympatriques de crustacés décapodes intertidaux ont été étudiées sur le terrain et au laboratoire quant aux mécanismes utilisés pour la défense contre les prédateurs. Les espèces sont sympatriques et représentent un gradient de l'intertidal supérieur (*Cyclograpsus lavauxi*) au

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subtidal (*Notomithrax ursus*) avec *Petrolisthes elongatus*, *Heterozius rotundifrons* et *Halicarcinus innominatus* intermédiaire dans la répartition tidale. Nous avons testé l'hypothèse que la diversité des traits défensifs augmenterait suivant un gradient tidal, de la haute à la basse mer. Toutes les espèces étaient notées sur le terrain sur leur capacité à s'adapter à la couleur du milieu et la tendance à autotomiser des appendices. En laboratoire, les individus ont été notés sur le délai jusqu'au premier mouvement suivant la perturbation, la vitesse maximale du mouvement, l'extension maximale du chélicépède, et les réponses aux odeurs d'alarmes spécifiques. Les tailles maximales des individus des différentes espèces ont été obtenues à partir des données publiées. Les cinq espèces différaient de façon significative dans les notes obtenues pour tous les traits de défense. *Halicarcinus innominatus* s'adapte le mieux au fond, de façon significative, *Petrolisthes elongatus* s'autotomise le plus facilement, *Heterozius rotundifrons* a montré les plus longues périodes d'immobilité après une perturbation, *Cyclograpsus lavauxi* se déplace le plus vite, et *Notomithrax ursus* a atteint la plus grande taille. Cependant, toutes les espèces ont utilisé des mécanismes multiples pour éviter les prédateurs. La somme des notes relatives aux sept différents critères ont révélé que l'échelle de diversité totale des critères de défense (1) ne variait pas suivant le gradient tidal et (2) montrait une variation étonnamment faible entre les différentes espèces.

INTRODUCTION

There are obviously a large number of biological mechanisms that decrease the probability of predation for any species of animal (Mitchell & Hazlett, 1996; Vermeij, 1982). Which categories of mechanisms are utilized by a particular species, depends upon both evolutionary history, which shapes the morphological, physiological, and behavioral features that allow some phenotypes to survive predation more successfully, and more plastic aspects of an animal's phenotype that may be affected by events encountered during its lifetime (Dukas, 1998). While many studies have focused upon the features of predators that help to determine the rate of successful predation (Curio, 1976), the features of prey are equally important in the predator-prey interaction.

A number of studies have documented the relationship between amount of predation pressure in a locale and the magnitude of certain defensive features. For example, the shells of related gastropods are thicker in the eastern Pacific compared to the Caribbean region, presumably reflecting the overall higher rate of predation there (Vermeij, 1978). Similarly, the gradient in shell thickness from temperate to tropical areas is a reflection of the greater abundance of predators that rely upon crushing in tropical waters (Vermeij, 1978).

In addition to looking at the relationship between predation pressure and defensive features across different geographic regions, it is also of interest to examine patterns at a more local scale. In this study, we investigated whether there are differences in the quality or quantity of defensive features among species along a local gradient of potential predation pressure. In particular, do species in different parts of the intertidal, from the lower intertidal where fish predation may be more

extreme to the higher intertidal with less extreme fish predation (Vermeij, 1978), have different syndromes of defensive features?

Secondly, we investigated whether some species tend to have just a few features that protect them from predation very well, or whether most species have a wide array of features, the sum of which add up to a high level of protection. Another way of posing this question is to ask if there are specialists among prey in defense strategy, or because each species must defend itself against an array of predators (Edmunds, 1974), are most species generalists with regards to their defense mechanisms? Another alternative would be for a species to have several specialized defensive features which it can employ depending upon the particular predator species present (McIntosh & Townsend, 1994).

We addressed these questions by examination of several features potentially related to predation avoidance in five of the most common species of intertidal decapods in New Zealand. Individuals of all five species tend to be found under rocks or in crevices at low tide and forage more at high tide (McLay, 1988). We examined morphological and behavioral features of these crustaceans and compared the ways in which species differed in all of these features. Because crustaceans generally do not rely upon chemical defenses (see Luckenbach & Orth, 1990, for a possible exception), this category of defensive features was not tested. The first hypothesis tested was that there would be a relationship between the sum of defensive features and location in the intertidal, reflecting stronger fish predation pressure lower in the intertidal. The second hypothesis tested was that all of the species would be similar in the "sum" of their defensive features.

METHODS

Study species

The five species were studied in the field near the Edward Percival Field Station, Kaikoura, New Zealand and in the laboratory at Canterbury University, Christchurch, New Zealand during January and February, 1998. The five species were the grapsid crab *Cyclograpsus lavauxi* H. Milne Edwards, 1853, the porcellanid anomuran *Petrolisthes elongatus* (H. Milne Edwards, 1837), the bellid crab *Heterozius rotundifrons* A. Milne Edwards, 1867, the hymenosomatid crab *Halicarcinus innominatus* Richardson, 1949, and the majid crab *Notomithrax ursus* (Herbst, 1788). In the rest of this paper we will refer to these species by their generic names. The fact that the species studied were all in different families, reduces the possibility of sharing features as a result of phylogenetic similarity. One of the behavioral features tested in all five species was the response to a chemical cue associated with predation, conspecific alarm odor, and the results of those tests

are reported elsewhere (Hazlett, in press). In addition, the effectiveness of the special appendage-extended posture of *Heterozius rotundifrons* is reported elsewhere (Hazlett & McLay, in press).

Background matching

A very common mechanism that affords some level of protection against visually orienting predators is background matching. We quantified the degree of background matching in the field for the five species. Crabs were located in the field at Kaikoura at low tide by turning over rocks. We utilized the method developed by Thacker et al. (1993) for quantifying colors and their extent of similarity. We characterized the color of the background on which crabs were found by matching a four square centimeter area directly under the crab with a particular paint chip color (Resene brand paint chip pages) from an array of 432 colors. Two observers independently picked out a color and when there were differences of opinion, a compromise was reached. We also scored the color of the crab using the same array of paint chips. In the case of *Notomithrax*, which is a decorating crab (Pack, 1982), the color scored was mostly determined by the algae on its carapace that the crab had placed there. We scored 20 individuals from 20 different rocks and their backgrounds for each species.

The colors of crabs and backgrounds were later visually matched to colors in the standard Methuen Handbook of Color. As described in Thacker et al. (1993), the 30 plates in this book, representing different hues, can be arranged in a color cylinder with tone increasing as one goes across a page from left to right and intensity decreasing as one moves down the plate. Thus each color can be described in terms of hue, tone, and intensity as a point in three-dimensional space (Thacker et al., 1993). For each crab and its background we determined the geometric distance between the color of the crab and the color of its background, and then compared these distances with ANOVA to test for differences among the species in the degree of color matching between crab and background. To determine if some species were found on a greater variety of background colors, we compared the variance of background colors using a bootstrap simulation technique (Thacker et al., 1993). This methodology is obviously not perfect in that the color vision of potential predators of these crustaceans is no doubt different from the color vision of humans (D'Eath, 1998). However, lacking full knowledge of which predators are most important and the exact nature of their color vision we utilized the method described above.

Size

The size of prey organisms almost always has an effect upon predation rate. Larger prey gain a refuge from predation because there is a smaller array of

predators that can successfully handle them (Persson et al., 1996; Werner & Gilliam, 1984; Wilbur, 1988). We ranked the crabs from the largest adult size in carapace width to the smallest, using data from the literature (McLay, 1988). While young individuals of all species would be expected to experience predation threat when small, they should vary in the extent of size refuges as adults.

Autotomy

Animals in a number of taxa have the capacity to autotomize parts of the body when disturbed, such as by a predator (Edmunds, 1974). Many species of Crustacea can autotomize limbs but the ease with which this occurs varies greatly among species (Bliss, 1960). We utilized a standard test to compare the frequency of cheliped autotomy among the five species of crustacea in the field. When individuals were found under a rock, the observer grasped an individual by one cheliped and lifted the animal above the substrate for one second. We recorded if the cheliped was autotomized for each of ten individuals for each species.

Delay to first movement

When animals are disturbed they may move away quickly, attempting escape, or remain stationary for some time, possibly avoiding detection. We tested 20 individuals of each species in the laboratory by picking them up, one at a time, and dropping them in an opaque plastic container (180 mm × 120 mm bottom dimensions) with about five cm water depth. We then timed how long before they first moved from their initial position. The species were compared by ANOVA to test for differences in the magnitude of delay to first movement following disturbance.

Speed of movement

Escape behavior in which the potential prey attempts to run away from a predator depends upon the ability to move more rapidly than predators. To compare the five decapod species, we placed adult individuals in one end of a rectangular container filled with sea water. Once the crab had started to move, we then "chased" it with a plastic ruler, making light tactile contact with appendages. We tried to make the animals move as fast as possible without actually pushing them along. We recorded the number of seconds it took to traverse the length of the container (46 cm) and converted the score for each animal to a cm/second value. ANOVA was used to compare the scores for the individuals among the five species.

RESULTS

Background matching

As shown in fig. 1, there was significant variation among the species in how closely they matched their background ($F = 3.59, P = 0.009$). Clearly individuals of *Halicarcinus* most closely resembled their background even though individuals were found on a wide range of background colors. Pairwise comparisons showed that *Halicarcinus* was significantly different from *Cyclograpsus* and *Heterozius* in the degree of color matching (fig. 1). Preliminary laboratory observations of individuals of *Halicarcinus* placed in different color environments indicated that this matching is an active process, which agrees with the findings of Melrose (1975). The dorsal carapace of these crabs is not heavily calcified and is actually quite clear, allowing chromatophores in the epidermis of the carapace to show through. These red, white, black and green chromatophores are concentrated or dispersed depending upon the color environment. When placed on a new color background, individuals of *Halicarcinus* can change color in about 30 minutes.

The other species that was difficult for a human collector to see, even though the color matching score was not very low, was the spider crab *Notomithrax*. This crab decorates its dorsal surfaces with algae and is thus difficult to detect. While some individuals decorated with red algae were found in areas of brown algae and

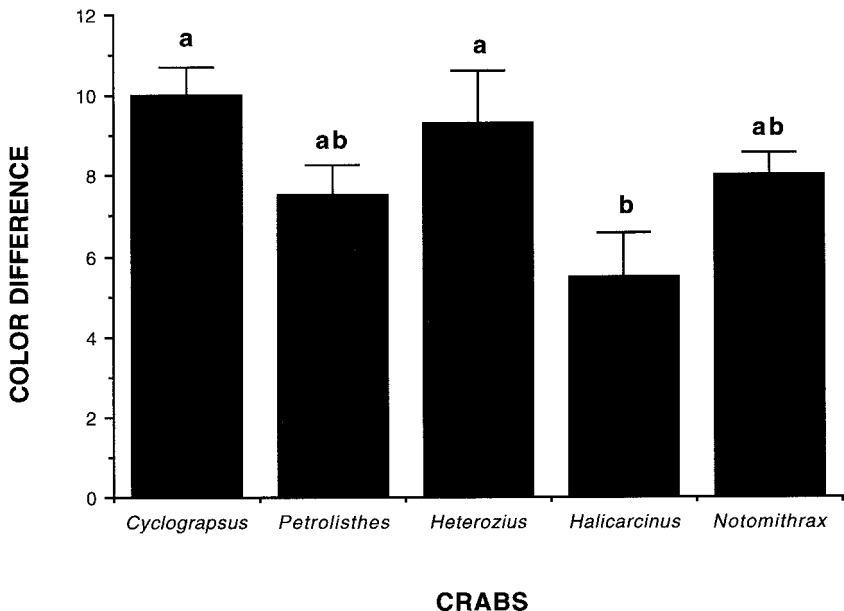


Fig. 1. Mean (+ S.E.) of the differences between the color of individual decapods and the color of their background in the field. $N = 20$. Different letters indicate species with significantly different scores by Tukey test comparisons ($P < 0.05$).

vice versa, thus the intermediate matching score, the crabs were still difficult to recognize due to the obscuring of their body outline by algae. Pack (1982) sampled over 800 crabs in nature and found that 89.6% carried at least some of the most common species of algae found in a particular area.

Pairwise comparisons of the variance in background coloration for the different crab species found only one significant difference, between the backgrounds for *Cyclograpsus* and *Petrolisthes* ($F = 6.0$, $P = 0.01$). Thus the majority of crabs were found on equally variable backgrounds and, in particular, *Halicarcinus* was found on backgrounds that were just as variable as those of the other species of decapods.

Size

The largest carapace width is attained by individuals of *Notomithrax* and the smallest by *Petrolisthes*. Individuals of *Cyclograpsus*, *Heterozius*, and *Halicarcinus* have intermediate size carapace widths (McLay, 1988). The maximum carapace widths recorded for the species, averaged for males and females are (1) *Notomithrax*, 39 mm, (2) *Cyclograpsus*, 27 mm, (3) *Heterozius*, 23 mm, (4) *Halicarcinus*, 17.2 mm, and (5) *Petrolisthes*, 16.2 mm (McLay, 1988).

Autotomy

The only individuals to autotomize a cheliped in the autotomy tests were individuals of *Petrolisthes* and all 10 individuals of that species that were tested did autotomize when picked up by one cheliped. In fact, the only way to collect individuals of this species with the chelipeds intact is to gently grasp the cephalothorax and try to avoid touching the chelipeds. The chelipeds of this species are not normally used in feeding as it is a filter feeder, utilizing the setose third maxillipeds for feeding (McLay, 1988), nor are they used extensively in social interactions (Molenock, 1976).

Delay to first movement

There were strong differences among species in the time before the first movement following the disturbance of being placed in a container ($F = 15.8$, $P = 0.000$) (fig. 2). There was a significantly longer delay for individuals of *Heterozius* than for any of the other four species. When disturbed, individuals of this species assume a catatonic-like state with the appendages fully extended and remain immobile for a number of minutes (Field, 1990; Hazlett & McLay, 2000). The other species that was slow to begin moving was *Halicarcinus*, which in the field is very difficult to see until it does move (fig. 2). The other three species were quite similar in their time to first movement.

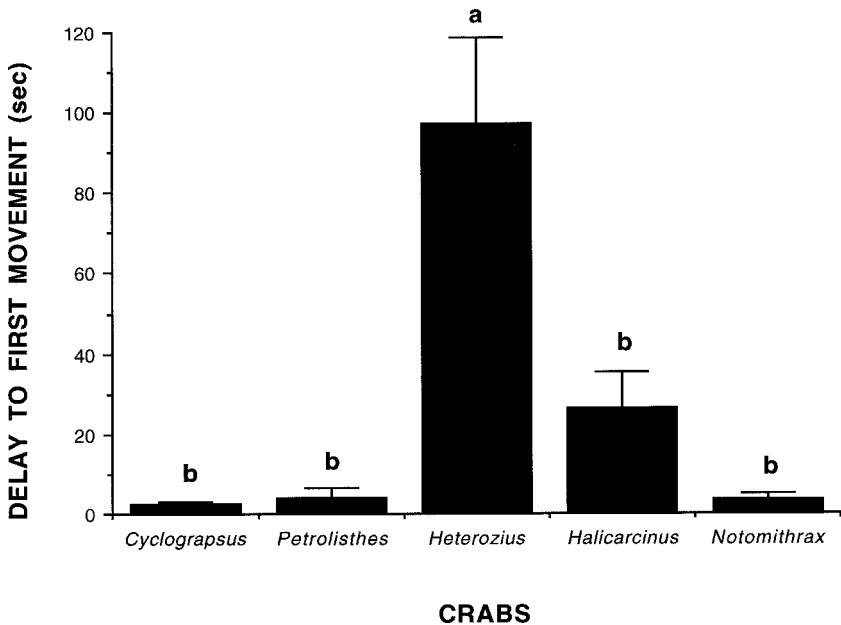


Fig. 2. Mean (+ S.E.) of the delay to first movement (seconds) following disturbance of individuals of the five species of decapods. $N = 20$. Different letters indicate species with significantly different scores by Tukey test comparisons ($P < 0.05$).

Speed of movement

There were also highly significant differences among the species in how fast they could be forced to locomote in the laboratory ($F = 31.35$, $P = 0.001$) (fig. 3). Clearly individuals of *Cyclograpsus* moved the fastest while individuals of *Halicarcinus* and *Heterozius* were the slowest.

Responses to alarm odor

As reported elsewhere (Hazlett, in press), the five species were tested for responses to conspecific alarm odors, obtained by crushing conspecific individuals and presenting a solution containing haemolymph to individuals. Comparisons of the frequency of behavior patterns with the frequencies shown during control periods showed changes in a number of behaviors. Individuals of *Heterozius rotundifrons* showed just one significant change in behavior which was an increase in time spent in a catatonic-like, appendage-extended state which is induced by tactile input. Individuals of *Cyclograpsus* and *Notomithrax* also showed a change in only one behavior (decreased locomotion upon introduction of alarm odor). *Halicarcinus* showed changes in two behaviors (increase in digging into the substrate and decrease of other movements), while individuals of *Petrolisthes* showed changes in three behaviors (increased time in lowered posture, decrease in locomotion, and decrease in all other movements).

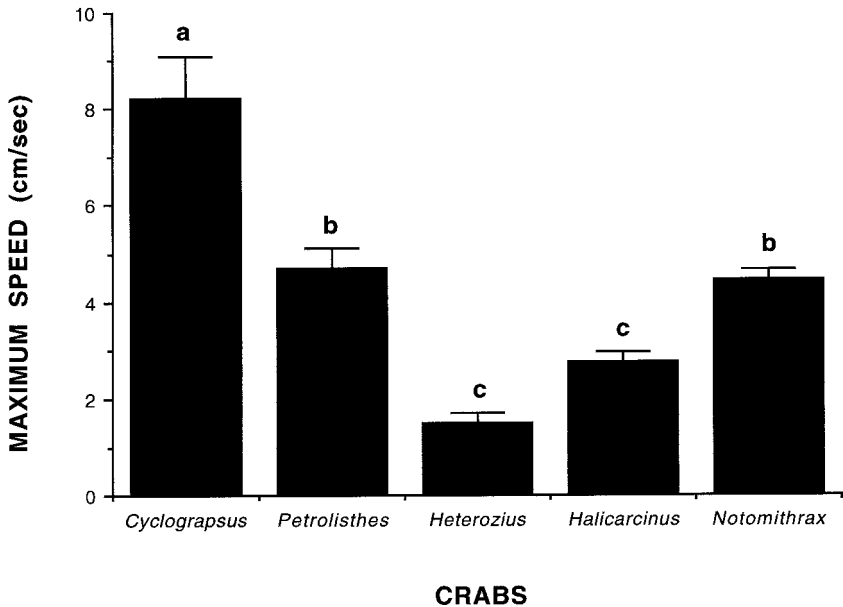


Fig. 3. Mean (+ S.E.) values for the maximum speed recorded for individuals of each of the five decapod species. $N = 20$. Different letters indicate species with significantly different scores by Tukey test comparisons ($P < 0.05$).

Maximum cheliped extension

As reported elsewhere (Hazlett & McLay, 2000), individuals of *Heterozius* can extend their chelipeds more fully than the other decapods. When disturbed, individuals extend their chelipeds a full 180 degrees apart and hold them rigid in that position for many minutes. This is distinctly further than the other species when they execute the defensive spread of the chelipeds. Among the other species tested in this study, *Halicarcinus* spread the chelipeds to about 15 degrees further than perpendicular to the transverse axis of the carapace and individuals of the other three species did not spread their chelipeds further than the mani being approximately parallel to each other, i.e., perpendicular to the transverse axis of the carapace.

Rank sum of defensive features

We ranked the five species of decapods for the five defensive measures reported in this manuscript as well as a ranking based upon the number of behavior patterns that changed when alarm odor was introduced (Hazlett, in press) and a ranking based upon the extent of cheliped extension when disturbed (Hazlett & McLay, 2000). The species were ranked from smallest difference in color matching to largest, longest delay in first movement to the shortest (because

TABLE I

Species' rankings for the defensive features scored for the five intertidal crustaceans studied: a score of 1.0 indicates the highest rank for a trait in terms of presumed predator avoidance while a score of 5.0 indicates the lowest rank for a trait

Crabs	Color match	Movement delay	Max. speed	Autotomy	Max. size	Response to alarm	Cheliped extension	Sum score
<i>Cyclograpsus</i>	4.5	3.5	1.0	3.5	2.0	4.0	4.0	22.5
<i>Petrolisthes</i>	2.5	3.5	2.5	1.0	5.0	1.0	4.0	19.5
<i>Heterozius</i>	4.5	1.0	4.5	3.5	3.0	4.0	1.0	21.5
<i>Halicarcinus</i>	1.0	3.5	4.5	3.5	4.0	2.0	2.0	20.5
<i>Notomithrax</i>	2.5	3.5	2.5	3.5	1.0	4.0	4.0	21.0

most predators respond to movement), from fastest locomotion to slowest, highest frequency of autotomy to lowest, largest adult size to smallest, greatest number of behaviors changed by detection of alarm odor to smallest, and the greatest extent of cheliped extension to the smallest. Scores for species that were not significantly different were assigned tied rank scores. We then summed the scores for these seven measures for each species. The summed rank scores ranged from 19.5 for *Petrolisthes* to 22.5 for *Cyclograpsus* (table I). This is a much smaller range of values than the 7.0 to 35.0 that would be theoretically possible for five species with seven rankings. The variation in this summed score is not significant (Friedman test, $F = 0.657$, $df = 4$, $P = 0.957$). Thus it appears that use of a combination of features is necessary for all species.

DISCUSSION

The array of defensive features shown by individuals of these five species, all from a similar intertidal area, is quite diverse. This diversity in defensive syndromes is somewhat surprising given that all these crabs probably face a similar array of predators and one might predict that one defensive mechanism or another might work best in that particular environment. Of course, the features we examined may well serve other functions in addition to predatory defense and thus be subject to multiple sources of selection.

While particular species of crabs tended to specialize or focus upon one aspect of predator defense measures, clearly species utilize a number of features to some degree. We can use the total ranking scores (table I) as some measure of the diversity of defensive features of these species. This would lead to a (statistically-not-significant) ranking of *Petrolisthes*, *Halicarcinus*, *Notomithrax*, *Heterozius*, and *Cyclograpsus*. If we rank these species according to their general location along a high intertidal to low intertidal gradient, the order would be *Cyclograpsus*,

Petrolisthes, *Heterozius*, *Halicarcinus*, and *Notomithrax* (cf. McLay, 1988). No statistical analysis is necessary to see that there is little agreement between the two rankings. This suggests that these data do not support the hypothesis that the diversity of the defensive syndromes of intertidal decapod crustaceans in a single habitat vary along a tidal gradient. The studies summarized by Vermeij (1978), many of which did suggest a gradient in predation defenses along a tidal gradient usually focused upon one aspect of predator defense. Thus shell thickness or degree of sculpturing of gastropod shells increases as predation pressure increases, lower in the intertidal (Vermeij, 1978). In the current study, we examined an array of defensive tactics rather than one or two particular features. It may well be that although the gradient in predation pressure in the intertidal has led to selection for an increase in one type of feature, that the variety of predators found in the intertidal has selected for a uniform diversity of tactics.

Interestingly, each of the five species ranked first in at least one of the defensive measures. *Petrolisthes* appears to utilize autotomy as an important defense when tactile contact is made but also utilizes speed and a diverse set of responses to alarm odor to reduce the probability that tactile contact is made. The overall score for *Halicarcinus* was determined, in part, because the delay in moving following disturbance is logically associated with its high degree of background matching. The responses to alarm odor by individuals of *Halicarcinus* (digging into the substrate and decrease of all other movements) further enhance the use of immobility and crypsis when danger is indicated.

The score for *Heterozius* may be primarily due to the reliance of that species on a special behavior (rigid immobility with limbs extended) as its primary defense mechanism. This one pattern is very effective in defense against predation unless the predators are over a certain size (Hazlett & McLay, 2000). The long delay in first movement, lack of autotomy of limbs, and slow movement are inter-related features that accompany this unusual defense posture. In a similar fashion, *Cyclograpsus* appears to rely primarily upon one defensive aspect, speed. Other features contribute to its defensive syndrome somewhat, but as any human collector/predator will acknowledge, grapsids tend to rely upon speed as a defensive mechanism.

We used a principal components analysis to further examine the syndromes of tactics used by the different species. The variation in rankings of tactics was largely explained (80%) by the first two factors. The distribution of the five species on the first two factors was quite distinct (fig. 4). The defensive features that contributed most heavily to Factor 1 were alarm odor responses, color matching, and autotomy while speed, cheliped extension, and size contributed the most to Factor 2. As shown in fig. 4, *Cyclograpsus* and *Notomithrax* clustered very closely in one region while the other three species were very distinct from that pair of species

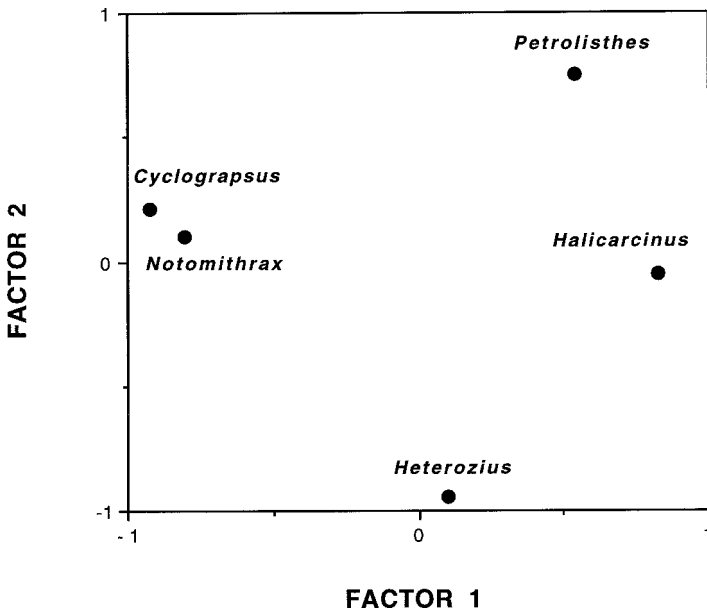


Fig. 4. Principal component analysis of the variation in rankings of the five species of decapods for the seven defensive features measured. Factors 1 and 2 explained 80% of the variance in the seven measures.

and from each other. This principal components analysis also does not support the hypothesis of a simple tidal gradient in defensive syndromes because *Cyclograpsus* and *Notomithrax* are the species furthest apart in their field distributions (highest intertidal and subtidal), this indicates further non-support of a simple tidal gradient in defensive syndromes. Indeed, the distinct spread of the species along the two axes suggests that individuals in different species might even be at an advantage if they do not use the same syndrome of tactics as other species in the area, *Cyclograpsus* and *Notomithrax* can utilize similar syndromes because they are distributed far enough apart in the environment that they may be facing different arrays of predators. *Cyclograpsus* in particular may be high enough in the intertidal to escape some fish predators but may be exposed more to bird predation. The importance to prey of the occurrence of multiple predators has been discussed in recent papers (Sih et al., 1998) but the possible role of multiple prey species in affecting the defensive tactics of individual prey species has not been addressed.

Both analyses utilized to examine the overall diversity of defensive tactics shown by these sympatric decapods indicate very strongly that the species are quite similar in the magnitude of the diversity of their syndromes. Perhaps this is to be expected since they are the five most common larger decapods, indicating they all have successfully survived in that environment. However, it is surprising that while some degree of specialization or reliance upon one or another tactic occurs, that

overall these unrelated species (five different families, two superorders) differ so little in the size of their predator defense packages. This may well be related to the generality of predators that prey upon all these species and if so, it would be very interesting to consider the defensive syndromes of species that are known to be subject to predators that are more specialized.

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