Host specialisation in trapeziid crabs: consequences for rarity at local scales

T.M. Sin\textsuperscript{1,2} and A.C. Lee\textsuperscript{2}

ABSTRACT

At local scales, the distribution and abundance of strongly habitat-associated organisms should be positively related to the amount of habitat available, but this relationship is highly dependent on the extent of specialisation for particular habitats. We examined habitat specialisation in seven species of crabs in the genus *Trapezia* from seven reefs in Kimbe Bay, Papua New Guinea to test predictions that species with wider host breadths would a) be more abundant and b) have wider local distributions. The results indicate that habitat specialisation is consequential in determining patterns of local abundance. The *Trapezia* species using wider ranges of pocilloporid coral species were also the most abundant. This pattern was disrupted when crab species specialised on highly abundant corals. Similarly, crabs that were habitat-generalists were found on more reefs than crabs that used only one or two coral species. These results suggest that species that are extreme habitat specialists may naturally exist in low numbers in reef communities. Furthermore, the loss of such organisms may not be detected by sampling methods using coarse taxonomic groupings. The relationship between habitat specialisation and rarity should therefore be an important consideration in designing reef monitoring studies.

Keywords Habitat specialisation, Rarity, Scale, Symbiosis, Management.

Introduction

Habitat availability and the organism’s responses to habitat are major factors limiting the distribution and abundance of species, and there is evidence that habitat diversity and abundance influence fish, coral and macroinvertebrate community structure on coral reefs (Sale 1978). Changes in habitat availability can result in population changes, depending on the degree to which available habitat is currently utilised. If organisms are habitat limited, their local distribution and abundance should be positively related to the amount of specific habitat available, and this relationship should be more robust in organisms specialised to particular habitats. The abundances of these organisms should be strongly correlated with the abundance of their specific habitats rather than total available space. In contrast, the abundances of species that are habitat generalists should be more closely correlated with total amount of habitat than the abundance of particular habitats (Hourigan et al. 1988).

Many coral reef organisms are involved in symbiotic associations: these can be extremely specialised, with discrimination occurring at the species level. This occurs in macrofauna such as anemonefish and coral gobies, as well as in invertebrates (Munday et al. 1997, Sin 1999). It is suggested that habitat specialisation is a strategy that allows persistence of inferior competitors in an ecosystem. While this is an obvious benefit, there may be other consequences. Habitat requirements may limit the distribution and abundance of organisms at a variety of spatial scales. Highly specialised species may have geographic ranges limited to that of their habitat. Gaston (1994) predicted that species using a narrow range of habitats (habitat specialists) would tend to be locally rare compared to species that use a wide range of habitats (habitat generalists). At large scales (100s to 1000s of kms), the distribution of an organism is thought to be limited by that of its preferred habitat (Gaston 1994, Gaston and Kunin 1997 for reviews). However, research by Sym's (1995) suggests that larval distribution may be more important than microhabitat associations at that scale. Differences in larval distribution may, in turn, be influenced by large scale oceanographic processes. Moreover, flexibility in habitat use, where a species’ habitat preferences varies among geographic locations, also reduces the importance of habitat associations in influencing large scale distributional patterns (Sin and Lee, unpublished). It appears that habitat requirements may be important primarily in smaller or meso-scale patterns of distribution (Sin and Kaly, unpublished ). For example, the distribution and abundance of *Tetralia* crabs on Australian reefs seem closely associated with that of their host corals (Sin 1999).

*Trapezia* crabs are small, obligate symbionts of corals. The family includes the genera *Tetralia*, *Tetraloides* and *Trapezia*, which are found exclusively on scleractinian corals from the families Acroporidae and Pocilloporidae. *Trapezia* are usually associated with *Pocillopora*, *Stylophora* and *Seriatopora*, and *Tetralia* with species of *Acropora* that form discrete colonies with bushy or corymbose growth forms (Knudsen 1967, Patton 1994). These are the most common symbionts of their host corals, with occupancy rates in excess of 90% (Abele 1976, Patton 1994). Although it was previously assumed that the crabs did not discriminate among congeneric species of host coral, Sin (1999) showed that *Tetralia* appears to select host corals rather than using them in strict accordance to availability. A range of host specialisation exists in this group of specialised animals, including some species that are restricted to one or two coral species within a locality. New evidence also suggests that these specialisation strategies may be rather flexible. Species that are apparent habitat specialists at one location may use a wider range of coral species at another (Sin and Lee, unpublished ), or switch host

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one location may use a wider range of coral species at another (Sin and Lee, unpublished), or switch host species in response to disturbance.

In this paper we describe patterns of host use by seven *Trapezia* species at Kimbe Bay, Papua New Guinea. We then examine the predictions that species with broad host breadths will a) be more abundant and b) have wider local distributions.

**Methods**

**Sampling**

Kimbe Bay is situated at New Britain, Papua New Guinea (5.36°S, 150.10°E). A small extent of reef fringed the bay, and there are numerous small patch reefs along the bay. Seven of these reefs within a 5 km radius were selected. All censuses were conducted using SCUBA apparatus. At each reef, 10 to 30 x 1 m belt transects were laid one metre above, and parallel to the crest. The starting point of each transect was haphazardly selected, but was within a metre radius of the last transect. All transects were more or less consecutive, and represented a single side of each reef. This was designed to minimise exposure-related differences in coral abundance among transects. All pocilloporid and acroporid corals within the belt were identified and counted.

Sampling of the symbionts was based on a visual census of the trapeziid crabs within each coral colony within the transect, and crabs were identified to species level and counted. Where there was doubt about the identity of the symbionts, they were collected for further examination. The accuracy of this sampling method was verified for both symbiont identification and for abundance estimates at Australian coral reefs. This experiment showed accuracies of 98% in identification and 97% for abundances.

**Analyses**

Chi-square tests were used to compare the observed distribution of each crab species to the frequency distribution of the coral species. Where significant differences were obtained, 95% confidence intervals were calculated using Bonferroni z-statistics around the proportion of coral used by each crab species to determine if that coral species was used more or less frequently than expected if host use was random (Sin 1999).

**Results**

Seven species of *Trapezia* were recorded from Kimbe Bay: *Trapezia cymodoce, T. ferruginea, T. guttata, T. punctipes, T. rufopunctata, T. septata* and *T. serenei*. These occurred solely on four pocilloporid corals, *Pocillopora damicornis, P. verrucosa, Seriatopora hystrix* and *Stylophora pistillata* (Table 1). No *Trapezia* were recorded from the acroporid corals censused.

**Table 1** Relative habitat availability and occurrence of crabs on coral species at Kimbe Bay, Papua New Guinea.

<table>
<thead>
<tr>
<th>Corals</th>
<th>P. damicornis</th>
<th>P. verrucosa</th>
<th>S. hystrix</th>
<th>S. pistillata</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of colonies</td>
<td>24</td>
<td>86</td>
<td>470</td>
<td>30</td>
<td>610</td>
</tr>
<tr>
<td>Proportion of colonies</td>
<td>0.04</td>
<td>0.14</td>
<td>0.77</td>
<td>0.05</td>
<td>1</td>
</tr>
</tbody>
</table>

**Table 2** Observed vs. expected number of *Trapezia* crabs found on pocilloporid corals in Kimbe Bay, Papua New Guinea.

<table>
<thead>
<tr>
<th>P. damicornis</th>
<th>P. verrucosa</th>
<th>S. hystrix</th>
<th>S. pistillata</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>T. cymodoce</td>
<td>8</td>
<td>9.1</td>
<td>30 (-)</td>
<td>32.7</td>
</tr>
<tr>
<td>T. ferruginea</td>
<td>6 (+)</td>
<td>2.3</td>
<td>22 (+)</td>
<td>8.2</td>
</tr>
<tr>
<td>T. guttata</td>
<td>3 (-)</td>
<td>12.6</td>
<td>2 (-)</td>
<td>45.1</td>
</tr>
<tr>
<td>T. punctipes</td>
<td>0 (-)</td>
<td>3.4</td>
<td>19 (+)</td>
<td>12.3</td>
</tr>
<tr>
<td>T. rufopunctata</td>
<td>0</td>
<td>0.1</td>
<td>0</td>
<td>0.4</td>
</tr>
<tr>
<td>T. septata</td>
<td>0 (-)</td>
<td>0.5</td>
<td>4 (+)</td>
<td>1.7</td>
</tr>
<tr>
<td>T. serenei</td>
<td>0 (-)</td>
<td>0.4</td>
<td>6 (+)</td>
<td>1.4</td>
</tr>
<tr>
<td>No. crabs on each coral species</td>
<td>17</td>
<td>83</td>
<td>563</td>
<td>39</td>
</tr>
</tbody>
</table>

(+) denotes observed numbers significantly more than expected, p<0.05, (-) denotes observed numbers significantly less than expected, p>0.05 * T. rufopunctata excluded from statistical analyses due to low numbers

A total of 610 coral colonies were censused in the survey, this represented a mean pocilloporid density of 0.29 m\(^{-2}\). The pocilloporid community was numerically dominated by *Seriatopora hystrix*, which made up 0.77 of the total number of pocilloporids recorded.

The crab community was dominated numerically by *T. guttata*, which contributed 44.3% of the total numbers sampled (Table 2). Initial qualitative examination of the distribution of crabs among the four coral species suggests a lack of host discrimination. All coral species were used to
some extent by each crab species (Table 2). Comparing the relative proportion of coral species used by each crab species with the proportions of coral species available gives evidence of discrimination. *Trapezia rafopunctata* did not occur in sufficient numbers for these analyses and so were excluded (Table 2).

Assigning a four-level scale to patterns of host use with respect to availability shows that the *Trapezia* species display a range of host specialisations (Table 3). *Trapezia cymodoce*, *T. ferruginea* and *T. guttata* used all four coral species, although with varying levels of preference. *T. punctipes* used three species, while *T. septata* and *T. serenei* used only two coral species. *T. cymodoce* and *T. ferruginea* were the most generalised in host use scoring nine and seven respectively, out of a maximum host breadth of 12. In contrast, *T. septata* and *T. serenei* (4, 3 respectively) were the most specialised, using only two of the coral species, *S. hystrix*. *T. cymodoce* and *T. ferruginea* were the most generalised in host use scoring nine and seven respectively, out of a maximum host breadth of 12. In contrast, *T. septata* and *T. serenei* (4, 3 respectively) were the most specialised, using only two of the coral species, *S. hystrix*. Very small numbers were occasionally found on all the other coral species.

Table 3. Host specialisation of *Trapezia* species on pocilloporid corals in Kimbe Bay, Papua New Guinea

<table>
<thead>
<tr>
<th></th>
<th><em>Pocillopora damicornis</em></th>
<th><em>Pocillopora verrucosa</em></th>
<th><em>Seriatopora hystrix</em></th>
<th><em>Syllaphora pustulata</em></th>
<th>Habitat breadth</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. cymodoce</em></td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td><em>T. ferruginea</em></td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td><em>T. guttata</em></td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td><em>T. punctipes</em></td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td><em>T. septata</em></td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td><em>T. serenei</em></td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>3</td>
</tr>
</tbody>
</table>

Legend: 0 = not used, 1 = used less than expected, 2 = used more than expected, 3 = used as expected.

Examining the relationship between host breadth and local abundance suggests that host specialisation tends to limit local abundances (Fig. 1). Total abundances of the specialised species, such as *Trapezia septata* and *T. serenei* were all less than 20, while the generalist *T. cymodoce*, which had a host breadth of 9 had more than 200 individuals (Fig. 1). However, two species do not fit this general trend. The intermediate *T. guttata* had the highest abundances at Kimbe Bay, with over 300 individuals (Fig. 1). In contrast, *T. ferruginea*, a host generalist, had lower numbers than either *T. cymodoce* or *T. guttata* (Fig. 1).

Similarly, host breadth appeared to have a positive influence on local distribution at Kimbe Bay. Host generalised species that used a wider range of host also occurred on more reefs than host specialised species (Fig. 2).

2. *Trapezia septata*, which preferentially uses a two coral species, was found on a single reef, while host generalists, *T. cymodoce* and *T. ferruginea*, occupied six and five reefs respectively, out of a maximum of seven (Fig. 2).

![Fig. 1 Numbers of crabs and host breadth of six *Trapezia* spp. at Kimbe Bay, Papua New Guinea. [CY = *Trapezia cymodoce*; FER = *T. ferruginea*; GUT = *T. guttata*; PUN = *T. punctipes*; SEP = *T. septata*; SER = *T. serenei*]](image1)

![Fig. 2 Numbers of reefs occupied and host breadth of six *Trapezia* species in Kimbe Bay, Papua New Guinea. [CY = *Trapezia cymodoce*; FER = *T. ferruginea*; GUT = *T. guttata*; PUN = *T. punctipes*; SEP = *T. septata*; SER = *T. serenei*]](image2)

**Discussion**

We examined relationships between host specialisation and patterns of local abundance and distribution at Kimbe Bay, Papua New Guinea. The results demonstrate for the first time, that species of *Trapezia*, like *Tetralia* (Sin 1999), discriminate among closely related host species, and display a range of host specialisations. This study also shows that host specialisation is also associated with patterns of local abundance. Host specialists tend to occur in lower numbers than host generalists, which tend to be numerically dominant. This is consistent with predictions made by Gaston (1994) and other researchers working in terrestrial and aquatic systems (Thompson et al. 1998, 1999).

However, deviations from this pattern occurred,
especially *Trapezia guttata* and *T. ferruginea*. The case of *T. guttata* may be explained by examining the abundances of the different coral species at the reefs. *Seriatopora hystrix* numerically dominated the pocilloporid guild at Kimbe Bay, accounting for 77.0% of total pocilloporid abundance (Table 1). It is possible that the high relative abundance of this coral species supported greater population sizes of crab species associated with it. Since *Trapezia guttata* was the only crab species that preferentially used *S. hystrix*, resource limitation may have been minimised for *T. guttata*, so that its numbers could be extremely high. The case of *T. ferruginea* may be a situation in which resource limitation is severe. *T. ferruginea* occupies much the same host breadth as *T. cymodoce* but was much lower in abundance than *T. cymodoce*. This may be because *T. cymodoce* is competitively superior to *T. ferruginea* and therefore restricts the latter to fewer coral colonies. This hypothesis can easily be tested using a combination of removal and exclusion experiments.

Host specialisation also influenced local patterns of distribution with host generalists tending to be more widespread, even at small spatial scales (up to 5 km). The host generalist, using a wider range of corals, were found on more reefs than host specialists. The latter species can therefore be classified as relatively rare based on numerical abundance, and on the fact the species occupying low proportion of areas sampled are also prone to extinction (Gaston 1994).

Host specialists may occur naturally in low abundances and in very localised aggregates in an ecosystem. Both these characteristics are used by Gaston (1994) to define rare species, and especially to identify species that are at high risk for local extinction. These species are highly susceptible to indirect disturbances that alter the quality and availability of their preferred habitats. In addition, they are at risk of extinction even from small, localised disturbances, although this may be mediated (at least in the short-term) by using alternative habitats (Sin, unpublished). Furthermore, since a range of habitat specialisation exists even within a genus, loss of such diversity may not be detected by sampling methods using coarse taxonomic groupings. The relationship between habitat specialisation and rarity is therefore an important consideration for monitoring and management strategies.

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**References**


