Overlaps in habitat use of fishes between a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan: Importance of the seagrass bed as juvenile habitat

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ABSTRACT: To clarify faunal overlap between a seagrass bed and adjacent coral and sand areas, and the number of reef fishes utilizing the seagrass bed as juvenile habitat, visual censuses were conducted at Amitori Bay, Iriomote Island, Japan. The numbers of species and individuals of fishes were significantly higher in the coral area than in the seagrass bed and sand area. Cluster and ordination analyses based on the number of individuals of each species demonstrated that the fish assemblage structure differed among the three habitats in each season, but with some overlaps. Approximately half the seagrass bed fishes occurred in the adjacent coral area (coral-seagrass species). Dominant species of coral-seagrass species utilized the seagrass bed as an important juvenile habitat. Thus, some overlaps in habitat use were present between the seagrass bed and adjacent coral area. Despite such overlaps, however, coral-seagrass species accounted for only approximately 15% of coral reef fishes overall, indicating that most of the latter hardly utilize the seagrass bed directly in the study area.

KEY WORDS: coral area, fish assemblage, juvenile habitat, microhabitat, ontogenetic habitat shift, Pacific, sand area, seagrass bed.

INTRODUCTION

Most coral reef fishes pass through a pelagic larval stage, following which individuals settle into coral and surrounding areas, and enter the benthic juvenile stage.¹ Seagrass beds and mangroves often cover extensive areas surrounding coral reefs, and habitats in these areas have been considered important nursery habitats for coral reef fishes. Hypotheses of nursery value of these habitats have been based on avoidance of predators,^{2,3} abundance of food,⁴ and higher interception rates of planktonic larvae.⁵ In fact, many studies on seagrass beds and mangroves in the Caribbean Sea have shown such areas to contain a high diversity and abundance of coral reef fishes.^{4,6-9} Once juvenile fishes outgrow the protection provided by these habitats, they migrate to coral reefs.^{6,8–13}

Many studies in the Caribbean Sea have recognized the importance of seagrass beds and man-

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groves as nurseries for many coral reef fishes, but the nursery function of these habitats in the Indo-Pacific is doubtful.^{14,15} In Papua New Guinea, for example, Quinn and Kojis made a direct, qualitative comparison of the fish fauna in a mangrove site near coral reefs and in a site remote from reefs, and detected little difference between them, with very few juvenile reef fishes utilizing both sites as juvenile habitats.¹⁶

To clarify how many and in what way reef fishes utilize seagrass beds as habitats, quantitative studies simultaneously comparing fishes in different habitats are needed. However, such studies are largely lacking, especially in the Indo-Pacific.^{5,9,17,18} Hence, little is known about relative fish abundance and species richness, and faunal overlaps between seagrass beds and adjacent habitats, including ontogenetic shifts in habitat use from juvenile to adult habitat association.

The present study was carried out on a fringing coral reef at Iriomote Island in the West Pacific, where the fish fauna of reef-associated seagrass beds is still poorly known, compared with that of the Caribbean.^{19,20} The aim of the present study was

to answer the following questions: (i) What kind of fishes utilize a seagrass bed and how does the fish assemblage structure in the seagrass bed differ from that in adjacent habitats?; (ii) Do adjacent habitats influence differences in fish assemblage structure among microhabitats within the seagrass bed?; (iii) Are there any faunal overlaps between such habitats, including ontogenetic shifts in habitat use from juvenile to adult reef association?; and (iv) Do seagrass beds in the West Pacific serve as important juvenile habitats for many reef species, as they do in the Caribbean?

MATERIALS AND METHODS

Study area

The study was conducted on the fringing reef at Amitori Bay (24°20'N, 123°42'E), situated on the western side of Iriomote Island, Ryukyu Islands, Japan (Fig. 1). The reef edge along the coast is



Fig. 1 Map of the study area at Amitori Bay, Iriomote Island. Three sites in the seagrass bed: CS, center of seagrass bed (60 m from the edge of the bed); SC, seagrass bed near the coral area (10 m from the edge of the bed); SS, seagrass bed near the sand area (10 m from the edge of the bed).

approximately 270 m from the shore. The coral area, from 160 m offshore to the reef edge, is composed primarily of both live and dead Acropora spp. and Porites spp. and coral rubble. The seagrass bed, adjacent to the coral area, extends along the coastline between 40 and 160 m from the shore. The vegetation within the bed is dominated by Enhalus acoroides and other plants, including Thalassia hemprichii, Syringodium isoetifolium and Cvmodocea rotundata. The mean shoot density of E. acoroides did not change seasonally (117.1 ± 30.2) [standard deviation] shoots/m²; one-way ANOVA, F = 1.47, P = 0.2), but a significant difference was observed in the mean height of seagrass leaves $(66.9 \pm 13.5 \text{ cm})$ in August $> 55.4 \pm 11.8$ cm in November $> 46.8 \pm 9.3$ cm in May > 23.9 ± 6.5 cm in February; Tukey–Kramer test, P < 0.05). The sand area is situated adjacent to the shoreline, characterized by a sandy bottom lacking vegetation. The three neighboring habitats (seagrass bed, coral area and sand area) are similar in some environmental characteristics, such as water temperature (approximately 25°C in November, 22°C in February, 26°C in May and 28°C in August), water depth (approximately 0.5-1.0 m at low tide and 2.0-3.0 m at high tide), salinity (approximately 34.5-35.5%) and underwater visibility (>15 m).

Sampling design

Visual censuses were made at five sites in the three habitats (three sites in the seagrass bed and one site each in the coral and sand areas) in November 1999 and February, May and August 2000, thereby covering each season. This census method has been considered to be effective in assessing fish densities in seagrass beds.²¹ For each census, five belt transects $(20 \text{ m} \times 1 \text{ m})$, parallel to the shore and separated from each other by at least 10 m, were established randomly at each site using a scaled rope. Each transect was approached slowly by a single diver using scuba and all fishes within the transect area were counted for 30 min. Individual fishes were identified to species and recorded as adults or juveniles on the basis of body size and coloration. Fishes that were difficult to identify to a species visually were collected and then identified in the laboratory. The scientific names of fishes followed Nakabo.²² Each census was made at high tide between 10.00 and 16.00 hours, each transect being censused once.

Three sites were set in the seagrass bed to clarify whether or not the adjacent coral and sand habitats influenced differences in fish assemblage structure among microhabitats within the seagrass bed (Fig. 1): site SC, seagrass bed near the coral area (10 m from the edge of the bed); site CS, center of seagrass bed (60 m from the edge of the bed); and site SS, seagrass bed near the sand area (10 m from the edge of the bed). Environmental characteristics such as seagrass species composition, seagrass leaf density and height, and substratum were similar among the three microhabitats.

To determine the habitat occurrence pattern of each fish species, the species were divided into the following seven habitat groups: (i) seagrass species, which appeared only in the seagrass bed; (ii) coral species; (iii) sand species; (iv) coral–seagrass species, which occurred in both the coral area and the seagrass bed; (v) seagrass–sand species; (vi) coral– sand species; and (vii) coral–seagrass–sand species.

Thirteen species that were abundant in the seagrass bed and also appeared in other habitats (>0.5 fish/transect during the study period in the seagrass bed) were selected so as to determine whether or not those species used the seagrass bed as an important juvenile habitat. In the present study, any habitat in which the number of juveniles was greater than the average individual number of the overall area in which juveniles occurred was defined as important juvenile habitat. Species richness and the individual density of all juvenile fishes were also compared among the seagrass bed and adjacent coral and sand areas to clarify whether the seagrass bed was truly utilized by many juveniles.

Data analysis

A two-way ANOVA was used to determine whether species and individual numbers of fishes censused were different among sites and seasons. Prior to the analyses, homogeneity of variances was improved by transformation of data to log (x + 1). If the ANOVA results indicated significant treatment effects at the level of P = 0.05, the Tukey–Kramer test was used to determine which means were significantly different.²³ Where ANOVA revealed a significant interaction between sites and seasons, a one-way ANOVA and post-hoc Scheffé's test were used to compare the means of one factor separately at each level of the other factor and vice versa.²⁴ Most ANOVA results are not presented in the present study because of space limitations.

The degree of similarity of fish assemblages between sites in each season was calculated using the Bray–Curtis similarity coefficient, based on the number of individuals of each species. Prior to the analysis, abundance data were transformed to $\log (x + 1)$ to normalize distributions and to stabilize variances. The resultant similarity matrix was subjected to cluster analysis (group-average mean linkage) and non-metric multidimensional scaling (MDS). Stress values calculated by the MDS procedure are a measure of how well the sample relationships are indicated by the dimensions (MDS providing a usable picture of sample relationships when the value is <0.2).²⁵ These analyses were performed using the CLUSTER and MDS programs on the PRIMER computer package (PRIMER v5, Plymouth, UK).²⁶

RESULTS

Fish fauna

During the study period, a total of 260 species in 44 families were counted in the seagrass bed and adjacent coral and sand areas (Appendix I). Of these, 70 species representing 24 families were observed in the seagrass bed, 205 fish species were observed belonging to 36 families in the coral area and 34 species were observed in 13 families in the sand area.

In terms of species number per family in the seagrass bed, Gobiidae (12 species, 17.1%) was the most dominant, followed by Labridae (11 species, 15.7%) and Mullidae (seven species, 10%). In terms of individual numbers, Gobiidae (29.1%), Labridae (22.2%) and Scaridae (13.9%) were dominant. In the coral area, Labridae (34 species, 16.6%), Gobiidae (33 species, 16.1%) and Pomacentridae (31 species, 15.1%) were the most dominant for species number, and Pomacentridae (39.4%), Gobiidae (29.5%) and Scaridae (8.9%) were the most dominant for the number of individuals. In the sand area, Gobiidae was dominant in both species (19 species, 55.9%) and individual (93.6%) numbers.

The most dominant species in the seagrass bed were *Stethojulis strigiventer* (8.8 fish per transect during the study period, 18.2% of total; Appendix I), *Apogon ishigakiensis* (6.0, 12.5%) and *Cryptocentrus caeruleomaculatus* (5.8, 12.0%). In the coral area, *Eviota bifasciata* (19.3, 9.3%), *Amblyglyphidodon curacao* (12.2, 5.8%) and *Chromis viridis* (12.2, 5.8%) were dominant. Three Gobiidae species, *Cryptocentrus cinctus* (3.9, 18.3%), *Cryptocentrus singapurensis* (3.0, 14.3%) and *Vanderhorstia ornatissima* (2.6, 12.1%) were abundant in the sand area.

Site and seasonal differences in assemblage structure

A significantly higher number of species was observed in the coral area than in each of the three seagrass sites (SC, CS and SS), regardless of season (Scheffé's test, P < 0.05; Fig. 2a). Comparing the number of species in each of the three seagrass sites with that in the sand area in each season, significantly higher numbers were found in the SC and CS sites than in the sand area only in August (Scheffé's tests, P < 0.05). No significant differences were obtained among the three seagrass bed sites in any season (Scheffé's tests, P > 0.05). Seasonal changes in species number in each seagrass bed site were found to be highest in August and lowest in February for each site (Tukey–Kramer test, P < 0.05).

The mean number of individuals per transect was also significantly greater in the coral area than in the three sites in the seagrass bed in every season (Tukey-Kramer test, P < 0.05; Fig. 2b). Comparing between the three seagrass bed sites and sand area, significantly higher numbers of individuals were found in the SC and CS sites than in the sand area in each season (Tukey-Kramer test, P < 0.05). Among the three sites in the seagrass bed, a significant difference was obtained only between SC and SS in each season (Tukey-Kramer test, P < 0.05). Significant seasonal differences were obtained for every study site (August > May = November > February; Tukey-Kramer test, P < 0.05).

Judging from the habitat occurrence pattern of each fish in the three habitats, the seagrass bed



Fig. 2 Mean numbers (±standard deviation) of (a) fish species and (b) individuals per belt transect (20 m², n = 5) at each site in each season.

fish assemblage largely comprised seagrass and coral-seagrass species, in terms of both total species and total individual numbers (Table 1). In the coral area, approximately 80% of total species and total individual numbers comprised coral species, the sand area being dominated by sand species.

The numbers of species and individuals of each habitat group at the five sites in each season are shown in Fig. 3. For species and individual numbers of the seagrass species group, there were no significant differences among the three seagrass bed sites in all seasons (two-way ANOVA, F = 2.5, P = 0.09 for both species and individual numbers; Fig 3a,b), whereas significant differences were obtained among seasons in all sites (August = May > November = February; Tukey-Kramer test, P < 0.05 for species and individual numbers). The coral-seagrass species group in the three sites in the seagrass bed showed a strong decrease in species and individual densities with increasing distance from the coral area in each season (SC > CS > SS; Tukey–Kramer P < 0.05for species and individual test. numbers; Fig. 3a,b), as well as significant seasonal changes in each of the three sites (August > May = November > February; Tukev-Kramer test, P < 0.05 for species and individual numbers). The number of species in the seagrasssand species group showed a significant seasonal difference between August and November in each of the three sites (Tukey–Kramer test, P < 0.05),

Table 1 Percentage contributions by species andindividuals for each habitat group †

	Species	Individuals
Habitat/habitat group	(%(n))	(%)
Seagrass bed		
Seagrass species	42.9 (30)	26.8
Coral-seagrass species	42.9 (30)	49.1
Seagrass-sand species	4.3 (3)	19.3
Coral-seagrass-sand species	10.0 (7)	4.8
Coral area		
Coral species	81.0 (166)	81.1
Coral-seagrass species	14.6 (30)	15.9
Coral-sand species	1.0 (2)	0.1
Coral-seagrass-sand species	3.4 (7)	2.9
Sand area		
Sand species	64.7 (22)	65.5
Seagrass-sand species	8.8 (3)	11.4
Coral-sand species	5.9 (2)	2.7
Coral-seagrass-sand species	20.6 (7)	20.4

[†]For example, seagrass species, which appeared only in the seagrass bed; coral–seagrass species, which occurred in both the coral area and the seagrass bed.



Fig. 3 Mean numbers (±standard deviation) of (a) fish species and (b) individuals of each habitat group per belt transect (20 m^2 , n = 5) at each site in each season. (\blacksquare) Seagrass species; (\blacksquare) coral-seagrass-sand species; (\blacksquare) coral-seagrass-sand species.

but no significant difference among sites (twoway ANOVÄ, F = 1.17, P = 0.3). Significantly higher numbers of individuals of the seagrass-sand species group were counted at the SS site than at the CS and SC sites in August only (Scheffé's tests, P < 0.05), a significant seasonal change being recorded only at the SS site (February = August > November and May = February, August and November; Scheffé's tests, P < 0.05). The numbers of species and individuals of coral-seagrass-sand species showed no significant difference among the three sites in the seagrass bed in each season (two-way ANOVA, F = 1.0, P = 0.4 for species number and F = 0.47, P = 0.6 for individual number), but showed significant seasonal changes at all sites (August = May = November > February; Tukey–Kramer test, P < 0.05 for species and individual numbers).

In the coral and sand areas, coral and sand species groups, respectively, dominated each season (Fig. 3a,b). The cluster analysis, based on the abundance of each species, showed that assemblages at each site in each season could be divided into three major groups with a similarity level of 30% (Fig. 4a): seagrass bed group, coral area group and sand area group. The results of the nonmetric MDS ordination paralleled those produced by the cluster analysis. The above three groups found in the cluster analysis were well separated from each other on the MDS plane (Fig. 4b).

In the seagrass bed group, fish assemblages in all seasons at the SC site, and in August at the CS and SS sites were similar to those of the coral area, whereas fish assemblages in other seasons at the CS and SS sites were similar to those of the sand area (Fig. 4a,b). Only fish assemblages at the CS and SS sites in February showed relatively high dissimilarity to others in the seagrass bed group, being more similar to fish assemblages in the sand area.



Fig. 4 (a) Dendrogram and (b) multidimensional scaling (MDS) ordination showing similarities between fish species based on their occurrence at five sites in three habitats in each season at Amitori Bay. Groups of sites in each season delineated at the 30% level in the dendrogram are circled in the ordination plot.

Seagrass bed as an important juvenile habitat

Of the 13 selected dominant seagrass bed fishes, nine species belonged to the coral–seagrass species group, each of them utilizing a part or all of the seagrass bed as an important juvenile habitat (Table 2). The remaining four species were included in the seagrass–sand and coral–seagrass– sand species groups, two species using the seagrass bed as an important juvenile habitat.

Stethojulis strigiventer, Cheilio inermis and Cryptocentrus caeruleomaculatus were significantly more abundant in the seagrass bed than in the adjacent coral and sand areas (Table 2). Both adults and juveniles of the three species were found in the seagrass bed, indicating that these species spend almost all of their life cycle in the seagrass bed. On the contrary, juvenile Scaridae and *Ctenogobiops pomastictus* were significantly more abundant in the coral area than in the seagrass bed.

Cheilodipterus quinquelineatus showed ontogenetic shifts in habitat utilization, juveniles occurring in the seagrass bed and coral area, and adults inhabiting the coral area (Table 2). Except for Scaridae spp., adults of each of the remaining 11 species were found in the seagrass bed, indicating that the latter constituted part of the adult habitat.

In the seagrass bed, a total of 65 juvenile species in 21 families were counted. In contrast, 156 juvenile species in 30 families occurred in the coral area and 26 species representing 11 families occurred in the sand area (Appendix I).

The coral area had a significantly higher number of juvenile species than the seagrass bed and sand areas in all seasons, the seagrass bed showing a significantly higher number of species than the sand area in August only (Scheffé's tests, P < 0.05; Fig. 5a). Seasonal changes in species numbers occurred in each habitat, with significantly higher numbers in August and the lowest numbers in February (Scheffé's tests, P < 0.05).

The individual number of juveniles was significantly higher in the seagrass bed than in the sand area in all seasons (Tukey–Kramer test, P < 0.05; Fig. 5b). However, it was significantly lower compared with that in the coral area in each of the four seasons. The highest number of juveniles was obtained in August and the lowest in February in each habitat (August > May > November > February; Tukey–Kramer test, P < 0.05).

Juveniles that occurred only in the seagrass bed represented 33 species (16 families), whereas 127 juvenile species (30 families) were recorded only in the coral area and 18 species (nine families) were recorded in the sand area (Appendix I). Dominant families in terms of the number of juvenile species counted only in the seagrass bed were Lethrinidae, Mullidae, Labridae and Gobiidae (four species, 12.1% for each family). In the coral area, Pomacentridae was the most diverse (25 species, 19.7%), followed by Labridae (23 species, 18.1%) and Gobiidae (17 species, 13.4%). The sand area was dominated by Gobiidae (10 species, 55.6%).

DISCUSSION

Fish fauna

In general, a common suite of temperate seagrass fish families includes Syngnathidae, Gobiidae and Monacanthidae (dominant in both species and

		M	lean individua	l number per t	ransect (juveni	les)		
				Seagrass bed				
Habitat group/family	Species	Sand area	SS	CS	SC	Coral area	Mobility	Category
Coral-seagrass species								
Apogonidae	Cheilodipterus quinquelineatus	I	$1.3 (1.30)^{\dagger}$	0.6(0.60)	0.3(0.30)	$1.5 (1.22)^{\dagger}$	R	IJН
Mullidae	Parupeneus ciliatus	I	$1.3 (0.88)^{\dagger}$	$0.5~(0.37)^{\dagger}$	0.2 (0.20)	0.5(0.00)	Λ	IJН
	Parupeneus multifaciatus	I	I	0.6^{a} (0.60)	$1.6^{\rm ab} \ (1.50)^{\dagger}$	$1.4^{\rm b} (0.70)$	Λ	IJН
	Parupeneus barberinus	I	0.6(0.45)	0.5(0.50)	$0.7 (0.70)^{\dagger}$	0.3 (0.26)	Λ	IJН
Labridae	Stethojulis strigiventer	I	5.5^{ab} (3.75)	$11.3^{\rm a}$ $(4.71)^{\dagger}$	$9.5^{a} (5.15)^{\dagger}$	$1.2^{\rm b}$ (1.15)	Λ	IJН
	Cheilio inermis	I	$0.7^{\rm ac} (0.48)^{\dagger}$	$0.6^{\rm ac} \ (0.25)^{\dagger}$	$0.9^{ m bc} (0.42)^{+}$	$0.1^{a} (0.00)$	Λ	IJH
Scaridae	Scaridae spp.	I	0.5^{a} (0.50)	4.7^{ab} (4.70)	$6.8^{ m bc}$ $(6.80)^{ m \dagger}$	$11.3^{\circ} (11.3)^{\dagger}$	Λ	IJН
Pinguipedidae	Parapercis cylindrica	I	0.3(0.30)	$0.9 (0.75)^{\dagger}$	$0.8 (0.60)^{\dagger}$	0.3 (0.24)	R	IJН
Gobiidae	Asterropteryx semipunctata	ļ	$0.8^{a} (0.80)$	1.1^{a} (1.0)	$8.3^{\rm b}$ (7.62) [†]	5.5° (3.97) [†]	R	IJН
Seagrass-sand species	Vandarboretia ornatiecima	יז ביו הבו\†	0 0 ab (0 30)				۵	
CODINAC	Cryptocentrus caeruleomaculatus	1.5^{a} (0.21)	$(0.00)^{+}$ (0.60) ⁺	$6.7^{\rm bc}$ (0.90) [†]	$\frac{-}{3.8^{ab}}$ (0.20)	1 1	4 24	IJH
Coral-seagrass-sand species								
Lethrinidae	Lethrinus harak	$0.5^{ab} (0.06)$	$1.3^{a} (0.57)^{\dagger}$	$1.0^{ab} (0.32)^{\dagger}$	$1.1^{\rm ab} (0.31)^{\dagger}$	$0.2^{\rm b} (0.00)$	> -	IJН
Gobiidae	Cienogobiops pomastictus	0.6^{a} (0.44)	$0.5^{m}(0.00)$	0.6^{a} (0.05)	0.7^{av} (0.00)	3.7° (0.34)	Х	
[†] Number of juveniles greater th ^{abccimificant} differences at D /	an the average juvenile number over all	sites where reco	orded (sites ider	ntified thus recog	gnised as importa	ant juvenile habi	tat (IJH)).	
CS, center of seagrass bed (60 m)	r from the edge of the bed); SC, seagrass h	bed near the cor	al area (10 m fro	om the edge of th	e bed); SS, seagra	ass bed near the s	sand area (10	m from the
edge of the bed).								
R, resident; V, visitor; –, not obs	served.							

 Table 2
 Mean densities per belt transect at each site of the 13 most abundant seagrass bed fishes that also occurred in other habitats (data pooled across census periods)

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Fig. 5 Mean numbers (±standard deviation) of (a) species and (b) individuals of juvenile fishes per belt transect (20 m², n = 15 for the seagrass bed, n = 5 for the coral and sand areas) in each habitat in each season.

individual numbers).²⁷ However, Labridae, Gobiidae and Scaridae were dominant in the present seagrass bed, *Stethojulis strigiventer, Apogon ishigakiensis* and *Cryptocentrus caeruleomaculatus* being the most abundant species. Similar phenomena were also found in a *Thalassia hemprichii*dominated bed at Ishigaki Island in the Ryukyu Islands.²⁰

Visual censuses in seagrass beds associated with coral reefs in the Caribbean have shown Scaridae, Haemulidae and Lutjanidae to be the dominant families (for both species and individual numbers) in the daytime, *Haemulon flavolineatum* and *Scarus iserti* being the most abundant species.^{4,8} These three dominant families were also abundant in daytime trawls.^{6,7} In the Pacific, based on extensive visual census studies in a variety of habitats in Cocos Lagoon, Guam, Jones and Chase recorded Labridae to be the most dominant family (for both species and individual numbers) in the seagrass bed, followed by Mullidae and Scaridae, *Stethojulis strigiventer* being the most abundant species.¹⁹

Scaridae was the common dominant family in both Caribbean and Pacific tropical seagrass beds. *Scarus iserti* and the seagrass-feeding scarid *Sparisoma radians* have been reported as abundant in Caribbean seagrass beds.^{4,6,8} In the present seagrass bed, in contrast, juveniles of the detritivorous Scaridae spp. were most abundant, followed by the seagrass-feeding scarids *Calotomus spinidens* and *Leptoscarus vaigiensis* (Appendix I).²⁸ The major differences in fish fauna between the Caribbean and West Pacific tropical seagrass beds included Haemulidae and Lutjanidae, being minor groups in the present study area (Amitori Bay) and Cocos Lagoon, whereas Labridae was less abundant in Caribbean seagrass beds.

Site and seasonal differences in assemblage structure

In the Caribbean, most seagrass bed fishes occur on coral areas (for example, approximately 70% of seagrass fish species have also been found on coral areas).⁸ During the present study, in contrast, only approximately 50% of the seagrass bed fishes also occurred on a coral area (coralseagrass group; Table 1). Because both species and individual numbers of that group were abundant at the SC site (Fig 3a,b), the structure of the fish assemblage at the SC site was more similar to that in the coral area than at other seagrass sites (CS and SS; Fig 4a,b). This phenomenon is concordant with the results of a study by Nagelkerken et al., which showed a strong decrease in density of reef species in seagrass beds with increasing distance from a coral area.8 Conversely, the influence of the sand area on fishes in the present

seagrass bed was not as clear, compared with that of the coral area. This is largely because the fishes in the sand area were dominated by resident Gobiidae, which do not make forays into the bed to feed.

According to the cluster and MDS analyses, fish assemblages in the seagrass bed, coral and sand areas were clearly separated each season in the present study. Approximately half the seagrass bed fishes were coral-seagrass species, but only approximately 15% of coral reef species were included in the latter group. Fish species that occurred exclusively in each habitat were abundant, dominant species being different in each habitat. This could explain the results of the cluster and MDS analyses. The phenomenon wherein the structure of the seagrass fish assemblage was different from those of the coral and sand areas agrees with the results of Jones and Chase obtained at Guam.¹⁹

Approximately 40% of coral reef species occurred in seagrass beds during the daytime in the Caribbean islands of Curaçao⁸ and Jamaica (T Nakai, unpubl. data, 2004). In the present study, only approximately 15% of reef species occurred in the seagrass bed, being similar to a result obtained in the *Thalassia hemprichii*-dominated bed at Ishigaki Island.²⁰ Significantly lower numbers of species and individuals in the seagrass bed compared with the coral area, as well as a different assemblage structure, suggest that the seagrass beds in the West Pacific are hardly utilized by many reef fishes.

Seagrass bed as an important juvenile habitat

The dominant species of coral-seagrass fishes, which make up approximately half the seagrass bed fishes recorded here, utilized the seagrass bed as an important juvenile habitat (Table 2). Clear habitat shifts with growth were shown by *Cheilodipterus quinquelineatus*, adults of which inhabit the coral area. In the remaining coral-seagrass species, however, both adults and juveniles occurred in the seagrass bed, indicating that the seagrass bed was used as part of the adult habitat as well as the juvenile habitat.

In the Caribbean, juveniles of Haemulidae and Lutjanidae are abundant in seagrass beds.^{6,8,9,18} A comparison between bays with and without seagrass beds in the Caribbean showed that these families were largely absent in bays lacking seagrass beds, suggesting that seagrass beds provide essential juvenile habitats for these families.¹⁸ In the seagrass bed of the present study, however, juveniles of these families were few, Lethrinidae,

Mullidae, Labridae and Gobiidae being the most diverse.

Seagrass beds have been considered important nursery habitat in the Caribbean.^{18,29} In the present study area, however, species and individual numbers of juveniles were significantly lower in the seagrass bed compared with those in the coral area. Although there were some overlaps in habitat use between the seagrass bed and adjacent coral area, coral-seagrass species accounted for only approximately 15% of coral reef fishes, indicating many coral reef fishes hardly utilize the seagrass bed as juvenile habitat in the study area. Such differences in the seagrass habitat utilization pattern of fishes between the Caribbean and present study site might have resulted from differences in tidal range and/or development of coral areas between the two regions. In Amitori Bay, which has a large tidal range (150 cm), seagrass habitats are not continuously available to the fishes because of exposure of seagrasses to air during low tide; this contrasts with the Caribbean, where seagrass habitats never fall dry because there is a small tidal range (30 cm).^{18,30} In addition, coral diversity is far higher in the West Pacific than in the Caribbean,³¹ suggesting that coral areas in the former provide suitable habitats for many reef fishes. Hence, the habitat function of seagrass beds for fishes might be different between the Caribbean and West Pacific. Further research is needed to investigate the possible mechanisms of such differences between the two regions.

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Family/Species	Sand area	Seagrass bed	Coral area
Muraenidae Echidna nebulosa	_	_	0.05 (J)
Synodontidae Saurida gracilis Synodus dermatogenys Synodus variegatus	0.05 (A) _ _	0.10 (J/A) _ _	0.10 (J) 0.05 (J) 0.10 (J)
Holocentridae Myripristis kuntee Neoniphon sammara Sargocentron diadema Sargocentron ittodai	- - - -	- - -	0.05 (A) 0.50 (J/A) 0.10 (A) 0.45 (J/A)
Aulostomidae Aulostomus chinensis	-	-	0.25 (J/A)
Fistulariidae Fistularia commersonii	0.05 (J)	_	_
Centriscidae Aeoliscus strigatus	_	0.32 (J/A)	-
Syngnathidae Corythoichthys haematopterus Hippocampus kelloggi	_ 0.05 (J)	0.05 (A) _	0.05 (A) _
Mugilidae Ellochelon vaigiensis	0.05 (A)	-	_
Hemiramphidae Hemiramphus far	_	0.02 (A)	-
Belonidae Tylosurus crocodilus crocodilus	_	_	0.05 (A)
Scorpaenidae Pterois antennata Scorpaenopsis oxycephala	- -	- -	0.05 (J) 0.05 (A)
Serranidae Cephalopholis miniata Cephalopholis urodeta Epinephelus merra Variola loui		- - -	0.15 (A) 2.00 (A) 1.05 (A) 0.30 (J/A)
Pseudochromidae Labracinus cyclophthalma Pseudochromis fuscus		-	0.35 (A) 0.25 (J/A)
Apogonidae Apogon ishigakiensis Apogon parvulus Apogon properuptus Apogon savayensis Cheilodipterus macrodon Cheilodipterus quinquelineatus Foa brachygramma Sphaeramia nematoptera	- - - - - - - -	6.03 (J/A) - - - 0.93 (J) 0.22 (J/A) 0.35 (J/A)	2.00 (J) 0.10 (J/A) 0.10 (A) 0.15 (J) 1.45 (J/A) –
Malacanthidae Malacanthus latovittatus	_	_	0.05 (A)
Carangidae Caranx melampygus Trachinotus baillonii	0.05 (J) 0.05 (A)	- -	- -

APPENDIX I Mean number of individuals per transect (20 m²; sand and coral areas, n=5; seagrass bed, n=15) in each habitat (data pooled across census periods)

Family/Species	Sand area	Seagrass bed	Coral area
Lutjanidae			
Aphareus furca	-	_	0.05 (A)
Lutianus bohar	-	_	0.05 (J)
Lutianus decussatus	-	_	0.35 (J/A)
Lutianus fulvus	0.20 (I)	_	-
Lutjanus gibbus	_	0.32 (J)	1.80 (J/A)
Caesionidae			
Caesio teres	_	_	0 10 (I)
Pterocaesio tile	_	_	0.60 (J)
Corrected of			0.00 ())
Gerrendae			
Gerres Oyena	—	0.02 (A)	-
Haemulidae			
Plectorhinchus albovittatus	-	0.02 (J)	_
Plectorhinchus chaetodonoides	-	0.02 (J)	0.05 (A)
Plectorhinchus lessonii	-	—	0.10 (J/A)
Plectorhinchus lineatus	-	_	0.10 (J/A)
Nemipteridae			
Scolopsis bilineata	_	_	0.15 (J/A)
Scolopsis lineata	-	0.02 (J)	0.10 (J/A)
Lethrinidae			
Lethrinus atkinsoni	_	0.48 (I)	0.10 (I/A)
Lethrinus genivittatus	_	0.12 (J/A)	-
Lethrinus harak	0.45 (I/A)	1.20 (I/A)	0.20 (A)
Lethrinus obsoletus	_	0.37 (1)	-
Lethrinus ornatus	_	0.08 (1)	_
Lethrinus snn	_	0.05 (J)	_
Monotaxis grandoculis	_	-	0.05 (I)
Mullidao			
Mulloidichthys flavolineatus		0.13(I/A)	
Darupopous barborinus	-	0.13(J/A)	0.25(I/A)
Parupanaus harberinoides	-	0.00(J/A)	0.23(J/A)
Paruponeus ciliatus	_	0.27 (J/A)	0.45(A)
Parupanaus cuclostomus	-	0.03 (J/A)	0.43(A)
Parupaneus indicus	0.05 (A)	 0.07 (I/A)	0.10(J)
Paruponous multifasciatus	0.03(A)	0.07 (J/A) 0.72 (I/A)	1.40 (I/A)
I upeneus munijascianas Ilpeneus tragula	- 0.05 (I)	0.12 (J/R)	1.40 (J/A)
Oberete de utilde e	0.00 ())	0.02 ())	
Chaetodon argentatue			0.05 (1/4)
Chaetodon argeniaius	=	—	0.25 (J/A)
Chaetodon auriga	=	—	0.25 (J/A)
Chaetodon auripes	=	—	0.15(A)
Chaeloaon ephippium Chaeloaon lunulatus	=	—	0.35 (J/A)
Chaetodon iunulaius	=	- -	0.85 (J/A)
Chaeloaon melannolus	=	0.02 (J)	
Chaetodon vijascialis	=	—	0.05 (A)
Chaeloaon unelensis	=		0.05(J)
Chaeloaon vagabunaus	-	0.03 (J/A)	0.25 (J/A)
Pomacanthidae			
Centropyge bispinosa	-	_	0.05 (A)
Centropyge ferrugata	-	-	0.90 (J/A)
Centropyge tibicen	-	—	0.20 (J/A)
Centropyge vrolikii	-	—	0.85 (J/A)
Chaetodontoplus mesoleucus	-	—	0.05 (J)
Pygoplites diacanthus	_	_	0.10 (J/A)

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Family/Species	Sand area	Seagrass bed	Coral area
Pomacentridae			
Abudefduf sexfasciatus	_	_	0.55 (J)
Amblyglyphidodon curacao	_	_	12.2 (J/A)
Amblyglyphidodon leucogaster	_	_	3.75 (J/A)
Amblyglyphidodon ternatensis	_	_	2.05 (J/A)
Amphiprion clarkii	_	_	0.45 (J/A)
Amphiprion frenatus	_	_	0.10 (I/A)
Amphiprion ocellaris	_	0.05 (J/A)	_
Cheiloprion labiatus	_	_	0.20 (A)
Chromis viridis	_	_	12.2 (I/A)
Chromis weberi	_	_	0.85 (I/A)
Chrysintera cyanea	_	_	6.65 (I/A)
Chrysintera narasema	_	_	2 10 (I/A)
Chrysiptera rex	_	_	0.50(I/A)
Chrysintera unimaculata	_	0.12 (I/A)	0.00(J/H) 0.45(J/A)
Dascyllus aryanys	_	0.12 ()/11)	2 85 (J/A)
Dascyllus reticulatus	_	_	0.50 (J/A)
Dascyllus trimaculatus			3.60(J/A)
Duscynus innucuunus Dischistodus prosonotaenia	_	- 0 43 (I)	0.70(J/A)
Hamighunhidodon plagiomatonon	—	0.43 ())	0.70(J/A)
Neoghuphidodon plagiometopon	—	—	0.95(J/A)
Neoglyphiaoaon meias	—	—	0.10(A)
Piecirogiyphiaoaon iacrymaius	—	—	0.30(J/A)
Pomacentrus alexanaerae	—	—	2.35 (J/A)
Pomacentrus amboinensis	—	—	9.00 (J/A)
Pomacentrus bankanensis	—	-	0.30(J)
Pomacentrus cnrysurus	-	0.13 (J)	0.55 (J/A)
Pomacentrus lepidogenys	-	-	0.55 (J/A)
Pomacentrus moluccensis	-	-	11.6 (J/A)
Pomacentrus philippinus	-	-	0.05 (J)
Pomacentrus vaiuli	—	—	0.05 (J)
Pomacentrus sp.	—	—	6.05 (J/A)
Stegastes lividus	—	—	0.05 (A)
Stegastes nigricans	—	—	0.45 (J/A)
Cirrhitidae			
Paracirrhites forsteri	_	_	0.05 (A)
Labridae			
Anamnees tuistii	_	_	0.05 (I)
Rodianus lovozonus	_	_	0.05(J)
Chailinus colobicus	_	_	0.05(J)
Cheilinus chlorourus	_	-	0.33(J/A)
Cheilinus fasciatus	_	0.07 (J7A)	0.10(J/A)
Cheilinus fusculus Cheilinus trilohatus	_	—	0.40(J)
Cheilinus un dultus	—	—	0.05 (A)
Cheilinus unaulius	—		0.05 (A)
	—	0.07 (J/A)	0.05(A)
Choeroaon anchorago	—	0.37 (J/A)	0.90 (J/A)
Cirrnilabrus spp.	-	-	2.40 (J)
Coris batuensis	-	-	0.35 (J/A)
Coris gaimard	-	-	0.05 (J)
Epibulus insidiator	-	_	0.05 (J)
Halichoeres argus	-	0.20 (J/A)	
Halichoeres marginatus	—	—	0.10 (J)
Halichoeres melanochir	—	_	0.05 (J)
Halichoeres melanurus	-	0.10 (J/A)	2.30 (J/A)
Halichoeres scapularis	-	-	0.15 (J)
Halichoeres trimaculatus	_	0.03 (J)	0.35 (J/A)
Hemigymnus fasciatus	-	-	0.10 (J)
Hemigymnus melapterus	_	_	0.40 (J/A)

Family/Species	Sand area	Seagrass bed	Coral area
Labroides dimidiatus	-	_	1.35 (J/A)
Labropsis manabei	_	_	0.05 (J)
Macropharyngodon meleagris	_	_	0.05 (J)
Novaculichthys macrolepidotus	_	0.07 (J/A)	-
Oxycheilinus bimaculatus	_	0.18 (J/A)	0.10 (J)
Oxycheilinus unifasciatus	_	_	0.05 (J)
Stethojulis bandanensis	_	_	0.30 (J/A)
Stethojulis strigiventer		8.77 (J/A)	1.15 (J/A)
Thalassoma hardwicke	_	-	0.90 (J/A)
Thalassoma lunare		-	0.10 (J/A)
Thalassoma lutescens	_	-	0.10 (J)
Xyrichtys dea	0.05 (J)	-	-
Labridae sp.1	_	-	0.05 (J)
Labridae sp.2	_	-	0.15 (J)
Labridae sp.3	_	0.13 (J)	-
Labridae sp.4	_	-	0.05 (A)
Labridae spp.	0.05 (J)	0.20 (J)	1.50 (J)
Scaridae			
Calotomus carolinus	-	_	0.10 (J)
Calotomus spinidens	-	2.42 (J/A)	-
Chlorurus sordidus	-	_	2.20 (J/A)
Hipposcarus longiceps	-	0.02 (J)	-
Leptoscarus vaigiensis	_	0.12 (J/A)	-
Scarus dimidiatus	_	_	1.00 (J/A)
Scarus festivus	_	-	0.15 (A)
Scarus forsteni	_	-	0.15 (J/A)
Scarus frenatus	_	-	0.05 (A)
Scarus ghobban	_	0.13 (J)	0.40 (J/A)
Scarus hypselopterus	_	-	0.80 (J/A)
Scarus niger	_	-	0.15 (J)
Scarus oviceps	_	-	0.20 (J)
Scarus prasiognathos	_	-	0.10 (J)
Scarus psittacus	_	-	0.05 (A)
Scarus rivulatus	_	-	1.25 (J/A)
Scarus schlegeli	_	-	0.50 (J/A)
Scaridae spp.	-	4.0 (J)	11.3 (J)
Pinguipedidae			
Parapercis cylindrica	-	0.65 (J/A)	0.25 (J/A)
Parapercis polyophthalma	_	_	0.50 (J/A)
Trintervgiidae			
Enneantervoius minutus	_	0.15 (I/A)	_
Helcogramma sp	_	_	0 10 (I)
Triptervgiidae spp.	_	_	0.15 (A)
Plonniidaa			0110 (11)
Atrosalarias fuscus holomolas			0.90 (1/4)
Econius variamaonsis	_	_	0.00(J/A)
Majacanthus atrodorsalis	_	_	0.20(J)
Meiacanthus arammistas	_		0.20 (A)
Detroscirtos mitratus	0.05 (1)	0.02 (A)	0.23 (A)
Petroscirtes militaitas	0.03 ())	-	-
Salarias fasciatus	_	0.03 (J/A)	0.40(1/4)
Salarias jascialias	_	_	0.40(J/A)
Gobiesocidae			
Diademichthys lineatus	-	-	0.05 (J)
Callionymidae			
Anaora tentaculata	-	0.10 (J/A)	-
Diplogrammus goramensis	0.05 (J)	_	-
Paradiplogrammus corallinus	_	_	0.15 (J)

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Family/Species	Sand area	Seagrass bed	Coral area
Gobiidae			
Amblyeleotris steinitzi	-	-	0.05 (J)
Amblygobius decussatus	-	-	0.05 (A)
Amblygobius hectori	-	-	0.85 (J/A)
Amblygobius phalaena	1.10 (J)	0.10 (J/A)	0.10 (J)
Asterropteryx ensifera	-	-	0.25 (J/A)
Asterropteryx semipunctata	-	3.38 (J/A)	5.45 (J/A)
Bryaninops erythrops	-	-	1.50 (J/A)
Bryaninops natans	_	_	3.45 (J/A)
Cryptocentrus albidorsus	-	0.07 (J/A)	-
Cryptocentrus caeruleomaculatus	1.50 (J/A)	5.77 (J/A)	-
Cryptocentrus cinctus	3.85 (J/A)	-	-
Cryptocentrus inexplicatus	0.05 (A)	_	-
Cryptocentrus singapurensis	3.00 (J/A)	_	-
Ctenogobiops crocineus	_	0.12 (J/A)	0.25 (A)
Ctenogobiops feroculus	0.15 (A)	_	-
Ctenogobiops formosa	0.55 (J/A)	_	0.15 (A)
Ctenogobiops pomastictus	0.55 (J/A)	0.58 (J/A)	3.70 (J/A)
Eviota bifasciata	_	_	19.3 (J/A)
Eviota nigriventris	_	_	1.30 (J/A)
Eviota prasites	_	_	2.35 (J/A)
Eviota sp.1	_	_	10.7 (J/A)
Eviota sp.2	_	_	2.65 (J/A)
Eviota sp.3	_	_	1.30 (J/A)
Eviota spp.1	_	0.27 (J/A)	-
Eviota spp.2	_	_	1.30 (J/A)
Favonigobius spp.	1.30 (J/A)	_	-
Fusigobius duospilus	_	_	0.10 (A)
Fusigobius neophytus	0.05 (A)	0.05 (J/A)	0.35 (A)
Fusigobius sp.	_	0.07 (J/A)	0.30 (J/A)
Gnatholepis anjerensis	_	_	0.15 (A)
Gnatholepis scapulostigma	_	_	1.30 (J/A)
Gobiodon okinawae	_	_	0.40 (J/A)
Gobiodon quinquestrigatus	_	_	0.10 (A)
Gobiodon sp.1	_	_	0.25 (A)
Gobiodon sp.2	_	_	0.05 (A)
Istigobius ornatus	0.45 (J/A)	_	-
Macrodontogobius wilburi	_	0.07 (J/A)	0.95 (J/A)
Mahidolia mystacina	0.05 (A)	_	-
Oplopomus oplopomus	0.75 (J/A)	_	-
Pleurosicya bilobata	_	0.03 (A)	-
Ptereleotris evides	_	_	0.05 (J)
Ptereleotris microlepis	1.70 (J/A)	_	-
Trimma caesiura	_	_	0.45 (J/A)
Trimma naudei	_	_	0.05 (A)
Trimma tevegae	_	_	1.45 (J)
Valenciennea longipinnis	1.05 (J/A)	_	-
Vanderhorstia ambanoro	0.10 (J/A)	_	-
Vanderhorstia ornatissima	2.55 (J/A)	3.50 (J/A)	-
Gobiidae sp.	0.05 (J)	_	-
Gobiidae spp.	0.90 (J)	_	0.75 (J)
Siganidae			
Siganus argenteus	_	_	0.25 (I)
Siganus corallinus	_	_	0.10 (A)
Siganus fuscescens	_	0.58 (I/A)	-
Siganus puellus	_	_	0.20 (A)
Siganus spinus	_	0.42 (I/A)	1.05 (I/A)
Siganus unimaculatus	_	_	1.10 (J/A)

APPENDIX I Continued

Family/Species	Sand area	Seagrass bed	Coral area
Zanclidae			
Zanclus cornutus	_	_	0.15 (J)
Acanthuridae			
Acanthurus blochii	_	_	0.30 (J/A)
Acanthurus mata	_	0.05 (J)	0.25 (J/A)
Acanthurus nigrofuscus	_	_	2.15 (J/A)
Acanthurus pyroferus	_	-	0.25 (J/A)
Acanthurus thompsoni	_	-	0.10 (J/A)
Ctenochaetus binotatus	_	-	0.30 (J/A)
Ctenochaetus striatus	_	-	0.60 (J/A)
Zebrasoma scopas	_	-	0.55 (J/A)
Zebrasoma veliferum	-	-	0.50 (J/A)
Sphyraenidae			
Sphyraena forsteri	_	0.30 (J/A)	-
Scombridae			
Euthynnus affinis	_	_	0.05 (A)
Bothidae			
Asterorhombus intermedius	0.10 (J)	_	-
Balistidae			
Balistapus undulatus	_	_	0.05 (J)
Sufflamen bursa	_	_	0.05 (J)
Sufflamen chrysopterum	_	_	0.10 (A)
Monacanthidae			
Acreichthys tomentosus	_	0.35 (J/A)	-
Oxymonacanthus longirostris	_	_	0.10 (A)
Paraluteres prionurus	_	_	0.10 (J)
Tetraodontidae			
Arothron nigropunctatus	_	_	0.05 (A)
0 <i>r</i>			

Growth intervals; A, adult; J, juvenile; –, not observed.