



Fish assemblage structure response to seagrass bed degradation due to overgrazing by the green sea turtle *Chelonia mydas* at Iriomote Island, southern Japan

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Abstract

The fish assemblage structure response to rapid degradation of *Enhalus acoroides* seagrass beds due to overgrazing by green sea turtles (*Chelonia mydas*) was investigated at Iriomote Island, southern Japan, by visual censusing of fish species in several microhabitats in and around the beds (i.e., dense seagrass bed, grazed bed, their boundaries, and adjacent sandy area). Fish assemblage structure differed among the seagrass microhabitats, both species and individual numbers being higher in microhabitats with seagrass compared to overgrazed beds and unvegetated sandy areas, together with different species composition. In the dense seagrass beds and boundary areas (the border area between dense seagrass beds and grazed areas), seagrass-associated fishes such as the rabbit fish *Siganus fuscescens* and cardinal fish *Ostorhinchus ishigakiensis* were abundant and comparable with those in other seagrass beds in the area. In addition, the fish assemblages in those microhabitats varied seasonally, fish abundance being greater in summer due to higher levels of recruitment. In the grazed bed, benthic gobies, such as *Ctenogobiops crocineus* and *Cryptocentrus caeruleomaculatus*, were dominant (similarly so in unvegetated sandy areas), and seasonal variations in such assemblages were relatively low compared to those in dense seagrass microhabitats. The decrease in the abundance and diversity of seagrass-associated fish in the grazed areas could be explained partly by the shortage of vegetation (< 20 cm in leaf length) for shelter and feeding throughout the year. The results suggested that the degradation of seagrass beds due to overgrazing by green turtles has a deleterious effect on fish assemblages, and that future conservation and management strategies for seagrass beds should consider both their associated fish communities and green turtles.

Keywords Fish assemblage · Seagrass · *Enhalus acoroides* · Green turtle · Seagrass degradation

Introduction

Seagrass beds typically support higher numbers of fish species and individuals than open sandy areas, serving as nursery habitats for many fish species, including several commercially important (Edger and Shaw 1995; Nagelkerken

et al. 2000; Dorenbosch et al. 2004; Nakamura and Sano 2004b). Such increased diversity is considered the result of seagrass beds being rich in invertebrates and therefore good feeding grounds for fishes (Heck et al. 2003; Nakamura and Sano 2005). In addition, seagrass habitats provide juvenile fishes with shelter against predators (Heck et al. 2003; Nakamura and Sano 2004a). Consequently, seagrass beds are considered to be essential for maintaining high levels of biodiversity in coastal ecosystems and local fisheries.

However, seagrass beds are rapidly declining around the world due to factors such as anthropogenic impact and climate change (Orth et al. 2006; Waycott et al. 2009). The loss of such beds results in a decrease in nursery and feeding grounds of seagrass-associated fishes, typically resulting in a significant decrease in numbers of fish species and individuals (Hughes et al. 2002; Nakamura 2010). Furthermore, seagrass degradation may also result in a decrease in the

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fish biodiversity of surrounding ecosystems, such as coral reefs, because some of them utilize seagrass beds as nurseries (Nagelkerken et al. 2002).

Recently, extensive seagrass degradation has become apparent around the islands of the Yaeyama archipelago in the Ryukyu Islands, southern Japan (Takeyama et al. 2014). Tape seagrass *Enhalus acoroides*, widely distributed throughout Indo-Pacific subtropical and tropical regions (Green and Short 2003), is widespread around the Yaeyama archipelago, the northern limit of its distribution (Toma 1999). However, a rapid decline in tape seagrass beds has been observed around Iriomote Island since 2013 (Takeyama et al. 2014). One of the most likely reasons for the observed decline has been excessive feeding by the green sea turtle *Chelonia mydas*. Although green turtles have been severely overhunted in the past, their populations have recovered rapidly in some regions (Chaloupka et al. 2008). However, an overabundance of green turtles, being primarily herbivorous and consuming large quantities of seagrass (Thayer et al. 1984), sometimes results in severe seagrass degradation (Fourqurean et al. 2010; Christianen et al. 2014). After a decline in local green turtle harvesting in the Yaeyama archipelago, which includes many green turtle spawning sites (Abe et al. 2004), the turtle population has increased (Kameda et al. 2017), resulting in severe overgrazing of the dense seagrass beds in Funauki and Amitori Bays on Iriomote Island, and their almost complete loss in 2013 (Takeyama et al. 2014).

Previous studies have shown that numerous fish species (including scarids, mullids, gobiids and labrids) utilize the seagrass habitats around the archipelago, the latter two families being dominant in both species and individual numbers (Nakamura and Sano 2004b). In addition, the juveniles of some coral reef fishes, such as the five-lined cardinalfish *Cheilodipterus quinquelineatus*, pacific yellowtail emperor *Lethrinus atkinsoni* and thumbprint emperor *Lethrinus harak*, all use seagrass beds for protection (Nakamura et al. 2012). Consequently, the fragmentation and degradation of seagrass habitats may lead to a decrease in formerly numerous fish species, as many depend on seagrass to some degree. However, relatively few studies have examined the response of fish assemblages to the decrease and degradation of seagrass beds, although the effects on fishes of complete loss of seagrass beds have been reported previously (Nakamura 2010). When green turtles graze exclusively on seagrass beds, the change in the habitat structure conferred by seagrass shoots is considerable (Lal et al. 2010; Kelkar et al. 2013), which may negatively impact seagrass fishes. However, such habitat fragmentation may also provide a variety of microhabitats of differing structural complexity, e.g., seagrass-remaining areas, grazed beds, and their boundaries. The responses of fishes to seagrass bed fragmentation are often complex and species specific, with macro-habitat use

patterns and dependence on seagrass beds differing among fish species (Horinouchi 2007). Accordingly, the effects on fish assemblages of seagrass degradation by turtle grazing should be assessed by comparing fish distribution among grazed/ungrazed seagrass microhabitats, so as to establish effective conservation and management strategies, which contribute to the high biodiversity of coastal ecosystems and local fisheries.

In the present study, we investigated the fish assemblage structure (i.e., numbers of species, individuals and species composition) in *E. acoroides* seagrass beds, which have been suffering fragmentation and decline due to overgrazing by green turtles, in northwestern Iriomote Island, Japan. Specifically, we compared fish assemblages among several microhabitats (dense seagrass beds, grazed beds, their boundaries and sandy areas) found in and around fragmented seagrass habitats, to clarify the response of each fish species to the grazing of seagrass by green turtles.

Materials and methods

Study site. The study was conducted in *Enhalus acoroides* seagrass beds at Hoshidate, northwestern Iriomote Island, Ryukyu Islands, Japan. The Yonada River drains into the inner area of the bay, which measures approximately 0.9 km across and opens to coral reefs offshore (Fig. 1). Ungrazed seagrass beds (> 50 cm in leaf length) concentrated near the center of the bay covered a total area of ca. 10 ha in 2013, a 25% reduction more or less of the area covered in 1974 (Takeyama et al. 2014). One of the reasons for the reduction in the area of the beds is considered to be overgrazing by green turtles, since most leaves on the outer edges of the beds were extremely short (< 20 cm in leaf length) with diagonally cut tips, characteristic of turtle grazing.

Four types of microhabitats within the present seagrass beds were identified: (1) areas of flourishing *E. acoroides* growth (hereafter referred to as “dense seagrass beds”), (2) areas where evidence of grazing by green turtles was clearly apparent (hereafter referred to as “grazed beds”), (3) boundary areas between dense seagrass beds and grazed beds (“boundary areas”), and (4) areas of sand flats near the seagrass beds (“sandy areas”) (Figs. 1, 2). Each microhabitat occurred in depths between 1.5 m and 2.0 m at high tide. The following surveys were conducted in each microhabitat at monthly intervals from April 2017 to March 2018.

Physical parameters. Water temperature was measured at 10 min intervals using a small data logger (HOBO U20-001-04-TI, Onset Ltd., America) in dense seagrass beds (N24°23'46.40", E123°45'06.50") from May 2017 to March 2018. The logger was attached to a rope and positioned 10 cm above the substrate using a buoy. Monthly mean values were calculated from the data to show seasonal

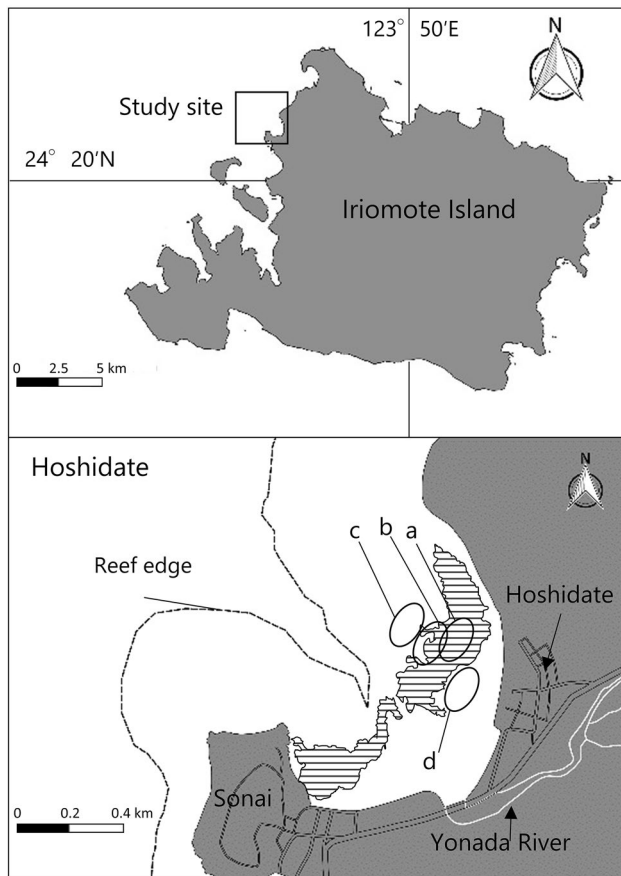


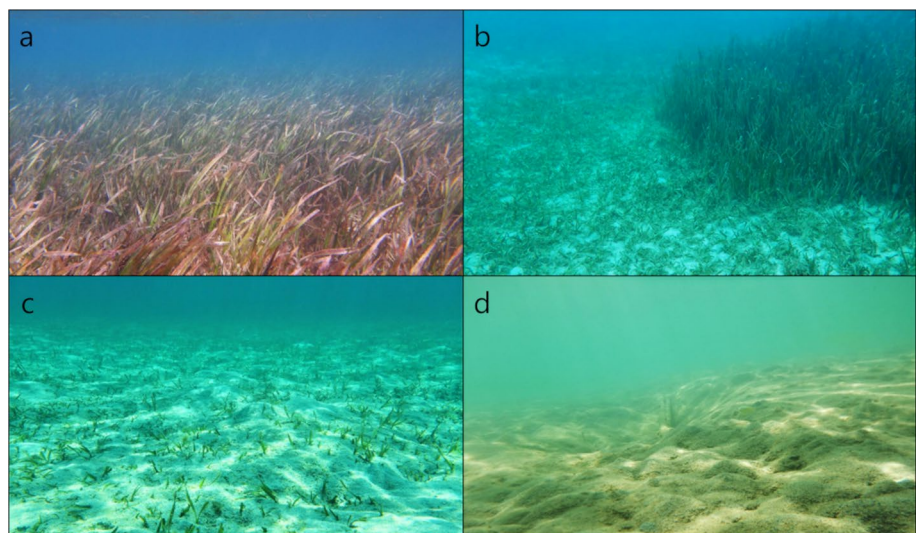
Fig. 1 Map of the study site at Iriomote Island, Ryukyu Islands, Japan. **a** Dense seagrass bed, **b** boundary area, **c** grazed bed, **d** sandy area. Hatched area indicates seagrass meadow consisting predominantly of *Enhalus acoroides* (Takeyama et al. 2014)

variations in water temperature. Shoot densities of *E.*

acoroides were determined by counting all of the shoots that had become established within a 1×1 m quadrat in each microhabitat in October 2017 (except the sandy area) (a total of five replicates separated from each other by at least 10 m). Leaf lengths were determined from five shoots randomly selected from each quadrat randomly established in each microhabitat at monthly intervals from May 2017 to March 2018, the longest leaf being measured to the nearest 1 cm. In the boundary areas, quadrats were established around the outer edge of the seagrass beds, a total of five shoots being selected randomly from inside and outside the seagrass outer edge.

Sampling design. The fish assemblage structures were determined from visual censuses conducted in each microhabitat at monthly intervals from April 2017 to March 2018. For each census, five 20×2 m linear transects were randomly positioned (parallel to the shore and separated from each other by at least 10 m). All of the fishes observed within the transects over a 20 min period (i.e., 1.0 m on either side of the center line transect) by an observer using goggles and a snorkel were counted. In the boundary areas, transects were established along the outer edge of the densely vegetated beds, fishes occurring within 1.0 m on either side of the seagrass edge being recorded. To reduce the possibility of a double count, we made an effort to maintain a swimming speed of about 1.0 m^{-1} , with a balance between swimming slow enough to identify fish species and record fish numbers and fast enough to reduce the possibility of a double count of the same fish, following to the previous study (Horinouchi et al. 2005). Each census was conducted at high tide between 09:00 and 17:00. Individual fishes were identified to species level following Okamura and Amaoka (1997), Seno et al. (2004) and Nakabo (2013).

Fig. 2 Different microhabitat types observed in the degraded seagrass bed. **a** Dense seagrass bed, **b** boundary area, **c** grazed bed, **d** sandy area



Fish species were classified into the following types by observation of their swimming, hovering, or resting behavior, following Park and Kwak (2018): (1) pelagic, fish species that swim over the seagrasses; (2) semi-benthic, fish species that swim and hover between the seagrass plants; (3) benthic, fish species that rest on the vegetated and unvegetated substrata.

Data analysis. During the study period, water temperature in the seagrass bed was lowest in February and highest in August (Fig. 3). Given the water temperature patterns at the study site, data were pooled as follows for each season: winter, January–March (21.5–23.6 °C); spring, April–June (27.3–29.3 °C); summer, July–September (30.2–30.6 °C); autumn, October–December (22.8–28.3 °C).

The mean numbers of fish species and individuals (/40 m²) were compared among microhabitats and seasons using a two-way ANOVA. When significant differences were observed ($p < 0.05$), post hoc Tukey–Kramer tests were applied. Because the first-order interactions were frequently significant, one-way ANOVAs and Tukey–Kramer tests were performed to compare the values among microhabitats in each season, and among seasons in each microhabitat. The same analyses were performed to analyze leaf length, the species and individual numbers of pelagic, semi-benthic and benthic fishes. Mean shoot densities were compared among microhabitats using a one-way ANOVA.

The degree of similarity in fish assemblages between each microhabitat and each season was estimated using the Bray–Curtis similarity coefficient, based on the number of individuals of each species. The resultant similarity matrix was subjected to cluster analysis using the group-average method. Species contributing to significant variation between the groups were identified using the SIMPER (similarity percentage) subroutine. All data were $[\log(x + 1)]$

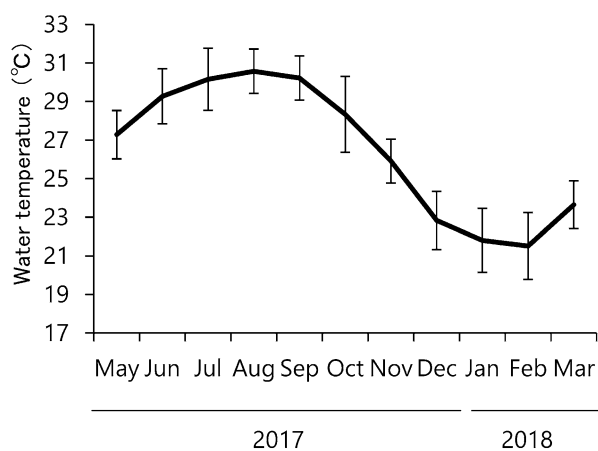


Fig. 3 Monthly mean water temperature (and standard deviation) calculated by the data measured at 10 min intervals in *Enhalus acoroides* seagrass beds at Hoshidate from May 2017 to March 2018

transformed prior to analyses. Large shoals of *Spratelloides delicatulus* were excluded from the above analyses, the occasional occurrence of the species in seagrass habitats likely distorting the results.

Results

The mean shoot density of *Enhalus acoroides* was 174.6 ± 12.6 shoots/m² (dense seagrass beds), 110.2 ± 11.1 shoots/m² (boundary areas), and 96.4 ± 14.6 shoots/m² (grazed beds), being significantly higher in the dense seagrass beds than in the boundary areas and grazed beds (Table 1).

Two-way ANOVAs revealed significant differences in the mean leaf length of *E. acoroides* among microhabitats and seasons, with an interaction among the latter (Table 1; Fig. 4). The mean leaf length in the dense seagrass beds was significantly greater than those in the boundary areas and grazed beds in all seasons. Additionally, in all microhabitats, except the sandy areas, mean leaf length was significantly greater in spring and summer compared with winter.

The fish surveys resulted in a total of 4,311 individuals, representing 17 families and 52 species, being observed over the course of the study period (Table 2). Of these, 2,639 individuals, representing 29 species (14 families) were observed in the dense seagrass beds, and 993 individuals, representing 31 species (16 families) in the boundary areas. A total of 412 individuals, representing 19 species (9 families), were observed in the grazed beds, and 267 individuals, representing 13 species (4 families), in the sandy areas.

The dominant species in the dense seagrass bed were *Siganus fuscescens* (a total of 1,428 individuals, 54.1% of total in the dense seagrass bed during the study period), *Ostorhinchus ishigakiensis* (500 individuals, 21.0%), *Cheilodipterus quinquelineatus* (173 individuals, 6.6%), *Stethojulis strigiventer* (167 individuals, 6.3%) and *Lethrinus harak* (111 individuals, 5.6%). In the boundary area, *Si. fuscescens* (247 individuals, 24.9% of total in the boundary area), *Ch. quinquelineatus* (174 individuals, 17.5%), *L. harak* (154 individuals, 16.1%), *Cryptocentrus caeruleomaculatus* (84 individuals, 8.5%) and *Cheilio inermis* (80 individuals, 5.0%) were most abundant. The dominant species in the grazed bed were *Ctenogobiops crocineus* (178 individuals, 43.2% of total in the grazed bed), *Cr. caeruleomaculatus* (140 individuals, 34.0%), *Ch. quinquelineatus* (37 individuals, 9.0%), *L. harak* (14 individuals, 3.4%) and *Amblygobius phalaena* (11 individuals, 2.7%), whereas *Oplopomus oplopomus* (113 individuals, 42.3% of total in the sandy area), *Cr. caeruleomaculatus* (83 individuals, 31.1%), *Cryptocentrus singapurensis* (29 individuals, 10.9%), *Ct. crocineus*

Table 1 Results of a one-way ANOVA comparing differences in shoot density among microhabitats, and a two-way ANOVA comparing differences in leaf length of *Enhalus acoroides* among microhabitats and seasons

Source	df	MS	F	P	Tukey–Kramer test
Shoot density					
Microhabitat	2	8711.00	52.76	<0.01	DB > BO = GR
Leaf length					
Microhabitat	2	5.19	911.40	<0.01	
Season	3	0.35	62.23	<0.01	
Microhabitat × season	6	0.08	13.21	<0.01	
Microhabitat in spring	2	0.53	117.40	<0.01	DB > BO > GR
Microhabitat in summer	2	1.67	620.30	<0.01	DB > BO > GR
Microhabitat in autumn	2	2.13	337.80	<0.01	DB > BO > GR
Microhabitat in winter	2	1.09	122.80	<0.01	DB > BO > GR
Season at dense seagrass beds	10	0.09	37.73	<0.01	Spring = Summer = Autumn > Winter
Season at boundary areas	10	0.09	20.46	<0.01	Spring = Summer = Autumn > Winter
Season at grazed beds	10	0.19	28.50	<0.01	Spring = Summer > Autumn > Winter

DB dense seagrass beds, BO boundary areas, GR grazed beds

(10 individuals, 3.7%) and *Valenciennea longipinnis* (8 individuals, 2.6%) were most abundant in the sandy area.

The mean numbers of both species and individuals differed significantly among microhabitats and seasons, an interaction among microhabitats and seasons also being evident (Table 3; Fig. 5). In most (all) seasons, the mean number of species (and individuals) was significantly higher in the dense seagrass beds than in the grazed beds and sandy areas, as well as highest in summer in each microhabitat.

The observed fishes included 3 pelagic (2 families), 26 semi-benthic (12 families) and 23 benthic (3 families) individuals (Table 2). The numbers of species and individuals of semi-benthic and benthic fishes, but not pelagic fishes,

differed significantly among microhabitats and seasons (Tables 4 and 5; Fig. 5). The mean numbers of species and individuals of semi-benthic fishes were significantly greater in the dense seagrass beds and/or boundary areas compared to grazed beds and/or sandy areas, and in most microhabitats, higher in summer than in other seasons. The mean number of benthic fish species was highest in dense seagrass beds and that of individuals, greatest in boundary areas. Those of both species and individuals were highest in summer (Tables 4 and 5).

A cluster analysis showed that the fish assemblages in each microhabitat and season could be divided into three major groups with a similarity level of 30% (Fig. 6). The fish assemblages in the dense seagrass beds constituted a group excluding other microhabitats (Group II). Similarly, the assemblage in the boundary areas constituted their own group, although it included the dense seagrass bed in winter (Group I). However, the assemblages in the grazed bed and sandy area were grouped together with the boundary area in winter (Group III). In Group I, which consisted mainly of assemblages in the boundary areas from spring to autumn, the semi-benthic *Si. fuscescens* and *L. harak*, and the benthic *Cr. caeruleomaculatus* were dominant, contributing markedly to the observed similarity from the results of the SIMPER analysis (Table 6). Group II comprised mainly the dense seagrass assemblages from spring to autumn, the semi-benthic *Si. fuscescens*, *L. harak*, and *O. ishigakiensis* being dominant, with the former two contributing significantly to the observed similarity. Conversely, in Group III, which comprised mostly the assemblages in the grazed bed and sandy area, the benthic *Cr. caeruleomaculatus*, *Ct. crocineus* and *O. oplopomus* were dominant, all contributing to the high level of similarity observed.

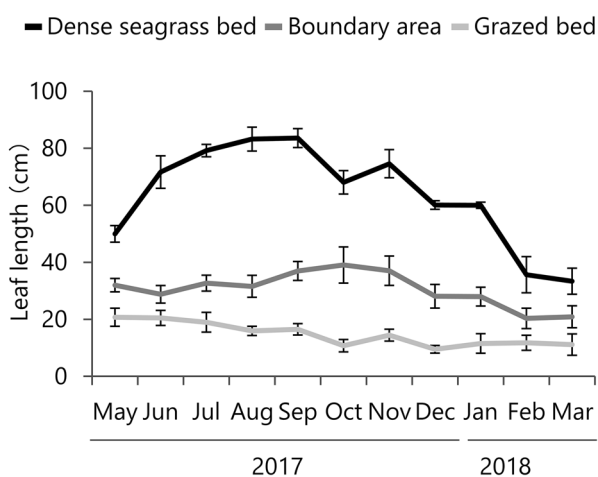


Fig. 4 Mean leaf length (and standard deviation) of *Enhalus acoroides* at each microhabitat ($n=5$) from May 2017 to March 2018. Black line indicates dense seagrass bed, dark-gray line indicates boundary area, and light-gray line indicates grazed bed

Table 2 Mean number of individuals of each fish species per transect (40 m², n = 5) at each microhabitat over time at Hoshidate

Family	Species	Type* 2017															
		Spring						Summer									
		Apr		May		Jun		Jul		Aug		Sep					
DB	BO	GR	SA	DB	BO	GR	SA	DB	BO	GR	SA	DB	BO	GR	SA		
Synodontidae	<i>Synodus dermatogenys</i>	B				0.2	0.2							0.2			0.2
Fistulariidae	<i>Fistularia commersonii</i>	P													0.2		
Centriscidae	<i>Aeoliscus strigatus</i>	S															0.8
Apogonidae	<i>Cheilodipterus quinquelineatus</i>	S	6.4		2.6	7.8		4.6	11.4	34.6	4.6	0.2	9.0	0.2	0.2		0.2
	<i>Ostorhinchus ishigakiensis</i>	S						0.8	64.6	8.2	0.8		37.4				8.8
	<i>Ostorhinchus properuptus</i>	S															1.0
Lutjanidae	<i>Lutjanus fulvus</i>	S							0.2							0.2	
	<i>Lutjanus fulviflamma</i>	S															0.4
Gerridae	<i>Gerrus oyna</i>	S							1.2				0.2				0.2
Haemulidae	<i>Plectorhynchus lessonii</i>	S							0.4				0.2				
Nemipteridae	<i>Scolopsis lineata</i>	S						0.6									
Lethrinidae	<i>Lethrinus harak</i>	S	1.0	0.2	0.2	0.4	0.6	0.6	3.4	2.4	1.0	1.6	1.6	2.2	0.4	4.8	14.0
	<i>Lethrinus nebulosus</i>	S							0.2	0.2							0.2
Scaridae	<i>Calotomus spinidens</i>	S											0.2	0.4			
	<i>Leptoscarus vaigiensis</i>	S							0.4				0.2				
	<i>Scarus rivulatus</i>	S											0.2				1.0
Mullidae	<i>Mullioichthys flavolineatus</i>	B												0.2			0.2
	<i>Parupeneus barberinoides</i>	B												0.2			
	<i>Parupeneus barberinus</i>	B	0.2					0.2									0.2
	<i>Parupeneus ciliatus</i>	B											0.2				
	<i>Parupeneus indicus</i>	B											0.2	0.4			0.2
	<i>Parupeneus pleurostigma</i>	B											0.2				
	<i>Upeneus tragula</i>	B							0.2						0.6		0.4
Pomacentridae	<i>Amblyglyphidodon leucogaster</i>	S												3.0			
	<i>Pomacentrus amboinensis</i>	S													0.2		
Labridae	<i>Cheilodactylus inermis</i>	S	0.2					0.2	0.8	0.8		0.6	0.6	0.2	1.8		0.6
	<i>Epibuttis insidiator</i>	S	0.2														
	<i>Haltichoeres orientalis</i>	S													0.2		
	<i>Haltichoeres trimaculatus</i>	S	0.8	0.2	0.6	0.6	0.2	0.2	0.2	0.2	0.2	0.2	0.6	0.2	0.2		0.2

Table 2 (continued)

Family	Species	Type* 2017																					
		Spring						Summer															
		Apr		May		Jun		Jul		Aug		Sep											
DB	BO	GR	SA	DB	BO	GR	SA	DB	BO	GR	SA	DB	BO	GR	SA								
Pinguipedidae	<i>Stethojulis strigiventer</i>	S																					
	<i>Paraperis cylindrica</i>	B				1.0	0.4	0.8	0.2				0.2	3.0	1.2		1.2	2.6					
Callionymidae	<i>Diplogrammus goramensis</i>	B																					
	<i>Amblyeleotris steinitzi</i>	B						0.2															
Gobiidae	<i>Amblygobius phalaena</i>	B						1.2															
	<i>Asterroperyx semipunctata</i>	B										0.6						0.4					
Gobiidae	<i>Cryptocentrus albidorus</i>	B	0.4		0.4																		
	<i>Cryptocentrus caeruleomaculatus</i>	B	0.8	0.6	2.6	0.6	0.2	2.0	1.6	1.6	0.8	1.0	1.6	1.2	1.4	2.2	2.6	0.2	1.6	4.8	2.2		
Gobiidae	<i>Cryptocentrus melanopus</i>	B										0.4									1.8		
	<i>Ctenogobius crocineus</i>	B																			1.3		
Gobiidae	<i>Ctenogobius pomasticus</i>	B																			0.2		
	<i>Favonigobius reichei</i>	B																			0.4		
Gobiidae	<i>Oplopomus oplopomus</i>	B											1.4								0.4	0.4	
	<i>Valenciennea longipinnis</i>	B																			3.8		
Gobiidae	<i>Valenciennea sexguttata</i>	B																				0.2	
	<i>Yongeichthys crinitiger</i>	B																				0.2	
Sigamidae	<i>Siganus fuscescens</i>	S	29.4											11.8								0.6	11.6
	<i>Siganus guttatus</i>	S																				25.6	1.6
Sigamidae	<i>Siganus spinus</i>	S	2.6																			0.2	0.2
	<i>Siganus virgatus</i>	S																					
Ephippidae	<i>Platax orbicularis</i>	S																					0.2
	<i>Sphyaena barracuda</i>	P																					
Sphyraenidae	<i>Sphyaena barracuda</i>	P																					
	<i>Sphyaena pinguis</i>	P																					3.2

Table 2 (continued)

Family	Species	Type* 2017												
		Autumn						Winter						
		Oct		Nov		Dec		Jan		Feb		Mar		
		DB	GR	SA	BO	GR	SA	DB	GR	SA	BO	GR	SA	
Synodontidae	<i>Synodus dermatogenys</i>	B												
Fistulariidae	<i>Fistularia commersonii</i>	P												
Centriscidae	<i>Aeoliscus strigatus</i>	S			0.4									
Apogonidae	<i>Cheilodipterus quinquelineatus</i>	S												
	<i>Ostorhinchus ishigakiensis</i>	S												
	<i>Ostorhinchus properopus</i>	S						0.2						
Lutjanidae	<i>Lutjanus fulvus</i>	S												
	<i>Lutjanus fulviflamma</i>	S	0.8		0.4	0.2								
Gerresidae	<i>Gerres oyena</i>	S	0.4											
Haemulidae	<i>Plectrohinchus tessoni</i>	S												
Nemipteridae	<i>Scolopsis lineata</i>	S												
Lethrinidae	<i>Lethrinus harak</i>	S	1.2	5.2	3.4	2.6	1.6	1.6	1.6	0.2	3.2	1.2		
	<i>Lethrinus nebulosus</i>	S												
Scaridae	<i>Calotomus spinidens</i>	S												
	<i>Leptoscarus vaigiensis</i>	S									4.0			
	<i>Scarus rivulatus</i>	S												
Mullidae	<i>Mulloidichthys flavolineatus</i>	B	1.2	1.0	0.2	1.8		2.0				0.2		
	<i>Parupeneus barberinoides</i>	B											0.2	
	<i>Parupeneus barberinus</i>	B		1.2	0.4	0.2		0.4				0.2		
	<i>Parupeneus ciliatus</i>	B												0.2
	<i>Parupeneus indicus</i>	B		0.2				1.0						0.2
	<i>Parupeneus pleurostigma</i>	B												
Pomacentridae	<i>Upeneus tragula</i>	B												
	<i>Amblyglyphidodon leucogaster</i>	S												
Labridae	<i>Pomacentrus amboinensis</i>	S												
	<i>Cheilodipterus</i>	S	0.2	3.2		0.6		0.4	0.2		1.2	1.2	1.8	0.2
	<i>Epibulus insidiator</i>	S												1.6
	<i>Halichoeres orientalis</i>	S												
	<i>Halichoeres trimaculatus</i>	S												0.2
Pinguipedidae	<i>Stethojulis strigiventer</i>	S	2.2	0.4	1.0	2.4		3.8			13.8	3.2	0.6	
	<i>Paraperis cylindrica</i>	B	0.4			0.2		0.4					0.2	0.2
Callionymidae	<i>Diplogrammus goramensis</i>	B												0.2

Table 3 Results of a two-way ANOVA comparing differences in the mean numbers of species and individuals per transect (40 m², $n=5$) among microhabitats and seasons

Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>	Tukey–Kramer test
Species					
Microhabitat	3	0.28	13.31	<0.01	
Season	3	0.74	35.64	<0.01	
Microhabitat × season	9	0.06	2.86	<0.01	
Microhabitat in spring	3	0.08	1.76	0.165	
Microhabitat in summer	3	0.17	9.18	<0.01	DB = BO > GR = SA
Microhabitat in autumn	3	0.15	12.70	<0.01	DB = BO > GR = SA
Microhabitat in winter	3	0.06	6.25	<0.01	DB > GR = SA
Season at dense seagrass beds	3	0.21	9.98	<0.01	Summer = Autumn > Spring = Winter
Season at boundary areas	3	0.49	18.90	<0.01	Summer > Spring = Autumn = Winter
Season at grazed beds	3	0.12	5.90	<0.01	Summer > Autumn = Winter
Season at sandy areas	3	0.10	6.53	<0.01	Summer = Autumn > Spring
Microhabitat	3	3.72	29.30	<0.01	
Season	3	3.29	25.85	<0.01	
Microhabitat × season	9	0.28	2.20	<0.01	
Microhabitat in spring	3	1.32	5.99	<0.01	DB > BO = GR = SA
Microhabitat in summer	3	1.69	12.82	<0.01	DB = BO > GR = SA
Microhabitat in autumn	3	1.16	12.90	<0.01	DB > BO > GR = SA
Microhabitat in winter	3	0.39	5.91	<0.01	DB > GR = SA
Season at dense seagrass beds	3	0.54	10.62	<0.01	Spring = Summer = Autumn > Winter
Season at boundary areas	3	2.05	10.65	<0.01	Summer > Spring = Winter
Season at grazed beds	3	0.78	8.38	<0.01	Summer > Spring = Autumn = Winter
Season at sandy areas	3	0.36	13.98	<0.01	Summer > Spring = Autumn = Winter

DB dense seagrass bed, BO boundary area, GR grazed bed, SA sandy area

Discussion

The present study revealed that the fish assemblage structures differed significantly among microhabitats within seagrass beds degraded by turtle grazing, the numbers of species and individuals being greater (and having different species composition) in the seagrass-remaining microhabitat compared to those in the grazed beds and sandy areas. As found in previous studies, common species, such as *Siganus fuscescens*, *Ostorhinchus ishigakiensis* and *Cheilodipterus quinquelineatus*, were abundant in dense seagrass beds and boundary areas (Nakamura and Tsuchiya 2008; Nakamura 2010). Conversely, like sandy area assemblages, which are characterized by relatively low species richness and abundance, the grazed beds supported less diverse fish assemblages (comprising mainly benthic species, such as the gobiids *Cryptocentrus caeruleomaculatus* and *Ctenogobius crocineus*).

Seagrass beds subjected to partial disturbance/degradation typically have patches where the leaves are shorter and less dense, which results in the fragmentation of large contiguous beds into smaller patches. Interestingly, the heterogeneity of such fragmented seagrass beds, which can contain habitat edges and seagrass patches that differ with respect to

canopy height, density, and area of exposed substrate, can sometimes support higher levels of species diversity compared to a single contiguous seagrass bed (Horinouchi et al. 2009). Horinouchi (2009) also demonstrated horizontal gradients in the fish assemblages found in and around seagrass beds with inside sand patches, the outer and inner boarder areas between the beds and sand areas sometimes having higher levels of species diversity and/or abundance than seagrass microhabitats, due to some group-forming goby juveniles, such as *Chaenogobius gulosus*, *Pterogobius zonoleucus* and *Gymnogobius heptacanthus*, favoring edge-type microhabitats. In the present study, however, such species did not occur in the boundary areas, semi-benthic seagrass-associated fishes (such as *Si. fuscescens* and *O. ishigakiensis*) instead being observed in both dense seagrass beds and boundary areas, occasionally moving in schools from the former to the latter, where their abundance was less. Contrary to this, the benthic goby *Cr. caeruleomaculatus*, also occurring in the dense seagrass and boundary areas, was more abundant in the latter. The distribution patterns of these fish types determined the boundary area assemblages, with similar or sometimes lower levels of species richness and abundance, and different species composition compared to those of the dense seagrass bed. These findings suggest that fish assemblages can change in a seagrass microhabitat

Fig. 5 Table 1 Results of a one-way ANOVA comparing differences in shoot density among microhabitats, and a two-way ANOVA comparing differences in leaf length of *Enhalus acoroides* among microhabitats and seasons. Mean numbers (and standard deviation) of (a) species and (b) individuals per transect (40 m², n=5) for each microhabitat use group in each microhabitat at Hoshidate from April 2017 to March 2018. Black bars indicate pelagic species, gray bars indicate semi-benthic species, and white bars indicate benthic species

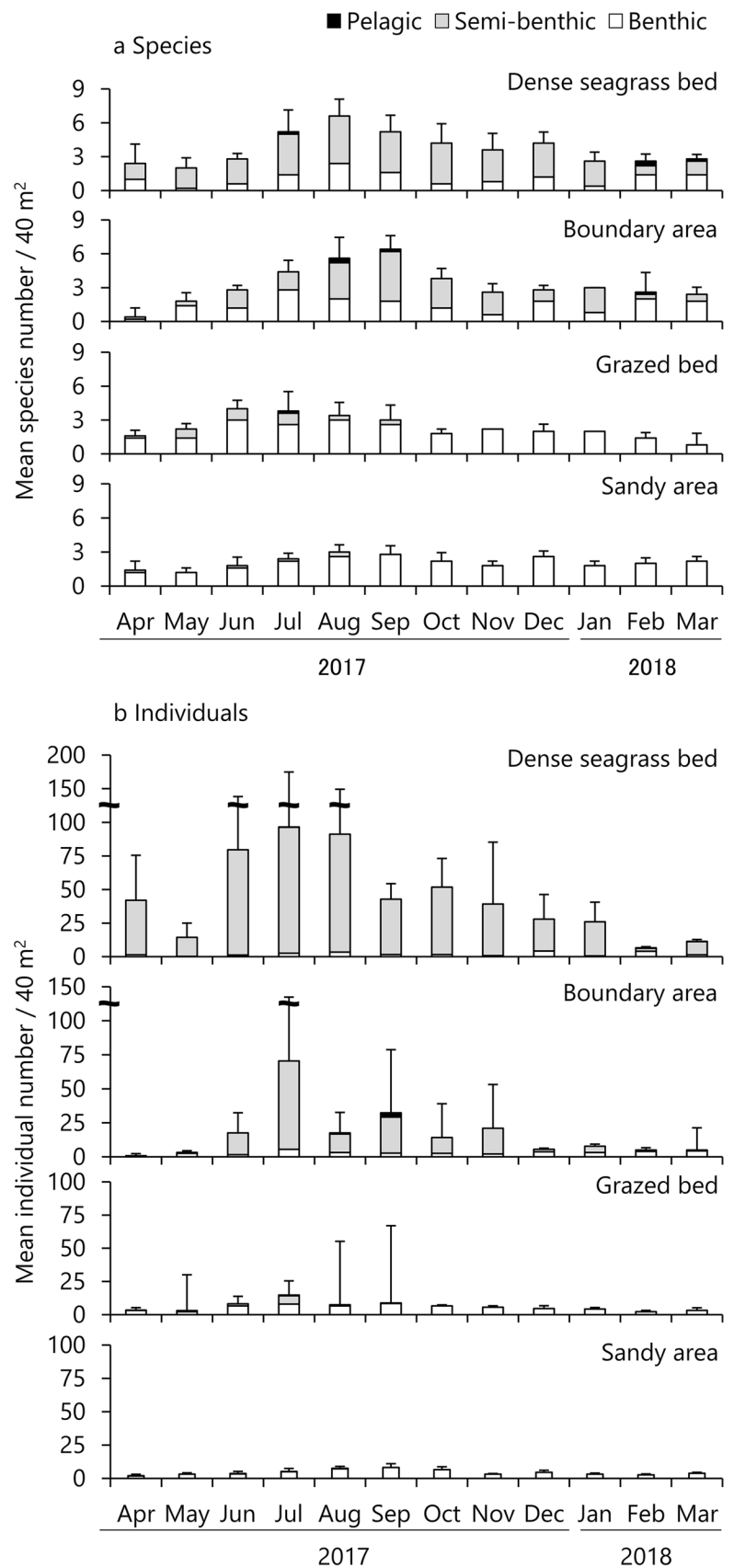


Table 4 Results of a two-way ANOVA comparing differences in the mean number of species in each fish type per transect (40 m², $n=5$) among microhabitats and seasons

Source	df	MS	F	P	Tukey–Kramer test
Pelagic fish					
Microhabitat	3	0.01	2.51	0.06	
Season	3	0.01	3.23	<0.01	Summer > Spring = Autumn
Microhabitat × season	9	0.01	0.96	0.48	
Semi-benthic fish					
Microhabitat	3	10.91	117.88	<0.01	
Season	3	2.16	23.28	<0.01	
Microhabitat × season	9	1.77	6.36	<0.01	
Microhabitat in spring	3	1.25	11.64	<0.01	DB > GR = SA
Microhabitat in summer	3	5.47	34.98	<0.01	DB = BO > GR = SA
Microhabitat in autumn	3	4.56	120.70	<0.01	DB = BO > GR = SA
Microhabitat in winter	3	1.39	20.32	<0.01	DB > BO = GR = SA
Season at dense seagrass beds	3	0.92	11.65	<0.01	Summer = Autumn > Spring = Winter
Season at boundary areas	3	2.67	12.11	<0.01	Summer > Spring = Winter
Season at grazed beds	3	0.31	5.75	<0.01	Summer > Autumn = Winter
Season at sandy areas	3	0.02	1.44	0.24	
Benthic fish					
Microhabitat	3	0.41	25.71	<0.01	DB > BO > GR = SA
Season	3	0.49	21.43	<0.01	Summer > Spring = Autumn = Winter
Microhabitat × season	9	0.03	1.74	0.08	

DB dense seagrass bed, BO boundary area, GR grazed bed, SA sandy area

when about half of the area is grazed (i.e., the boundary area, containing both seagrass-remaining and grazed areas). In addition, the fish assemblages in such microhabitats varies seasonally, with fish abundance increasing in the summer due to high levels of fish recruitment. For example, juvenile *Si. fuscescens* and *O. ishigakiensis* were observed in June to September in seagrass bed microhabitat during this study, corroborating previous studies conducted in other seagrass beds (Nakamura et al. 2004b; Nakamura and Tsuchiya 2008).

On the other hand, the fish assemblages in the areas of completely grazed seagrass differed significantly to that in dense seagrass beds, with lower fish species richness and abundance. The grazed bed assemblages were dominated mostly by benthic gobies, such as *Cr. caeruleomaculatus* and *Ct. crocineus*, similar to the assemblages associated with the sandy areas. Moreover, seasonal variations in the grazed bed assemblage were relatively small as no summer recruitment of seagrass-associated fish was found. The decline in species and individual numbers of seagrass-associated fishes in the grazed bed may be attributed to decreases in the canopy height (< 20 cm) and shoot density compared to those in dense seagrass beds, since a reduction of seagrass structure typically has an adverse effect on seagrass fishes (Hughes et al. 2002). Gullstorm et al. (2008) reported that seagrass coverage and canopy height have a marked effect on the species richness of juveniles in seagrass beds. One of the primary factors responsible for the reduced fish species

diversity in grazed beds may be a reduction in the shelter provided by seagrasses. Nakamura and Sano (2004a), who undertook tethering experiments to evaluate the predation risk for two juvenile fish species, demonstrated that the presence of seagrass cover had a positive effect on the survival of juvenile *Stethojulis strigiventer* and *O. ishigakiensis*. For fishes that depend on seagrass for protection from predators, the grazed areas, with their extremely low canopies and densities, may be unsuitable habitats. However, some benthic gobies, such as *Cr. caeruleomaculatus* and *Ct. crocineus*, were abundant in grazed areas. These bottom-dwelling gobies may not necessarily utilize seagrass beds for shelter, due to their adaptation to unvegetated areas where they often utilize the burrows of alpheid shrimps for protection. Similar significant changes in fish assemblages have been observed in areas around Iriomote Island, where seagrass beds have been completely lost (Nakamura 2010). The overall findings suggest, therefore, that declining seagrass areas due to turtle grazing negatively impact seagrass fish assemblages, to a similar extent as complete seagrass loss, even though low shoot height/densities remain in the grazed areas.

In addition to the sheltering effects of seagrass meadows, food availability can influence fish distribution patterns. The density of invertebrates, such as gammaridean amphipods and harpacticoid copepods, is higher in seagrass beds than on unvegetated substrata (Ansari et al. 1991; Nakamura and Sano 2005), such small crustaceans being important food items for seagrass fishes (Nakamura et al. 2003). Similar

Table 5 Results of a two-way ANOVA comparing differences in the mean number of individuals of each fish type per transect (40 m², n=5) among microhabitats and seasons

Source	df	MS	F	P	Tukey–Kramer test
Pelagic fish					
Microhabitat	3	0.02	1.68	0.173	
Season	3	0.02	2.28	0.08	
Microhabitat × season	9	0.01	0.66	0.744	
Semi-benthic fish					
Microhabitat	3	60.50	143.11	<0.01	
Season	3	9.32	22.04	<0.01	
Microhabitat × season	9	7.46	5.88	<0.01	
Microhabitat in spring	3	13.47	20.82	<0.01	DB > BO = GR = SA
Microhabitat in summer	3	28.13	60.79	<0.01	DB = BO > GR = SA
Microhabitat in autumn	3	20.19	100.10	<0.01	DB > BO > GR = SA
Microhabitat in winter	3	6.17	16.25	<0.01	DB > BO = GR = SA
Season at dense seagrass beds	3	5.87	6.85	<0.01	Summer = Autumn > Winter
Season at boundary areas	3	9.95	16.39	<0.01	Summer > Spring = Autumn = Winter
Season at grazed beds	3	0.93	4.44	<0.01	Summer > Autumn = Winter
Season at sandy areas	3	0.02	1.44	0.24	
Benthic fish					
Microhabitat	3	1.51	30.04	<0.01	BO > DB > GR = SA
Season	3	0.86	17.06	<0.01	Summer > Spring = Winter, Autumn > Spring
Microhabitat × season	9	0.07	1.34	0.22	

DB dense seagrass bed, BO boundary area, GR grazed bed, SA sandy area

Table 6 Results of SIMPER analysis showing the contributions of selected fish species to the overall similarity of each group based on the cluster analysis

Group/species	Type*	Mean ind.**	Contribution (%)
Group I			
<i>Siganus fuscescens</i>	S	4.7	48.7
<i>Lethrinus harak</i>	S	1.9	16.6
<i>Cryptocentrus caeruleomaculatus</i>	B	1.3	15.0
<i>Cheilio inermis</i>	S	1.1	8.9
<i>Stethojulis strigiventer</i>	S	2.4	5.6
Group II			
<i>Siganus fuscescens</i>	S	30.9	85.1
<i>Lethrinus harak</i>	S	2.2	6.2
Group III			
<i>Cryptocentrus caeruleomaculatus</i>	B	1.9	66.2
<i>Ctenogobiops crocineus</i>	B	1.2	19.6
<i>Oplopomus oplopomus</i>	B	0.8	7.3

Group I boundary areas in spring, summer and autumn, and dense seagrass bed in winter, Group II Dense seagrass beds in spring, summer and autumn, Group III Grazed beds in all seasons, sandy areas in all seasons, and boundary area in winter

*Type types of fish based on their swimming, hovering and resting behavior. S semi-benthic fish, B benthic fish

**Mean ind. mean number of individuals per transect (40 m², n=5) in each group

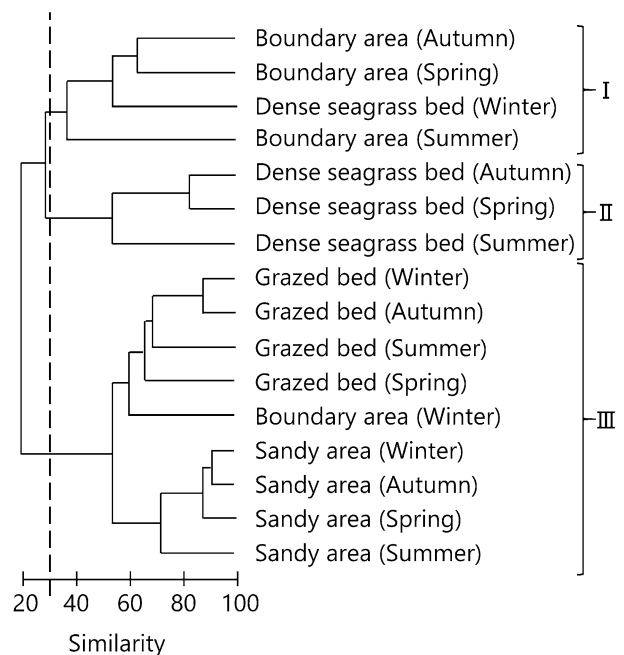


Fig. 6 Dendrogram from the cluster analysis indicating similarities among fish assemblages, based on the mean number of individuals of each fish species in each microhabitat in each season at Hoshidate

prey organisms associated with seagrass may decrease in grazed beds, leading to a decrease in seagrass fishes. However, data on prey abundance were not obtained during the present study, and further study is awaited.

The present study revealed that the degradation of seagrass beds due to overgrazing by green turtles had a negative effect on seagrass fish assemblages, with seagrass-associated fish species in the newly grazed beds declining and being replaced by bottom-dwelling gobies. In the event that such degradation of seagrass habitat progresses further in the Yaeyama archipelago, most of the seagrass-associated fish species are likely to be significantly reduced or lost, with a shift in the fish assemblage structure toward that encountered in areas with sandy/muddy substrates. Importantly, habitat alteration may lead to declines in the overall fish diversity and fisheries resources in areas where green turtles have become abundant. Accordingly, monitoring of areas of seagrass beds as well as the number of green turtles, a previously protected species, should be continued to design and optimize local fisheries management strategies and conservation policies for the region.

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