

Species-specific habitat distribution of coral reef fish assemblages in relation to habitat characteristics in an Okinawan coral reef

Atsushi Nanami^{a,b}, Moritaka Nishihira^a, Takao Suzuki^a & Hiroyuki Yokochi^c

^a*Biological Institute, Graduate School of Science, Tohoku University, Sendai 980-8578, Japan*

^b*Current address: National Research Institute of Fisheries Engineering, Fisheries Research Agency, Ebikai, Hasaki, Kashima-gun, Ibaraki, 314-0421, Japan (e-mail: nanami@affrc.go.jp)*

^c*Okinawa Regional Research Center, Tokai University, Amitori, Iriomote, Okinawa 907-1435, Japan*

Received 12 June 2002 Accepted 3 March 2004

Key words: habitat association, coral morphology, habitat characteristics, Pomacentridae, Gobiidae, Labridae

Synopsis

We determined the species-specific habitat associations of coral reef fishes and environmental characteristics in an Okinawan coral reef in Japan. We focused on three families (Pomacentridae, Gobiidae and Labridae) and attempted to determine differences in habitat utilization. We selected six sites along the coast of Amitori Bay, from the entrance to the innermost part, in order to cover a wide range of habitat characteristics (exposed habitat, semi-exposed habitat and sheltered habitat). The species diversity of coral assemblages was greater at the exposed and semi-exposed habitats, whereas branching coral mostly covered the sheltered habitat. The environmental factors that determine the species-specific spatial association in fishes differed among families. Both biological characteristics (coral morphology and coral species diversity) and physical characteristics (water depth and wave exposure) affected the spatial association of pomacentrids and gobiids. In contrast, physical characteristics such as substrate complexity and water depth affected the species-specific spatial association of labrid species. Further study is needed to determine the ecological factors that regulate the species-specific habitat preference in Okinawan coral reefs.

Introduction

The distribution of organisms relative to their habitat is of central importance to ecology. The nature of this distribution provides initial insight into the types of ecological processes that regulate populations and assemblages. In reef fish ecology, species-specific microhabitat associations of fishes have been widely reported (reviews in Jones 1991, Williams 1991). Numerous studies have shown that the local scale abundance of coral reef fishes is correlated with coral cover (e.g., Bell & Galzin 1984, Munday et al. 1997, Munday 2000), availability of shelter holes (Roberts & Ormond 1987, Hixon & Beets 1993), structural complexity

(Luckhurst & Luckhurst 1978, Sano et al. 1984, 1987, McCormick 1994, Nanami & Nishihira 2002), and biological or structural characteristics of habitat zones (Yamamoto 1976, Clarke 1977, Alevizon et al. 1985, Green 1996, Chabanet et al. 1997). Although a fundamental aim of ecological studies is to understand how fishes respond to the heterogeneity of reef substrata over a wide range of spatial scales, few studies on the association between coral reef fish and reef habitat have been carried out in Japan. Exceptions include work by Yamamoto (1976) showed that the species compositions and spatial distributions of 25 pomacentrid species roughly corresponded to the coral zonation (e.g., coral coverage and coral

morphology) on a small spatial scale (within 100 m) in an Okinawan coral reef in Japan. Nanami and Nishihira (2002) studied the spatial differences between fish assemblage structures on a rocky reef flat and an adjacent sandy sea bottom (separated by 100 m) in Okinawa, and they found that the fish assemblage structures were substantially different and that the difference was maintained during a 2-year study period. Unfortunately, there have been few studies in which fish-habitat association was investigated on a broader spatial scale (>1 km) in an Okinawan coral reef. Most of the data on ecology of reef fish assemblages have been obtained from studies conducted along the Great Barrier Reef and in Caribbean Sea, and there is relatively little in Okinawan coral reefs. Results of studies at Okinawan coral reefs with the aim of determining the validity of proposed mechanisms underlying the organization of reef fish assemblages should therefore contribute to a more comprehensive understanding of the ecology of reef fish assemblages.

The purpose of the present study is to examine population densities and reef fish assemblage structures of three families (Pomacentridae, Gobiidae and Labridae) within six habitats in Amitori Bay, Iriomote Island, Okinawa, Japan in order to determine species-specific habitat variations in coral reef fish assemblages.

Materials and methods

Study site

The study site was located on a fringing reef in front of the Okinawa Regional Research Center, Tokai University, Amitori Bay, Iriomote Island, Okinawa, Japan ($24^{\circ}20'N$, $123^{\circ}42'E$) (Figure 1). We selected six sites along the coast, from the entrance to the innermost part of Amitori Bay, in order to cover a wide range of habitat characteristics (Figure 1). The six sites were classified into three kinds of habitat: (1) exposed habitat (site 1 and site 2), (2) semi-exposed habitat (site 3 and site 4) and (3) sheltered habitat (site 5 and site 6). The exposed habitat was located in the area most exposed to wave action from northwest swells. The semi-exposed habitat was located near the center of Amitori Bay and had a lesser degree of wave

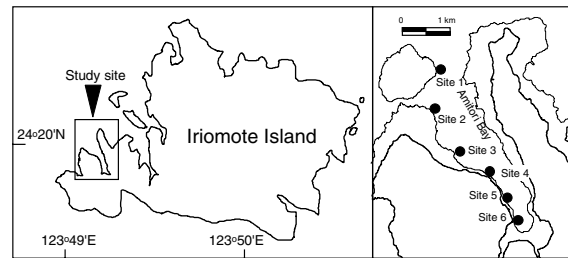


Figure 1. Map of Iriomote Island and six sites that were selected along a 2-km-long section of the coast of Amitori Bay. The six sites were composed from 3 type habitats such as exposed sites (site 1 and site 2), semi-exposed sites (site 3 and site 4) and sheltered sites (site 5 and site 6). At each site, one quadrats ($4\text{ m} \times 4\text{ m}$ in area) were established at the depth of 2, 5 and 10 m.

exposure. The sheltered habitat was located in the innermost area of Amitori Bay and was exposed to very little wave action. In order to clarify the differences between fish assemblage structures at the six sites and at three water depths, one permanent quadrat ($4\text{ m} \times 4\text{ m}$) was established at each depth of 2, 5 and 10 m at each site (total of 18 quadrats). Quadrats at each site were separated by more than 5 m except for at site 1, one at a depth of 5 m and one at a depth of 10 m, which were separated about 2 m due to the existence of a steep reef slope. The spatial distributions of coral colonies within each quadrat were recorded in detail on maps by the following procedure. Iron rods were used to divide each quadrat into 64 ($50\text{ cm} \times 50\text{ cm}$) sections. All corals in each section in each quadrat were recorded by a digital video camera. Maps of each permanent quadrat showing the positions and sizes of all coral colonies, including living and dead corals, were made from the video images, and corals present in the quadrats were classified by their morphology into six categories (branching, tabulate, massive, encrusting, leafy, and dead coral skeleton). Corals were classified into these categories because previous studies in which corals were classified by morphology demonstrated species-specific habitat association of fishes (e.g., Itzkowitz 1977, Syms 1995).

Analysis of habitat characteristics

From the maps, the projected areas of all coral colonies were visually measured by following

procedure. Each section (50 cm × 50 cm) was divided into 25 (10 cm × 10 cm) sub-sections. If corals occupied the entire sub-section, the coverage of coral in the sub-section was estimated as 100 cm² (10 cm × 10 cm). If corals partially occupied the sub-section, the coverage of coral in the sub-section was estimated as 50 cm² (5 cm × 10 cm). The diversity of the six coral categories was estimated using Shannon's Index: $H' = -\sum p_i \ln(p_i)$, where p_i is the proportion of the total area covered by the i th coral category. We defined the value as "coral diversity".

Since coral in each of the quadrats had created a complex substratum and provided habitat spaces for fishes, quantification of the complexity of the substratum was considered necessary. The complexity of the substratum in each quadrat was quantified by the following technique. Iron rods were driven into the substrate at the four corners of each quadrat. Ropes were then stretched horizontally from each rod at a height of 50 cm, and each quadrat was divided into 64 (50 cm × 50 cm) sections. We then measured the height of the coral (accurate to 1 cm) at 25-cm intervals along the nylon ropes. The squared differences between the heights of consecutive irregularity values (25-cm intervals) were summed, and the value was defined as "substrate complexity".

Measurement of sedimentation

Gleason et al. (1979) and Ward et al. (1984) demonstrated that sedimentation retention is greater at sites of low wave exposure in shallow areas. Although we were not able to measure the intensity of wave exposure directly, we considered the quantitative estimation of sedimentation to represent the intensity of wave exposure. In order to determine the difference between degrees of sedimentation accumulation in the 18 quadrats, slate plates (10 cm × 10 cm) were set near each permanent quadrat in August 1999. At each quadrat, four plates were placed on rocks and left for two days. It was found that a 2-day setting of the plates was sufficient for sediment to accumulate on the plate. After two days, the plates were carefully placed in zip-type plastic bags. There was

little disturbance of sediment matter that had accumulated on the plates during this procedure. In the laboratory, the dry weight of sediment matter was measured.

Fish census

Surveys of fish assemblages in the 18 quadrats were conducted in July and August 1999. Species names, locations where individual fish were observed, life-history intervals (adults or juveniles), and estimated total length for each fish were recorded. Identification of fish species was based on Masuda & Kobayashi (1994). Terminal-phase adults and initial adults in labrid species were included.

The censuses were carried out using the method of Nanami & Nishihira (2002). Each permanent quadrat was divided into 64 (50 cm × 50 cm) sections by iron rods, and data were recorded while swimming along these rods. Data were recorded three times for each quadrat. In the first census, the fishes showing little attachment to the quadrat and swimming away from the quadrat in response to the approach of the diver (A. Nanami) were recorded. In the second census, the fishes showing strong site-attachment and not swimming out of the quadrat in response to the approach of the diver were recorded. In the final census, small cryptic fish (e.g., gobiids), that may have been missed in the first and second censuses, were recorded. The first, second and third censuses were recorded immediately after one another. This procedure was carried out three times for each quadrat, and each data set represented the average number of fishes recorded in the three consecutive surveys. Further details and merits of the procedure are described by Nanami & Nishihira (2002).

Data analysis

The similarity in environmental conditions in the eighteen quadrats was estimated by correspondence analysis (CA). Interpretation of the results of the CA was based on the plots of environmental variables and quadrats using the first two axes of the analysis. We selected 10 environmental variables: coverage of six coral categories (branching,

massive, tabulate, leafy, encrusting and dead corals), coral diversity, substrate complexity, depth and density of sedimentation.

Since three families (Pomacentridae, Labridae and Gobiidae) were the most dominant Families in terms of abundance (totally 68.2%; Pomacentridae: 20.4%, Labridae: 9.6% and Gobiidae: 38.2%) and species richness (totally 52.0%; Pomacentridae: 18.5%, Labridae: 21.2% and Gobiidae: 12.3%), we selected these three families for analyses. Species-specific spatial variations for Pomacentridae, Gobiidae and Labridae in the 18 quadrats were estimated using canonical correspondence analysis (CCA). CCA was performed using CANOCO (ter Braak & Smilauer 1998). Ten environmental variables (coverage of six coral categories, coral diversity, substrate complexity, depth and sedimentation) were selected to explain the relationship between habitat characteristics and fish fauna. Each data set represented the average number of fishes for a set of three con-

secutive surveys for each quadrat. Common species of Pomacentridae, Gobiidae and Labridae were selected for analysis to determine whether there was species-specific habitat preference in the 18 quadrats (Appendix 1). Rare species (i.e., species for which the total abundance in the 18 quadrats was less than two individuals) were omitted from the analysis. Finally, 19 species of Pomacentridae, 12 species of Gobiidae, and 13 species of Labridae were selected for the CCA. The environmental variables that were significant when correlated with the ordination axis were identified.

Results

Habitat characteristics

Habitat characteristics are shown in Table 1. Coral coverage ranged from 27.7% (2C) to 66.8% (1B). Generally, coral diversity was greater in the

Table 1. Description of the study sites using three quadrats (each 4 m × 4 m in area) per site established in Amitori Bay, Okinawa, Japan.

Site	Habitat	Quadrat code	Depth (m)	Coral coverage (%)	Coral diversity	Coral category	Substrate complexity	Sedimentation (mg dry wt./100 cm ² /48 h)
Site 1	Exposed	1A	2	52.6	1.64	B, D, E, L, M, T	112.1 ± 22.1	26.03 ± 5.11
		1B	5	66.8	1.71	B, D, E, L, M, T	143.2 ± 22.5	15.67 ± 5.92 ^a
		1C	10	41.3	1.72	B, D, E, L, M, T	374.8 ± 98.6	15.31 ± 3.11
Site 2	Exposed	2A	2	42.2	1.23	B, D, E, L, M, T	129.4 ± 7.6	33.92 ± 14.38
		2B	5	48.0	1.36	B, D, E, L, M, T	165.6 ± 24.1	78.03 ± 52.45
		2C	10	27.7	0.96	B, D, E, L, M, T	151.4 ± 43.7	50.48 ± 4.43
Site 3	Semi-exposed	3A	2	49.5	1.43	B, D, E, L, M, T	129.3 ± 27.8	32.71 ± 7.16
		3B	5	54.5	1.53	B, D, E, L, M, T	179.1 ± 48.0	34.55 ± 20.29
		3C	10	43.9	1.67	B, D, E, L, M, T	192.8 ± 64.2	44.22 ± 14.70
Site 4	Semi-exposed	4A	2	63.2	1.28	B, D, E, L, M, T	182.9 ± 40.5	42.72 ± 19.91
		4B	5	37.1	1.46	B, D, E, L, M, T	197.9 ± 92.8	25.35 ± 8.81
		4C	10	40.7	1.10	B, D, E, L, M, T	106.2 ± 27.3	29.94 ± 2.11
Site 5	Sheltered	5A	2	29.7	1.39	B, D, E, M, T	201.6 ± 61.0	84.30 ± 28.92
		5B	5	36.1	0.05	B, T	284.4 ± 90.8	140.6 ± 54.12
		5C	10	33.0	0.03	B, E, L	249.6 ± 60.5	134.7 ± 26.53
Site 6	Sheltered	6A	2	37.5	1.39	B, D, E, L, M, T	181.6 ± 48.3	175.8 ± 46.62
		6B	5	77.5	0.00	B	256.1 ± 77.1	129.9 ± 53.04
		6C	10	60.4	0.16	B, D, E, M	184.9 ± 34.3	106.9 ± 37.66

For measurement for coral diversity, substrate complexity (±SD) (n = 9) and sedimentation (±SD) (n = 4), see text. Coral morphology is described by the following abbreviations: B, branching; E, encrusting; M, massive; T, tabular; L, leaf; D, dead coral skeletons.

^aOnly two plates were available (n = 2).

exposed habitat (site 1 and site 2) and semi-exposed habitat (site 3 and site 4) because all six coral categories were observed in these sites (Table 1). In contrast, branching coral (*Acropora echinata*) mostly covered the quadrats in sheltered and deeper habitats (5B, 5C, 6B and 6C), and the coral diversities were extremely low in these four quadrats (coral diversity = 0–0.16, Table 1). The density of the sedimentation was significantly greater at sheltered sites (exposed habitat = semi-exposed habitat < sheltered habitat, Scheffe's test, $p < 0.001$) ($n = 22$ –24). This suggest that the degree of wave exposure was significantly greater in the exposed and semi-exposed habitats (site 1–site 4) than in the sheltered habitat (site 5 and site 6). The substrate complexities in the exposed habitat, semi-exposed habitat and sheltered habitat were not significantly different (Scheffe's test, $p > 0.05$) ($n = 54$).

The CA showed that the exposed habitat (site 1 and site 2) and semi-exposed habitat (site 3 and site 4) had minus scores on the first CA axis, except for 2C and 4C (Figure 2). Seven quadrats (1A, 1B, 2A, 2B, 3A, 3B and 4A) were characterized by a high degree of coverage of four types of corals (encrusting, tabular, massive and dead coral skeletons) and by a high degree of coral diversity.

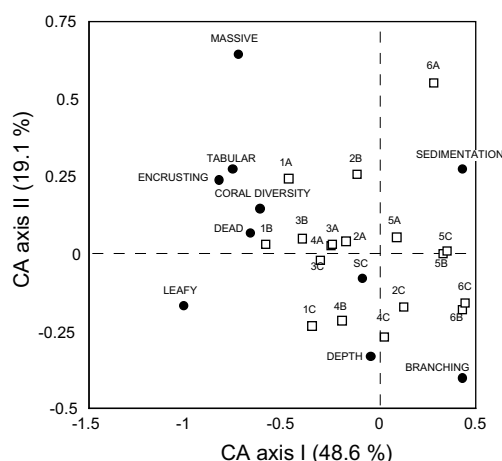


Figure 2. Result of CA to explain the similarity of habitat characteristics among 18 quadrats. Black symbols and white symbols represent the environmental variables and quadrats, respectively.

Three quadrats (1C, 3C and 4B) were characterized by a high degree of coverage of leafy coral. In contrast, the sheltered habitat (site 5 and site 6) had plus scores on the first axis (CA axis I). The density of sedimentation was high in 6A, whereas branching corals were dominant in 6B and 6C. In general, the exposed habitat and semi-exposed habitat were characterized by high coral diversity, whereas higher density of sedimentation (degree of wave exposure being low) and high coverage of branching corals characterized the sheltered habitat.

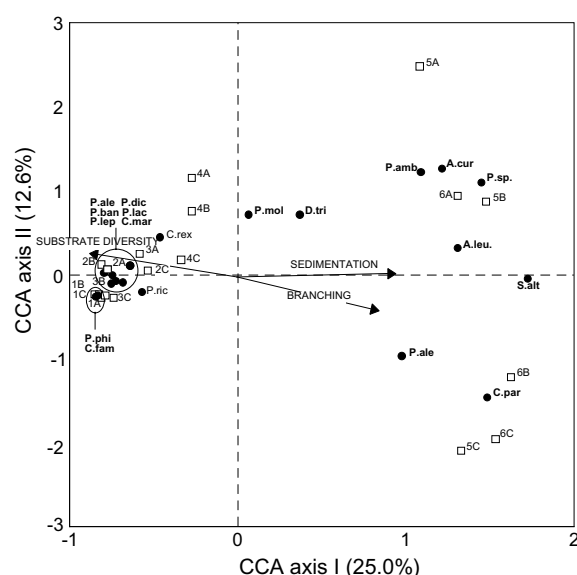


Figure 3. Result of CCA for 19 species of pomacentrids explaining the species-specific spatial distribution among 18 quadrats. Vectors, white symbols and black symbols represent the environmental variables, quadrats and species, respectively. The species names were indicated by abbreviations: A.cur = *Amblyglyphidodon curacao*; A.leu = *Amblyglyphidodon leucogaster*; C.fun = *Chromis funea*; C.mar = *Chromis margaritifer*; C.par = *Chrysiptera parasema*; C.rex = *Chrysiptera rex*; D.tri = *Dascyllus trimacuratus*; P.dic = *Plectroglyphidodon dickii*; P.joh = *Plectroglyphidodon johnstoniatus*; P.lac = *Plectroglyphidodon lacrymatus*; P.ale = *Pomacentrus alexanderae*; P.amb = *Pomacentrus amboinensis*; P.ban = *Pomacentrus bandanensis*; P.leu = *Pomacentrus lepidogenys*; P.mol = *Pomacentrus moluccensis*; P.phl = *Pomacentrus philippinus*; P.ric = *Pomacentrus richardsoni*; S.alt = *Stegastes altus*.

Species-specific habitat association of fishes

A total of 43 species (23 genera) and 1914 individuals of fishes were recorded for the three families (Appendix 1). The results of CCA indicated that biological characteristics (coral diversity and branching corals) and physical characteristics (sedimentation \equiv wave exposure) affected the spatial distribution of pomacentrids (CCA axis I and CCA axis II had eigenvalues of 0.871 and 0.442, respectively). Pomacentrid assemblage could be clearly divided into two groups along the six sites (Figure 3), i.e., a group inhabiting exposed and semi-exposed habitats (site 1–site 4) that had minus scores on CCA axis I, and a group inhabiting sheltered habitat (site 5 and site 6) that had plus scores on CCA axis I. CCA axis II mainly indicates the difference along coverage of branching corals in the pomacentrid assemblage structures. The differences along CCA axis II in pomacentrid assemblage structures was less clear in the exposed habitat (site 1 and site 2) and in one semi-exposed habitat (site 3), relatively clear in one semi-exposed habitat (site 4), and markedly clear in the sheltered habitat (site 5 and site 6) (Figure 3). Nine species (*Pomacentrus lepidogenys*, *Pomacentrus philippinus*, *Pomacentrus bankanensis*, *Plectroglyphidodon dickii*, *Plectroglyphidodon johnstonlatus*, *Plectroglyphidodon lacrymatus*, *Chromis margaritifer*, *Pomachromis richardsoni* and *Chromis fumea*) preferred the exposed and semi-exposed habitats (site 1–site 3). Three species (*Chrysiptera rex*, *Pomacentrus moluccensis* and *Dascyllus trimaculatus*) were observed around a semi-exposed habitat (site 4), but several individuals of these three species were also observed at other sites (site 2–site 6) (Appendix 1). In contrast, seven species that inhabited sheltered sites showed clear differences along CCA axis II. Three of these species (*Pomacentrus* sp., *Pomacentrus amboinensis* and *Amblyglyphidodon curacao*) inhabited a shallow area (2 m in depth), two species (*Stegastes altus* and *Amblyglyphidodon leucogaster*) inhabited a an area of medium depth (5 m in depth), and two species (*Pomacentrus alexanderae* and *Chrysiptera parasema*) inhabited a deep area (10 m in depth).

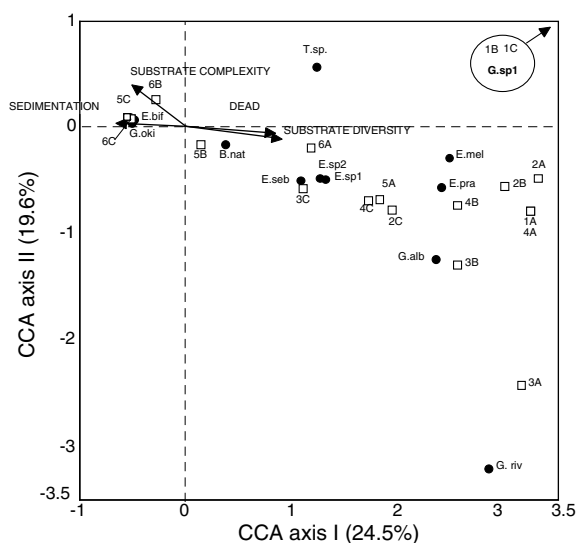


Figure 4. Result of CCA for 12 species of gobiids explaining the species-specific spatial association among 18 quadrats. Vectors, white symbols and black symbols represent the environmental variables, quadrats and species, respectively. The species names were indicated by abbreviations: B.nat = *Bryaninops natans*; E.bif = *Eviota bifasciata*; E.mel = *Eviota melasma*; E.pra = *Eviota prasina*; E.seb = *Eviota sebreei*; E.sp1 = *Eviota* sp.1; E.sp2 = *Eviota* sp.2; G.alb = *Gobiodon albofasciatus*; G.oki = *Gobiodon okinawae*; G.riv = *Gobiodon rivulatus*; G.sp1 = *Gobiodon* sp.1; T.sp. = *Trimma* sp. Since the score for *Gobiodon* sp., 1B and 1C lies off the plot at ((3.62, 9.49), (4.45, 11.77) and (4.49, 13.61) respectively), the solid symbols for them are not indicated.

For gobiids, a species-specific spatial distribution was not clearly observed, although several species tended to show species-specific spatial distribution (Figure 4) (CCA axis I and CCA axis II had eigenvalues of 0.750 and 0.599, respectively). Four species (*Bryaninops natans*, *Eviota bifasciatum*, *Eviota* sp. 2 and *Gobiodon okinawae*) were mainly observed at sheltered sites (site 5 and site 6) (Figure 4, Appendix 1). In contrast, the other eight species did not show clear spatial distributions (Figure 4, Appendix 1). Since the direction and length of two vectors, coral diversity and substrate complexity, seem to be the main environmental variables along CCA axis I and CCA axis II, these two environmental variables were considered to be the main factors determining the spatial distribution of gobiid assemblage (Figure 4).

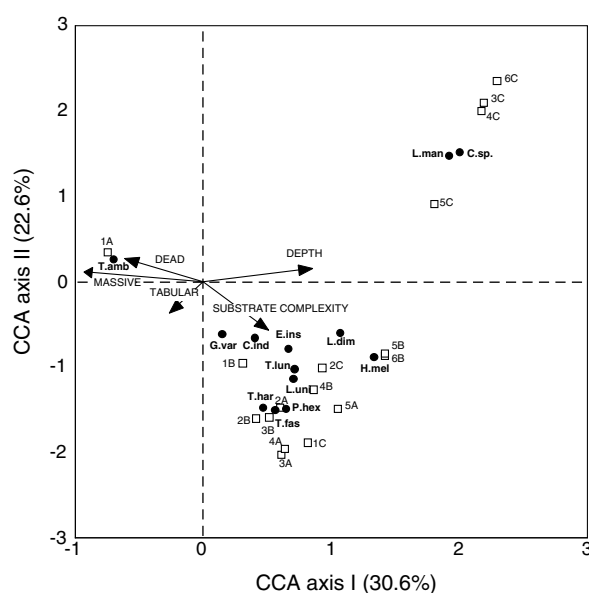


Figure 5. Result of CCA for 13 species of labrids explaining the species-specific spatial association among 18 quadrats. Vectors, white symbols and black symbols represent the environmental variables, quadrats and species, respectively. The species names were indicated by abbreviations: C.ind = *Cheilinus indulatus*; C.sp. = *Cirrhiabrus* sp.; E.ins = *Epibulus insidiator*; G.var = *Gomphosus varius*; H.mel = *Halichoeres melanurus*; H.fas = *Hemigymnus fasciatus*; L.uni = *Labrichthys unilineatus*; L.dim = *Labroides dimidiatus*; L.man = *Labropsis manabei*; P.hex = *Pseudocheilinus hexataenia*; T.amb = *Thalassoma amblycephalum*; T.har = *Thalassoma hardwickii*; T.lun = *Thalassoma lunare*.

The labrid assemblage structures could be divided into three groups (Figure 5) (CCA axis I and CCA axis II had eigenvalues of 0.875 and 0.647, respectively). One species, *Thalassoma amblycephalum*, was dominant in the most-exposed and shallowest area (1A). In contrast, most of the labrid species (10 species: *Gomphosus varius*, *Cheilinus fasciatus*, *Epibulus insidiator*, *Halichoeres melanurus*, *Hemigymnus fasciatus*, *Labrichthys unilineatus*, *Labroides dimidiatus*, *Pseudolabrus japonicus*, *Thalassoma hardwickii* and *Thalassoma lunare*) selected sites where habitat complexity was high (Figure 5). Differences at the six sites and at the three depths among the 10 species were not clear. Other species (two species: *Cirrhiabrus* sp. and *Labropsis manabei*) were observed in four quadrats in deeper areas (3C, 4C, 5C and 6C). These results suggest that the spatial pattern of labrid species except for *T. amblycephalum* was influenced by physical

characteristics such as substrate complexity and water depth.

Discussion

The present study demonstrates that species-specific spatial distribution of coral reef fishes and spatial distribution was substantially affected by the habitat characteristics in an Okinawan coral reef (Figures 3–5). These results of the present study are consistent with results of several other studies demonstrating species-specific habitat associations for pomacentrids (Yamamoto 1976, Clarke 1977, Itzkowitz 1977), gobiids (Munday 2000, 2002) and labrids (Green 1996). For pomacentrids, coral morphology and coral diversity and sedimentation (\equiv wave exposure) determine the spatial distribution. Although a

variety of processes could produce this pattern, it is most easily explained by broad-scale habitat selection (Wellington 1992, Gutiérrez 1998). Settling individuals may use the presence of conspecific individuals as a cue for suitable habitat characteristics (Sweatman 1983, 1985, Jones 1987a, b, Booth 1992). Those studies demonstrated that growth was reduced by intraspecific competition (Jones 1987a, b, Booth 1995), but survivorship may be increased in larger groups (Booth 1995). Elucidation of habitat selection and/or intraspecific interactions may be important for understanding species-specific spatial differences for pomacentrids.

For gobiids, only four species (*Bryaninops nantans*, *Eviota bifasciatum*, *Eviota* sp. 2 and *Gobiodon okinawae*) were commonly observed in the sheltered habitat. This is partly consistent with the findings that wave exposure determines the spatial difference of coral-dwelling gobies (Munday et al. 1997, Munday 2000). Munday (2002) suggested that interspecific interactions operate in the spatial distribution of four coral-dwelling gobies. Figure 4 shows that coral diversity and substrate complexity also seem to be the main factors responsible for spatial distribution of gobiid fishes. Gobiid fishes analyzed in the present study were cryptic species, and substrate complexity created by diverse corals might affect the habitat association of gobiid fishes. Further studies are needed to clarify the effect of interspecific competition and habitat structure on spatial distribution of gobiids.

The species-specific habitat association of labrids was less clear than for that of pomacentrids and gobiids (Figure 5). Substrate complexity and depth were correlated with the abundance of most of the labrid species, and coral morphology itself was not a major determinant for habitat association of labrids (Figure 5). Similar results were obtained by Green (1996), suggesting that labrids have a large home range that may encompass a variety of habitat features and they are unlikely to show strong association with specific habitat characteristics. Another reason why the labrids show few habitat associations

with coral morphology and/or coral diversity might be their behavioral traits. Spatial distribution of labrids seems to be affected by social interactions with other fishes rather than distribution and availability of certain kinds of habitats (Jones 1984). In contrast, although some labrid species show different spatial patterns of habitat by adults and recruits, Green (1996) suggested that recruitment patterns of juveniles is important in structuring patterns of habitat use of labrids. Further studies are required to test these hypotheses.

In conclusion, the present study suggested that habitat characteristics such as coral diversity, coral morphology, substrate complexity, water depth and wave exposure are one of the factors responsible for species-specific spatial association in coral reef fishes. These species-specific habitat associations might be due to habitat selection at the time of juvenile settlement and/or inter- and intra-specific competition. If so, differences between species compositions at different habitat sites would not change over time, and the degree of temporal stability in species composition of fish assemblages at particular sites would be high. Further studies are needed to determine what ecological factors regulate species-specific habitat associations of fishes in an Okinawan coral reef.

Acknowledgements

We thank Hiroyoshi Kohno, Ken Sakihara, Nagahiro Nakazato, Toshiaki Nakamura, and the Okinawa Regional Research Center, Tokai University, for assisting in the field work, and four anonymous reviewers for their comments on the manuscript. This study was supported in part by a grant-in-aid (no. 09NP1501) for creative basic research program (DIVER) from the Ministry of Education, Science, Sports and Culture, Japan. This paper is a contribution from the Okinawa Regional Research Center, Tokai University.

Appendix 1. List of pomacentrids, labrids and gobiids observed in Amitori Bay, Okinawa, Japan. Six sites were selected, and quadrats (each 4 m × 4 m in area) were established at depths of 2, 5 and 10 m at each site. In total, 18 quadrats were established. Numbers are the densities of species in each quadrat. Three consecutive surveys were conducted, and the average number was used for analysis.

Species name	Code	Site 1			Site 2			Site 3			Site 4			Site 5			Site 6			Total
		1A	1B	1C	2A	2B	2C	3A	3B	3C	4A	4B	4C	5A	5B	5C	6A	6B	6C	
Pomacentridae																				
<i>Amblyglyphidodon curacao</i>	A. cur										1.0			23.3	16.0		2.7	5.0	48.0	
<i>Amblyglyphidodon leucoga</i>	A. leu			1.0			0.3				1.0	1.0			37.0	1.0	0.7	5.3	47.3	
<i>Chromis funea</i>	C. fun			5.3															5.3	
<i>Chromis margaritifer</i>	C. mar	5.3	7.7	3.0	6.3	7.0		1.7	1.0										32.0	
<i>Chrysiptera parasema</i>	C. par														4.3	2.0	1.0	8.3	35.3	51.0
<i>Chrysiptera rex</i>	C. rex				3.7	2.0					5.7	1.0								12.3
<i>Dascyllus trimaculatus</i>	D. tri							3.0	0.7					2.7	1.7			1.0	9.0	
<i>Plectroglyphidodon dickii</i>	P. dic	5.3			1.7						1.3								8.3	
<i>Plectroglyphidodon johnstonianus</i>	P. joh		2.7	4.3	1.3	0.5	1.0		0.7		0.3								10.8	
<i>Plectroglyphidodon lacrymatus</i>	P. lac	1.0	11.0	0.7	2.3	5.0		1.3	4.0	2.0	0.7								28.0	
<i>Pomacentrus alexanderae</i>	P. ale	0.3			0.3				1.0			2.0			2.0	4.5		9.3	19.5	
<i>Pomacentrus amboinensis</i>	P. amb													3.0			1.3	4.3		
<i>Pomacentrus bankanensis</i>	P. ban		0.7	5.3		7.5	2.7	2.7	2.3	2.7	5.5	2.3							31.7	
<i>Pomacentrus lepidogenys</i>	P. leu	19.3	52.3	19.3	5.3	6.0	1.3	6.7	14.0	9.7	5.0	12.7							151.7	
<i>Pomacentrus moluccensis</i>	P. mol						6.7				8.0	6.5	6.7		7.3		1.0	0.7	36.8	
<i>Pomacentrus philippinus</i>	P. phi	4.0	4.0	8.0						5.0									21.0	
<i>Pomacentrus richardsoni</i>	P. ric	12.7	2.0	0.7			18.3	6.7											40.3	
<i>Pomacentrus sp.</i>	P. sp.													1.7			2.3	0.3	4.3	
<i>Stegastes altus</i>	S. alt													0.3	3.7			3.0	7.0	
Labridae																				
<i>Chelinus indulatus</i>	C. ind	2.0	4.7	0.3				0.3			2.0								9.8	
<i>Cirrhitabrus sp.</i>	C. sp.			0.3				4.7				13.7		0.7	3.0		0.3	1.0	23.7	

Appendix 1. (Continued)

Species name	Code Site 1			Site 2			Site 3			Site 4			Site 5			Site 6			Total
	1A	1B	1C	2A	2B	2C	3A	3B	3C	4A	4B	4C	5A	5B	5C	6A	6B	6C	
<i>Epibulus insidiator</i>	E. ins	1.3	0.7	1.0	0.7								1.0	1.3	0.5		0.3		6.8
<i>Gomphosus varius</i>	G. var	3.0	2.7		0.7	1.0	0.3	1.3		0.3									9.7
<i>Halichoeres melanurus</i>	H. mel		0.3								1.0	0.3	2.0	3.0	1.0		1.3		9.0
<i>Hemigymnus fasciatus</i>	H. fas				0.3	1.5				0.3			0.7						2.8
<i>Labrichthys unilineatus</i>	L. uni	1.3	1.0		1.0	2.5	0.3	0.3	0.3	0.3	0.5		0.3				0.3		9.0
<i>Labroides dimidiatus</i>	L. dim	0.3	0.3	0.7			0.3	0.7	0.3		1.0	1.0	1.0						4.3
<i>Labropsis manabei</i>	L. man				0.3	0.3			0.7			2.0							3.3
<i>Pseudocheilinus hexataenia</i>	P. hex		7.3		2.7	4.0	0.7	1.0	1.3	0.7									17.7
<i>Thalassoma amblycephalum</i>	T. amb	144	2.7		0.7	2.0													167.3
<i>Thalassoma hardwickii</i>	T. har	0.3	0.7		0.3	0.5	0.7			1.3	0.5		0.3						4.7
<i>Thalassoma lunare</i>	T. lun		1.7							1.0		0.3	1.3						4.3
Gobiidae																			
<i>Bryatinops natans</i>	B. nat								16.7					22.0	21.0	31.0		13.3	104.0
<i>Eviota bifasciata</i>	E. bif								8.0			1.0		37.0	571		5	118	740.3
<i>Eviota melasma</i>	E. mel	0.7	0.3	0.3	0.3	2.0	1.0	0.7	2.3	0.7	8.5	1.0	3.7			0.3			32.2
<i>Eviota prasina</i>	E. pra	1.3				0.3		1.3		1.3	0.5	0.3				2.7			7.8
<i>Eviota sebreei</i>	E. seb					1.7			3.3						0.5	3.0			8.5
<i>Eviota</i> sp. 1	E. sp1				0.5	4.0	1.0	7.0	21.3	8.0	11.0		1.3	5.0	9.0	4.7			81.8
<i>Eviota</i> sp. 2	E. sp2					0.7				1.0	1.3		34.0	8.3	5.0	12.0		1.0	63.3
<i>Gobiodon albofasciatus</i>	G. alb						2.7	6.7	3.0	1.0									13.3
<i>Gobiodon okinawae</i>	G. oki																7.3		7.3
<i>Gobiodon rivulatus</i>	G. riv						2.0									0.3			2.3
<i>Gobiodon</i> sp. 1	G. sp1	1.0	4.0													1.0			6.0
<i>Trimma</i> sp.	T. sp.		0.3							0.3			2.0			1.7	1.0	0.3	5.7
Pomacentridae Total		48.0	80.3	47.7	0.0	21.0	23.0	35.3	0.0	15.3	27.7	22.0	0.0	38.3	64.7	7.5	0.0	4.3	568.8
Labridae total		151.0	15.0	10.7	0.0	6.7	11.5	1.7	0.0	2.3	3.7	5.7	0.0	6.7	5.0	0.0	0.0	2.3	272.5
Gobiidae total		2.0	1.3	4.7	0.0	0.3	2.5	7.7	0.0	7.7	16.0	53.7	0.0	41.0	72.3	606.5	0.0	56.7	1072.7
Total		201.0	96.7	63.0	0.0	28.0	37.0	44.7	0.0	25.3	47.3	81.3	0.0	86.0	142.0	619.0	0.0	61.0	1914.0

References

- Alevizon, W., R. Richardson, P. Pitts & G. Serviss. 1985. Coral zonation and patterns of community structure in Bahamian reef fishes. *Bull. Mar. Sci.* 36: 304–318.
- Bell, J.D. & R. Galzin. 1984. Influence of live coral cover on coral-reef fish communities. *Mar. Ecol. Prog. Ser.* 15: 265–274.
- Booth, D.J. 1992. Larval settlement patterns and preferences by domino damselfish *Dascyllus albisella* Gill. *J. Exp. Mar. Biol. Ecol.* 155: 85–104.
- Booth D.J. 1995. Juvenile groups in a coral reef damselfish: Density-dependent effects on individual fitness and population demography. *Ecology* 76: 91–106.
- Chabanet, P., H. Ralambondrainy, M. Amanieu, R. Faure & R. Galzin. 1997. Relationships between coral reef substrata and fish. *Coral Reefs* 16: 93–102.
- Clarke, R.D. 1977. Habitat distribution and species diversity of chaetodontid and pomacentrid fishes near Bimini, Bahamas. *Mar. Biol.* 40: 277–289.
- Gleason, M.L., D.A. Elmer, N.C. Pien & J.S. Fisher. 1979. Effects of stem density upon sediment retention by salt marsh cord grass *Spartina alterniflora* Loisel. *Estuaries* 2: 271–273.
- Green, L.A. 1996. Spatial, temporal and ontogenic patterns of habitat use by coral reef fishes (Family Labridae). *Mar. Ecol. Prog. Ser.* 133: 1–11.
- Gutiérrez, L. 1998. Habitat selection by recruits establishes local patterns of adult distribution in two species of damselfishes: *Stegastes dorsopunicans* and *S. planifrons*. *Oecologia* 115: 268–277.
- Hixon, M.A. & J.P. Beets. 1993. Predation, prey refuges and the structure of coral reef fish assemblages. *Ecol. Monogr.* 63: 77–101.
- Iitzkowitz, M. 1977. Spatial organization of the Jamaican damselfish community. *J. Exp. Mar. Biol. Ecol.* 28: 217–241.
- Jones, G.P. 1984. The influence of habitat and behavioural interactions on the local distribution of the wrasse, *Pseudolabrus celidotus*. *Environ. Biol. Fishes* 10: 43–58.
- Jones, G.P. 1987a. Competitive interactions among adults and juveniles in a coral reef fish. *Ecology* 68: 1534–1547.
- Jones, G.P. 1987b. Some interactions between residents and recruits in two coral reef fishes. *J. Exp. Mar. Biol. Ecol.* 114: 169–182.
- Jones, G.P. 1991. Postrecruitment processes in the ecology of coral reef populations: a multifactorial perspective. pp. 294–328. *In*: P.F. Sale (ed.), *The Ecology of Fishes on Coral Reefs*, Academic Press, San Diego.
- Luckhurst, B.E. & K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Ecol. Prog. Ser.* 49: 317–323.
- Masuda, H. & Y. Kobayashi. 1994. *Grand Atlas of Fish Life Modes* (in Japanese). Tokai University Press, Tokyo. 465pp.
- McCormick, M.I. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Mar. Ecol. Prog. Ser.* 112: 87–96.
- Munday, P.L. 2000. Interactions between habitat use and patterns of abundance in coral-dwelling fishes. *Environ. Biol. Fishes* 58: 355–369.
- Munday, P.L. 2002. Does habitat availability determine geographical-scale abundance of coral-dwelling fishes? *Coral Reefs* 21: 105–116.
- Munday, P.L., G.P. Jones & M.J. Caley. 1997. Habitat specialization and the distribution and abundance of coral-dwelling gobies. *Mar. Ecol. Prog. Ser.* 152: 227–239.
- Nanami, A. & M. Nishihira. 2002. The structure and dynamics of fish communities in an Okinawan coral reef: effects of coral-based habitat structures at sites with rocky and sandy sea bottoms. *Environ. Biol. Fishes* 63: 353–372.
- Roberts, C.M. & R.F. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar. Ecol. Prog. Ser.* 41: 1–8.
- Sano, M., M. Shimizu & Y. Nose. 1984. Changes in structure of coral reef fish communities by destruction hermatypic corals: observational and experimental views. *Pacific Sci.* 38: 51–79.
- Sano, M., M. Shimizu & Y. Nose. 1987. Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. *Mar. Ecol. Prog. Ser.* 35: 267–275.
- Sweatman, 1983 Sweatman, H.P.A. 1985. The influence of adults of some coral reef fishes on larval recruitment. *Ecol. Monogr.* 55: 469–485.
- Swearer, S.E., J.E. Caselle, D.W. Lea & R.R. Warner. 1999. Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402: 799–802.
- Syms, C. 1995. Multi-scale analysis of habitat association in a guild of blennioid fishes. *Mar. Ecol. Prog. Ser.* 125: 31–43.
- ter Braak, C.J.F. & P. Smilauer. 1998. *CANOCO Reference manual and user's guide to Canoco for Windows: Software for Canonical Community Ordination (Version 4)*. Microcomputer Power, Ithaca, New York, 351 pp.
- Ward L.G., W.M. Kemp & W.R. Boyton. 1984. The influence of wave and seagrass communities on suspended particulates in an estuarine embayment. *Marine Geol.* 59: 85–103.
- Wellington, G.M. 1992. Habitat selection and juvenile persistence control the distribution of two closely related Caribbean damselfishes. *Oecologia* 90: 500–508.
- Williams, D.Mc.B. 1991. Patterns and processes in the distribution of coral reef fishes. pp. 437–474. *In*: P.F. Sale (ed.), *The Ecology of the Fishes on Coral Reefs*, Academic Press, San Diego.
- Yamamoto, T. 1976. Seasonal variations in abundance, size compositions and distributional patterns of residing damselfishes in Sesoko Island, Okinawa. *Sesoko Marine Science Laboratory Technical Report* 4: 19–42.