Analysis of spatial niche structure in coexisting tidepool fishes: null models based on multi-scale experiments

Seiji Arakaki*† and Mutsunori Tokeshi

AMBL, Kyushu University, Amakusa 863-2507, Japan

Summary

1. Fundamental and realized spatial niches were investigated through a combination of laboratory and mesocosm experiments, field observations and null model analysis in three intertidal gobiid species (Bathygobius fuscus, Chaenogobius annularis and C. gulosus). Null models based on the results of single-species experiments were used to assess interspecific spatial use and coexistence on two different scales: (i) microhabitats within a tidepool (‘microhabitat’ scale); and (ii) distribution among a set of tidepools (‘habitat-wide’ scale).

2. Patterns of microhabitat use varied from single to paired treatments, depending on paired species. Realized overlap of microhabitat use was smaller than would be expected from single-individual situations for intraspecific combinations, but not for interspecific ones.

3. Patterns of tidepool occupancy (a measure of spatial niche breadth) in the mesocosm were influenced by interspecific interactions. Two Chaenogobius species, but not B. fuscus, decreased tidepool occupancy in the hetero-specific treatments compared with the mono-specific ones. For all interspecific combinations, spatial overlap (habitat-wide scale) was significantly lower than the values expected from mono-specific situations. The results also indicated a possible trade-off between competitiveness and growth efficiency in these fishes.

4. Interspecific spatial overlap in the field was similar to that in the mesocosm experiment and the pattern of coexistence of gobiids can be explained by the results of our experiments.

5. This study demonstrates that niches of intertidal fishes may experience modifications under the influence of species interactions and that null models based on controlled experiments can greatly facilitate the deciphering of such changes in niche structure.

Key-words: coexistence, competition, intertidal, intra-/interspecific interactions

Introduction

The niche concept has been central to community ecology, on which major theoretical and empirical studies have been undertaken (e.g. Grinnell 1914; Elton 1927; Hutchinson 1957; MacArthur 1958; Pulliam 2000; Chase & Leibold 2003; Odling-Smee, Laland & Feldman 2003; Tilman 2004; McGill et al. 2006; Pearman et al. 2008; Levine & HilleRisLambers 2009). Species coexistence cannot be discussed fully without referring to the niche and the aspects of resource utilization (Hutchinson 1957; Schoener 1974), both of which have important implications for species assembly, species abundance and competitive/non-competitive relations (Tokeshi 1999). The shape and volume of niche may be altered through biotic interactions, most notably competitive relations on ecological and evolutionary time scales (Connell 1983; Schoener 1983; Morin 1999; Pearman et al. 2008). Conversely, the consequences of competitive interactions may be revealed through a comparison between the fundamental and the realized niche, which would lead to a better understanding of the mechanics of community organization and species coexistence.

Space is an important dimension of niche which may be shared or partitioned by co-occurring species (Schoener 1974; Tokeshi 1999), reinforcing the view that resource partitioning in terms of space is central to species coexistence (e.g. Rosenzweig 1981). Fundamental spatial niche depends on the ecophysiological and other traits of a species, forming the basis of species-specific occurrence patterns which in turn are closely influenced by requirements for food, reproduction, avoidance of predators/competitors and some adverse

*Correspondence author. E-mail: arakaki@ambl-ku.jp
†Present address: Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus, 3422 Sesoko, Motobu, Okinawa, Japan 905-0227.
environmental conditions. The distribution of species and, consequently, species composition and coexistence in a community reflect some modifications of the fundamental spatial niches of different species. Possible effects of competition on habitat use (i.e., changes in spatial niche), in particular, have often been inferred through experimental manipulations of competitor abundance in various assemblages (e.g., Crowell & Pimm 1976; Black 1979; Hairston 1980; Pacala & Roughgarden 1982; Elmgren et al. 1997; Lee & Silliman 2006) including fishes (e.g., Werner & Hall 1976, 1977; Munday, Jones & Caley 2001; Schofield 2003). However, assessment of changes in spatial niche is not straightforward with experiments, as biological realism may be sacrificed and density and species identity cannot always be independently controlled in mixed-species situations. In this respect, incorporation of null model approaches may be of some value, but there has been no attempt to explore the possibility of combining manipulative experiments with null model analyses to elucidate patterns of niche shifts.

Despite numerous ecological studies on intertidal fishes, mechanisms and relative importance of different types of biotic interactions in community organization still remain obscure (see Gibson & Yoshiyama 1999). As the number of tidepools available at low tide time is limited, space is probably the most important niche dimension for intertidal fishes. Indeed, previous studies noted differences in spatial use (e.g., Gibson 1972; Davis 2000) and the possible roles of intra-/interspecific competition for space in structuring intertidal fish communities (e.g., Stephens et al. 1970; Nakamura 1976; Mayr & Berger 1992; Pfister 1995, 2006; Faria & Almada 2001). There is, however, a paucity of information on variable patterns of intra- and interspecific space use on different scales of intertidal habitat.

The objective of this work was to investigate the patterns of fundamental and realized spatial niche in intertidal gobid species through a combination of laboratory and mesocosm experiments and null model analysis. Here, fundamental spatial niche was interpreted as spatial patterns shown by individuals of a species, either singly or as group of individuals. Null models were constructed from data derived from single-species/individual experiments in which there was no influence of inter-/intraspecific interactions. Spatial niche was considered on two different scales (microhabitat and habitat-wide) to examine the varied influences of biotic interactions on the patterns of space utilization and species coexistence in this assemblage. In assessing the influences of biotic interactions, growth was also taken into account alongside changes in space use.

Materials and methods

STUDY SITE AND FISH SPECIES

Field observation and fish collection were carried out on a moderately wave-exposed rocky shore of Shikizaki (32°31′N, 130°01′E) on the Amakusa-Shimoshima Island, south-western Japan. The study site had a tidal amplitude of about 3.5 m and was exposed for a distance of about 80 m seaward at the low tide. Tidepools of various sizes formed on this relatively flat rocky shore. The observation area and the collection site were separated by > 100 m and an extra large tidepool (c. \(3 \times 10^4 \) m\(^2\)) in between. Thus, there was no or negligible effect of fish collection on the observation area.

Gobiidae and Blenniidae were particularly abundant in the study site, with the former being dominant at all tidal levels, especially in the upper intertidal, constituting about 90% of tidepool fish community (Arakaki & Tokeshi 2006). Three common gobid species chosen for the present study, Bathygobius fuscus (Rüppell), Chaenogobius annularis Gill and Chaenogobius gulosus (Sauvage), comprised over 80% of tidepool fish fauna throughout the year. All three species are adapted for benthic life with similar maximum body sizes (c. 10 cm total length), compressed body shape and cryptic coloration, and are known to consume small benthic animals (Dōtu 1955; Sasaki & Hatatori 1969).

Field observations on tidepool use were conducted in the same season as the mesocosm experiment (June–August 2003, see below). A total of 34 tidepools of various sizes (surface area 500–9500 cm\(^2\)) were chosen from the mid to upper intertidal zones [170–255 cm above mean lower low water (MLLW)]. Species and their abundances were recorded by direct visual observation at day-time new moon spring low tide. We confirmed that this method had a similar accuracy of sampling as fish collection using anaesthetics (Arakaki & Tokeshi 2006).

LABORATORY EXPERIMENT ON MICROHABITAT USE

A laboratory experiment was carried out to examine the patterns of microhabitat utilization under the influence of biotic interactions. The present experiment with paired individuals complemented our previous experiment (Arakaki & Tokeshi 2005) that dealt solely with single-individual situations; results from both were used in the present study. Individuals of three species used in the experiment were collected using a hand net from the collection site. Fishes were carefully brought back to the laboratory in a container within 10 min of collection. All individuals were identified to species but sexes were not separated, as Chaenogobius spp. could not be sexed on the basis of external morphology. Fishes were selected for similar body sizes (mean TL ± ISD, B. fuscus = 38.5 ± 4.2 mm, C. annularis = 36.1 ± 2.2 mm and C. gulosus = 39.4 ± 2.6 mm). Each species was kept separately in aquaria (62 × 38 × 15 cm) containing a bed of small stones with a flow-through seawater system for 7 days prior to the experiment. The fish were fed daily with pieces of shrimps, crabs and molluscs collected from the field. The acclimatization period of 7 days was considered appropriate for these gobid fishes, though shorter than in other studies (Mayr & Berger 1992; Griffiths 2002; Schofield 2003).

The experiments were conducted in rectangular opaque aquaria (37 × 25 × 14 cm, corresponding in size to small natural tidepools), each of which was subdivided into four equal quarters by thin reten- dance walls (2 cm high, 0.8 mm thick) and a square stone plate (10 cm × 10 cm) was placed in the centre to serve as a rooftop such that a fish could use the shaded space below as shelter (Fig. 1a). Each quarter of an aquarium was allotted with one of four types of substrate, (i) sand (diameter, 0.25–1.0 mm); (ii) coarse sand (1.0–5.6 mm); (iii) gravel (5.6–19 mm); and (iv) bare rock (stone tile); the positioning of the four substrates in an aquarium was determined randomly for each setup. Substrates were collected from the field and separated using sieves of different mesh sizes in the laboratory. Stone tiles used as bare rock were preconditioned in the field for a year prior
null model analysis

Null models were employed to evaluate the effects of biotic interactions. A single most crucial element of null modelling concerns
the creation of ‘null expectation’, a pattern in which a focal biological phenomenon is absent. In the case of biotic interactions, the situation without such interactions cannot in principle be re-created from observed data as there is generally no guarantee that the aspect of relevance extracted from the data concerned has not been influenced by those interactions, past and present. In the present study our rationale was to construct null models based on experimental manipulations in which a single species/individual was present, thereby guaranteeing that the expected patterns were devoid of biotic interactions. For the microhabitat (laboratory) experiment, the null model involved randomization based on two single-individual experimental results to create null expectation of (pairwise) space use. For the habitat-wide (mesocosm) experiment, the null model was generated by randomly combining two single-species (not individual) experimental results. The choice of individual-based or species-based procedures was related to the fact that individual-based situations become less realistic as spatial scale increases; while a single-individual situation is relevant at microhabitat or ‘within-pool’ scale, it is not at habitat-wide or ‘among-pool’ scale. Note that these two analyses for different spatial scales involved different details of null model construction, as explained below.

**Microhabitat overlap (laboratory experiment)**

Overlap ($M_0$) in microhabitat use was calculated as,

$$M_0 = \sum \min(P_{x(i)}, P_{y(i)})$$

where $P_{x(i)}$ and $P_{y(i)}$ are the proportional use of the $j$th (micro-) habitat by species/individual $x$ and $y$, respectively. Proportional use was based on the 30 position data for each individual from the laboratory experiment. The index ranged from 0 (no overlap) to 1 (complete overlap) (Tokeshi 1986, 1999). Realized (observed) overlap values were compared with expected values derived from the data of single-individual experiment (conducted under the same setup, Arakaki & Tokeshi 2005), assuming that paired fishes behave in the same manner as in a single-individual situation (i.e. not influenced by other individuals). To generate the expected pattern, a computer simulation was performed in which fishes were re-distributed among ten microhabitats according to the probabilities equalling the observed proportions of microhabitats occupied in the single-individual experiment (Table 1). This re-distribution process was repeated 30 times for each fish individual to generate a set of space-use (30 positions) data, which was then used to calculate spatial overlap for a particular pair of individuals. The whole procedure was replicated 1000 times with random selection of individuals to obtain the mean with 95% range for each intra-/interspecific combination.

**Tidepool occupancy and overlap (mesocosm experiment)**

Tidepool occupancy, expressed as the proportion of tidepools occupied out of total, represents a measure of spatial niche breadth on the mesocosm scale. Realized tidepool occupancy and overlap in tidepool use under hetero-specific mixtures were compared with the expected occupancy/overlap values based on the mono-specific treatment in the mesocosm experiment. To derive expected values, the following procedure was taken: (1) data on 24 individuals of each species were randomly extracted from the mono-specific treatment (a total of 39 ($B. fuscus$), 43 ($C. annularis$) and 45 ($C. gulosus$) individuals, excluding those with incomplete spatial data), (2) for each pair of species (a total of 48 individuals), tidepool occupancy was calculated for (i) each species separately and (ii) the two species together (‘combined’ occupancy); note that this value is equal to or smaller than the smaller of 1.0 and the addition of two separate occupancy values, depending on the degree of overlap in spatial distribution between the two species), (3) for each pair of species, spatial overlap ($M_0$) was calculated, using each tidepool as unit of habitat. In addition, ‘observed’ values of intraspecific overlap in tidepool use were obtained by randomly dividing the observed mono-specific set of 48 individuals into two groups (each with 24 individuals) and calculating the spatial overlap between the two groups. These procedures were repeated 1000 times to obtain the mean and 95% range of occupancy and overlap values. Although data were collected on 10–14 consecutive occasions (designated as $t1$ to $t10/t14$), only those of the last three occasions ($t8$–$t10$ or $t12$–$t14$) were subjected to this analysis, as these represented more reliable ‘settled’ patterns.

Interspecific spatial overlap was also calculated for field-derived data, separately for each species combinations on monthly occasions.

**Change in tidepool use (mesocosm experiment)**

Effect sizes were calculated for three aspects of habitat-wide space utilization in the mesocosm experiment: (i) number of ‘displaced’ individuals (i.e. those located outside the 24 aquaria in the mesocosm), (ii) upper/lower positioning (the ratio of individuals located in the upper and lower tidepools) and (iii) level of aggregation, expressed as Morisita’s index ($I_m$). In meta-analyses, the ‘effect size’ ($D$) is calculated by standardizing the difference between ‘control’ and ‘experimental’ groups (Gurevitch et al. 1992; Gurevitch & Hedges 2001). In our analysis, the mean values in the hetero-specific treatment ($X_h$) and that in the mono-specific treatment ($X_m$) correspond to the ‘experimental’ and the ‘control’ group, respectively. Thus, positive/negative values of $D$ imply departures of the hetero-specific situations from the mono-specific ones. We calculated the effect size $D$ using the pooled standard deviation ($S$) of the mono-specific and the hetero-specific treatments.

### Table 1. Frequencies of microhabitat use (% inside/outside shelter) by three gobid species, under single-individual conditions

<table>
<thead>
<tr>
<th>Microhabitat category</th>
<th>Sand</th>
<th>Coarse sand</th>
<th>Gravel</th>
<th>Bare rock</th>
<th>Above plate</th>
<th>Side wall</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>B. fuscus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day</td>
<td>6/7</td>
<td>1/7/17/9</td>
<td>12/1/23/8</td>
<td>0/8/21</td>
<td>1/7</td>
<td>3/3</td>
</tr>
<tr>
<td>Night</td>
<td>2/5</td>
<td>2/5/14/2</td>
<td>3/3/42/9</td>
<td>2/1/7/9</td>
<td>1/3</td>
<td>0</td>
</tr>
<tr>
<td><strong>C. annularis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day</td>
<td>24/6</td>
<td>14/6/6/3</td>
<td>15/8/8</td>
<td>9/2/38</td>
<td>0/4</td>
<td>5/4</td>
</tr>
<tr>
<td>Night</td>
<td>5/8</td>
<td>5/8/7/9</td>
<td>15/4/21/7</td>
<td>2/9/5</td>
<td>2/9</td>
<td>20/4</td>
</tr>
<tr>
<td><strong>C. gulosus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day</td>
<td>0/0</td>
<td>45/4/04</td>
<td>50/0</td>
<td>4/2/0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Night</td>
<td>42/5</td>
<td>5/4/2/5</td>
<td>29/6/54</td>
<td>12/9/0/4</td>
<td>0/4</td>
<td>0/8</td>
</tr>
</tbody>
</table>
\[ D = \frac{X_e - X_s}{S} \]

\[ S = \sqrt{\frac{(N_e - 1)S_e^2 + (N_s - 1)S_s^2}{N_e + N_s - 2}} \]

where \( S_e, S_s, N_e, \) and \( N_s \) are the standard deviation (S) and the number of cases (N) of the hetero-specific treatment (e) and the mono-specific treatment (s), respectively. The term \( J \) corrects for bias due to small sample size:

\[ J = 1 - \frac{3}{4(N_e + N_s - 2) - 1} \]

**Growth in the mesocosm experiment**

Growth rates, expressed as (\( TL_2 - TL_1 \)/\( TL_1 \)) (where \( TL_1 \) and \( TL_2 \) are length at the start and the end of experiment, respectively), were compared between the mono-specific and the hetero-specific treatment using the Kruskal–Wallis test with Scheffe’s post hoc test. For \( B. fuscus \), the Mann–Whitney U-test was used to compare the mono-specific treatment (sample size was reduced to 37 due to missing values) and the mixture with \( C. annularis \); the data on \( B. fuscus + C. gulosus \) combination were incomplete due to typhoon interruption. There were no significant differences in the initial mean size of introduced fishes among all treatment groups (ANOVA, \( P > 0.05 \)).

Standardized mean differences of growth rates between the hetero-specific and the mono-specific treatment were also calculated in the same way as mentioned above (change in tidepool use). In this analysis, mean growth in the hetero-specific treatment (\( X_e \)) and that in the mono-specific treatment (\( X_s \)) correspond to the ‘experimental’ and the ‘control’ group, respectively.

**Results**

**MICROHABITAT USE AND OVERLAP (LABORATORY EXPERIMENT)**

On the microhabitat scale, the patterns of substrate use under mixed situations departed significantly from those expected under single situations for all combinations and times of day (chi-squared test with Bonferroni correction, \( P < 0.05 \)) (Table 2). In contrast, the patterns of shelter use showed no such difference (Mann–Whitney U-test with Bonferroni correction, corresponding to \( P > 0.05 \)) except for the \( C. annularis + C. gulosus \) pair by daytime. Realized values of intraspecific overlap in microhabitat use were significantly lower than would be expected from single situations in two Chaenogobius species and marginally so in \( B. fuscus \) (Fig. 2). In contrast, realized values of interspecific overlap showed no significant departure from expected values, except the \( C. annularis + C. gulosus \) pair by daytime. \( Ca + Cg \) was the only combination showing a clear difference in overlap pattern between day and night.

**TIDEPOOL OCCUPANCY AND OVERLAP (MESOCOSM EXPERIMENT)**

Tidepool occupancy of \( B. fuscus \) under interspecific mixtures showed no significant departure from the mono-specific situation, while \( C. annularis \) and \( C. gulosus \) showed some significant departures (Fig. 3). Chaenogobius annularis had a significant reduction in tidepool occupancy when mixed with either \( B. fuscus \) or \( C. gulosus \). Realized occupancy of \( C. gulosus \) varied depending on paired species: it was smaller when mixed with \( C. annularis \) but tended to be similar/slightly larger when mixed with \( B. fuscus \) than would be expected under mono-specific situations. Realized total (combined) occupancy of the \( B. fuscus + C. gulosus \) pair was larger than the expected value, while values for \( B. fuscus + C. annularis \) and \( C. annularis + C. gulosus \) pairs were smaller.

In all hetero-specific treatments, realized overlap values in the mesocosm were significantly smaller than would be expected from the mono-specific treatments and similar to observed values in the field (Fig. 4). The observed values of overlap in the field were apparently small compared with expected values of the mesocosm except for the June data of

![Table 2. Comparison of microhabitat use between single and mixed treatments of tidepool fishes. Changes in microhabitat use when mixed with other conspecific/heterospecific individual are tested for each focal species by the chi-squared test for substrate use and the Mann–Whitney U-test for shelter use. *P < 0.05 with Bonferroni correction.](image_url)
B. fuscus + C. gulosus combination. Observed intraspecific spatial overlap had similar magnitudes in the three species, being slightly shifted towards larger values than the expected interspecific overlap of B. fuscus + C. annularis and B. fuscus + C. gulosus pairs.

CHANGE IN TIDEPOOL USE (MESOCOSM EXPERIMENT)

Three gobiid species showed contrasting patterns of tidepool use under the hetero-specific treatment compared with the mono-specific one (Fig. 5). Chaenogobius gulosus paired with C. annularis showed a significant increase in the number of displaced individuals, while other species and species combinations showed no change (Fig. 5a). Two Chaenogobius species significantly changed their upper/lower positioning depending on paired species, while B. fuscus did not (Fig. 5b). Chaenogobius annularis tended to shift towards the lower intertidal when mixed with other species, particularly C. gulosus. In contrast, C. gulosus moved towards the upper intertidal when mixed with B. fuscus, but towards the lower intertidal when mixed with C. annularis. The degree of aggregation significantly increased in C. annularis but not in other species (Fig. 5c).

GROWTH IN THE MESOCOSM

Chaenogobius annularis showed significantly reduced growth rates in hetero-specific treatments compared with the mono-specific treatment (Fig. 6a Kruskal–Wallis test with Scheffe’s post hoc test, $P < 0.05$). Bathygobius fuscus showed a similar trend, with a reduced growth rate in the mixture with C. annularis (Mann–Whitney U-test, $P < 0.05$) compared

with the mono-specific treatment; the \( B. fuscus \) + \( C. gulosus \) combination was similar to \( Bf + Ca \), though its small sample size did not allow a definite comparison. In contrast, no significant difference in growth rates between treatments was detected for \( C. gulosus \). These trends were also demonstrated by the standardized mean difference of growth rates (Fig. 6b), with \( B. fuscus \) and \( C. annularis \) (but not \( C. gulosus \)) experiencing a negative effect from the presence of other species.

**DISTRIBUTION IN THE FIELD**

Three gobiid species showed distinct patterns of vertical distribution, with peak densities consistently found at different tidal levels (Fig. 7). *Chaenogobius gulosus* was more evenly distributed from the mid intertidal upwards with relatively higher abundances in the upper intertidal, \( B. fuscus \) was most abundant in the mid-low intertidal and \( C. annularis \) was concentrated in the lowest zone.

**Discussion**

**ANALYSIS OF FUNDAMENTAL VS. REALIZED SPATIAL NICHE**

A combination of habitat-use experiments on different spatial scales and null model analyses allowed the evaluation of intra- and interspecific interactions in the spatial utilization and community organization of intertidal fishes. In previous studies the effect of species interactions on community structure has been examined through either experimental (e.g. Black 1979; Pacala & Roughgarden 1982; Elmberg et al. 1997; Munday, Jones & Caley 2001; Schofield 2003) or analytical approaches (e.g. Sale 1974; Lawlor 1980; Tokeshi 1986; Winemiller & Pianka 1990; Tokeshi & Romero 2000; Gotelli & Rohde 2002). Experimental approaches can focus on a particular factor or factors to clarify mechanisms, but may not adequately reflect complex natural situations in which species interactions are embedded. In contrast,
null model analyses are more effective in revealing unexpected patterns and under situations where experimental approaches are difficult or not feasible and the assumption of conventional statistical tests are violated (Gotelli & Graves 1996; Morin 1999). Construction of appropriate null models, however, is problematic (Colwell & Winkler 1984; Gilpin & Diamond 1984; Gotelli & Graves 1996). Unlike previous studies, our null model used the expected values of spatial occupancy and overlap derived from experiments without intra-/interspecific interaction on different spatial scales. This null model analysis based on experimental results is considered less bias-prone and will allow a more rigorous examination of the pattern of resource utilization and mechanisms of community organization.

The results can be represented in a schematic diagram depicting fundamental and realized patterns of space use (Fig. 8). Most notably, B. fuscus showed no difference between fundamental and realized spatial niche, while the two Chaenogobius species showed differences. Chaenogobius annularis had reduced occupancy under hetero-specific treatments (i.e. with both C. gulosus and B. fuscus) and its area of use shifted towards the lower intertidal with a stronger tendency of aggregation. In contrast, C. gulosus had different responses depending on mixed species. When combined with B. fuscus, C. gulosus shifted towards the upper intertidal without decreasing its occupancy, leading to a reduced interspecific overlap. With C. annularis, C. gulosus showed a shift towards the lower intertidal and increased displacement of individuals, suggesting the potential effect of interspecific interactions.

Chaenogobius annularis obviously decreased its occupancy when mixed with B. fuscus, while the latter did not show an apparent change. Interestingly, C. annularis reduced spatial overlap with B. fuscus by aggregating in lower tidepools, suggesting that species interaction may generate vacant space (in this case the upper intertidal) as part of a realized pattern.

In the combination of B. fuscus and C. gulosus, overlap was reduced not through a decrease in tidepool occupancy but through a shift by C. gulosus towards the upper tidal zone. Consequently, the realized total occupancy of B. fuscus and C. gulosus was greater than the expected combined occupancy of the two species. This demonstrates that the range of fundamental space use may be expanded as well as reduced under the influence of interactive relationship. In other words, species interactions could induce expansion of niche at least on one dimension (i.e. space).

Patterns of species assembly represent a summary picture of the interactions and non-interactions characterizing a particular assemblage of species (Tokeshi 1999). Extrapolation of our experimental results is helpful for understanding the patterns in the field, though care should be taken in considering multi-species situations. Bathygobius fuscus mainly occurred in the mid-low intertidal and, together with C. gulosus, appeared to have forced C. annularis into the lowest zone. Chaenogobius gulosus was relatively more abundant towards the upper intertidal, possibly due to the dominance of B. fuscus in the mid-low intertidal. In addition, the observed overlap in the field was similar to the realized overlap of tidepool use in the mesocosm experiment. It may be conjectured that there is a common or similar effect of species interaction with regard to space use under both experimental and field conditions. Overall, our results lend support to a view that ongoing competitive interactions work as a driver in the organization of intertidal fish assemblages.

**PATTERNS ON DIFFERENT SPATIAL SCALES**

Resource use overlap does not directly represent occurrence and/or intensity of competition (e.g. Morin 1999; Munday, Jones & Caley 2001), but differences in overlap between different situations suggest the presence of some forces which
can modify the shape and volume of niche (Tokeshi 1999). Our experiments on different spatial scales revealed different patterns of spatial use overlap even for the same species combination. It is interesting that for all interspecific combinations realized spatial overlap was significantly reduced on the habitat-wide scale (mesocosm experiment) but not on the microhabitat scale (laboratory experiment). Reduction in spatial overlap on the habitat-wide scale mostly resulted from differential tidal height distributions of three gobids, while on the microhabitat scale relatively high interspecific overlap was partly due to intensive interactions such as chasing and attacking when confined in a tidepool. In contrast, reduction in intraspecific overlap on the microhabitat scale was due to individuals of each gobiid species showing flexible substrate choices under intraspecific conditions, leading to spatial segregation of conspecifics within a tidepool. While conspecific individuals of Chaenogobius species used different substrate types to remain in the shelter, under interspecific encounters C. gulosus excluded C. annularis from the shelter, resulting in the latter’s reduction of shelter use (by day, Table 2).

Thus our results indicate that patterns of interaction and spatial utilization vary and different processes of community organization may operate on different spatial scales. Overall, interspecific spatial segregation seems to occur mainly on the habitat-wide scale, while intraspecific segregation is more likely on the microhabitat scale. In this respect, the pattern in the aquarium experiment is considered to represent interactions at low tide (within a tidepool) while the pattern in the mesocosm reflects interactions at low and high tide (within/among tidepools).

The results of growth measurements in the mesocosm experiment suggest that C. annularis experienced negative impacts of interspecific interaction on its growth on the habitat-wide spatial scale. In terms of proximate mechanisms, this may have been attributable to (i) direct interspecific competition, or (ii) its indirect effects through greater intraspecific aggregation in some pools resulting in stronger intraspecific competition. These direct and indirect effects of interspecific interactions are not mutually exclusive and our data do not allow their separate recognition. Nevertheless, the mesocosm experiment has confirmed that the negative effect of interspecific competition on growth is larger than that of intraspecific competition.

Environmental variability is generally much larger among tidepools than among microhabitats within a tidepool. Hilton, Wellenreuther & Clements (2008) showed that physiological differences underpin habitat divergence in sympatric congeneric intertidal fishes. This might apply to the present study where reduced interspecific overlap occurred on a habitat-wide scale. Overall, habitat-wide space partitioning seems relatively more important than microhabitat partitioning in a tidepool, as far as small (< 1 m²) and shallow (< 9.5 cm mean depth) tidepools are concerned. Fishes can move between tidepools at high tide while they have to stay in one tidepool at low tide time. Given large environmental variability of tidepools (Metaxas & Scheibling 1993), it is advantageous to have phenotypic niche flexibility (e.g. Nakano, Fausch & Kitano 1999) allowing the use of different tidepools, especially for competitively inferior species. In addition, species- and size-related microhabitat utilization (Arakaki & Tokeshi 2005) may lessen the negative impact of interactions among intertidal fishes.

**COMPETITIVE COEXISTENCE**

The present study suggests competitive coexistence in this assemblage forming intricate interspecific relations among fish species but with no absolute dominant in terms of both space use and feeding efficiency. Bathygobius fuscus and C. gulosus had variable negative impacts on the habitat utilization and growth of other species, while C. annularis was generally on the receiving end of influence. The negative effect of interactions on growth apparently worked in an asymmetric manner from C. gulosus to other species, while that between B. fuscus and C. annularis occurred in a symmetric manner. Although a superior competitor for space use, B. fuscus seemed to spend much energy in competitive interactions, often resulting in reduced growth. In contrast, C. gulosus may feed and grow more efficiently by changing patterns of space use. Thus, the results of the present study point to a possible trade-off between competitiveness and growth efficiency in these fishes, an aspect which is worth investigating further.

The fact that C. annularis is apparently an inferior competitor for space raises a question about how it can coexist with competitive superior species in the system. Chaenogobius annularis’ space use was suppressed by other species, especially B. fuscus, though it can potentially use a wider range of tidepools than B. fuscus does. In this respect, C. annularis may be considered a generalist that can use part of the resource spectrum that is less exploited by specialist species (Wilson & Yoshimura 1994; Olson, Mittelbach & Osenberg 1995). Indeed, C. annularis showed varied microhabitat use and a wide range of spatial distribution in the field (Arakaki & Tokeshi 2005). Moreover, C. annularis had less continuous use of the same tidepool while C. gulosus tended to stay in the same tidepool (Sasaki & Hattori 1969), suggesting that the former has higher mobility among variable habitat patches.

Rosenzweig (1981) pointed out that habitat selection can lead to competitive coexistence with some density-dependent processes. In the present study, varied patterns of habitat selection occurred on different spatio-temporal scales. As tidepools represent periodically ‘patchy habitats’ (i.e. boundaries disappear at high tide), intensive competition is probably restricted to local, short time scales in tidepools. On the other hand, moving between tidepools also implies associated risks of predation, physical injury and failure to find suitable habitats. Therefore, the balance between the benefits/costs of moving and staying is considered an important aspect of their coexistence. To some extent tidepool fish assemblages may be supported by a process similar to metapopulation dynamics (Gilpin & Hanski 1991; Hanski 1999) whereby individuals
lost from particular tidepools (local extinction) are replaced by those surviving in other habitats (regional maintenance).

Conclusion

Our integrative approach combining experimental and null model analyses revealed the alteration of fundamental spatial niche coupled with a reduction in growth under interspecific interactions. Variable patterns of change in space utilization indicated the operation of scale-dependent processes in intertidal fish assemblages, whereby interspecific interactions were more evident on a microhabitat scale and interspecific ones on a habitat-wide, mesocosm scale. Field-observed patterns of spatial distribution and overlap matched the experimental results, suggesting that the organization of intertidal fish assemblage is at least partly governed by competitive interactions for space use. Intertidal fishes achieve coexistence by adjusting and modifying their fundamental niches to mitigate the negative impact of biotic interactions in patchy and heterogeneous tidepool environments. The present study has demonstrated that the application of experiment-based null model analysis is an effective tool for clarifying the dynamic aspects of niche and species coexistence.

Acknowledgements

We thank all members of the Amakusa Marine Biological Laboratory, especially Y. Nozawa, T. Hirakawa, K. Tokieda and E. Londoño-Cruz, and student participants of the summer field course for invaluable help with preliminary trials of the aquarium experiment. We are also indebted to reviewers who provided useful comments on our earlier drafts. Part of this research was supported by the 21st Century COE programmes of the Kyushu University and the University of the Ryukyus and the GCSE programme of the Kyushu University from the Ministry of Education, Culture, Sports and Technology, the Kyushu University P & P programme and the Japan Society for the Promotion of Science (‘Grant-In-Aid’ nos. 14235013 and 14340246 to MT and 21770826 to SA). Our experimental protocols followed the guideline of the Ichthyological Society of Japan for the use of fishes in research (2003).

References


Spatial niche in intertidal fish assemblage


Received 8 December 2009; accepted 5 August 2010

Handling Editor: Martin Genner