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Relation	

Temporal changes of the fish community in a seagrass bed after disappearance of vegetation caused by disturbance of the sea bottom and sediment deposition

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Abstract:	To investigate the response of the fish community structure to a natural disturbance in their habitat, fish abundance, biomass and species composition were analyzed in relation to temporal variability of environmental conditions in a seagrass <i>Zostera marina</i> bed. A total of 3,024 fishes belonging to 46 taxa (22 families) were collected by quantitative sampling for 10 years from 2007 to 2016 in the Seto Inland Sea, southwestern Japan. Seagrass shoot density decreased to less than 1/20 of its original density after disappearance of vegetation caused by heavy rain in the fall of 2011 and the area did not recover for the next five years. In order to analyze temporal changes of fish community, the fish was divided into three groups depending on their habitats or lifestyles: pelagic or migratory species (PM), sand or mud bottom-associated species (SM) and seagrass (<i>Z. marina</i>)- or substrate (rocky bottom including macrophytes)- associated species (ZS). Multiple regression analysis showed seagrass shoot density had the most significant effect on biomass of ZS among the three groups, with higher fish biomass under higher seagrass shoot density. Fish community composition changed after the disappearance of the seagrass vegetation coverage with an increase in abundance of SM during the five-years of the post-disturbance period. Seagrass vegetation was concluded to affect temporal change of fish community structure through a stronger influence on fish species that are more dependent on seagrass bed as habitat.

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1 Running Head:
2 Temporal change of fish community in seagrass bed

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7 **disappearance of vegetation caused by disturbance of the sea**
8 **bottom and sediment deposition**

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31 Abstract

32

33 To investigate the response of the fish community structure to a natural disturbance in their habitat,
34 fish abundance, biomass and species composition were analyzed in relation to temporal variability of
35 environmental conditions in a seagrass *Zostera marina* bed. A total of 3,024 fishes belonging to 46
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49

50 **Keywords:** Natural disturbance; Seto Inland Sea; species change; succession; vegetation; *Zostera*
51 *marina*

52

53 INTRODUCTION

54

55 Disturbance caused by anthropogenic and natural forces on an ecosystem is known to greatly affect
56 the plant and animal communities (Foster *et al.*, 1998; Nyström *et al.*, 2000; Johnson & Miyanishi,
57 2010; Turner, 2010). Some of the disturbance caused by natural forces happens suddenly and is
58 therefore difficult to predict. To evaluate the effects of a natural disturbance, it is necessary to collect
59 and compare data before and after the event. In addition to the data collection just before and after the
60 event, long-term monitoring as well as spatial comparison would also be useful to clarify the process
61 of community succession (Larkum *et al.*, 2007; Jelbart *et al.*, 2007; Hori *et al.*, 2009).

62 In marine coastal ecosystems, flooding and tsunamis are typical examples of natural disturbance
63 that directly affect ecosystems and plant and animal communities owing to organisms being swept

64 away and to the drastic changes in e.g. physical, chemical and biological properties of their habitats
65 (Atwater & Moore 1992; Nakaoka *et al.*, 2006; Jaramillo *et al.*, 2012). Furthermore, biological
66 communities at higher trophic levels suffer from indirect effects through changes in the habitat
67 conditions (e.g. bottom sediments and plant vegetation: Muraoka *et al.* 2017). However, information
68 on the effect of natural disturbances on the fish community is very limited (Shoji & Morimoto, 2016;
69 Noda *et al.*, 2017) while there have been observations on the short-term impact of the disturbances on
70 the benthic communities on seagrass beds (Nakaoka *et al.*, 2006; Whanpetch *et al.*, 2010), the sandy
71 bottom (Seike *et al.*, 2013) and rocky reefs (Jaramillo *et al.*, 2012; Takami *et al.*, 2013). The difficulty
72 in quantitative sampling of fish and the greater effort required for fish surveys have restricted the
73 evaluation of the effects of natural disturbance on fish communities (Beck *et al.*, 2000). Monitoring of
74 the fish community through the periods before and after a natural disturbance is indispensable to better
75 understand the impacts of disturbance.

76 Seagrass *Zostera marina* beds are one of the most important ecosystems that serve as a habitat for
77 a variety of marine organisms. Among the world's ecosystems, seagrass (including *Zostera* spp. and
78 related species) beds provide ecosystem services with high economic values (Costanza, 1997; Ellison
79 *et al.*, 2005; Orth *et al.*, 2006). Many fish species are dependent on seagrass beds for their spawning,
80 feeding, refuge from predators and inhabitation (Heck *et al.*, 1989; Boström *et al.*, 2006; Larkum *et al.*
81 *et al.*, 2007). The abundance of fishes associated with seagrass beds has been reported to fluctuate
82 depending on spatial and temporal variabilities in seagrass vegetation (Jelbart *et al.*, 2007; Hori *et al.*,
83 2009; Raventos *et al.*, 2009; Shoji *et al.*, 2017). Changes in fish community after the decline of seagrass
84 beds resulting from eutrophication, physical disturbance and a resurgence of wasting disease have been
85 observed in the North Atlantic (Hughes *et al.*, 2002). In recent studies, drastic changes in the fish
86 community in seagrass beds following an abrupt decrease in seagrass vegetation coverage have been
87 reported. On the Pacific coast of northern Japan after the tsunami following the 2011 Tohoku
88 earthquake off the Pacific coast, the dominant fish species (fishes associated with seagrass beds and
89 substrates: rocky bottom including macrophytes) changed to sand or mud bottom-associated fish
90 species after the disturbance of bottom sediment (Shoji & Morimoto, 2016; Noda *et al.*, 2017). In these
91 previous studies, however, the periods of the observations (one to three years) are limited just before
92 and after the natural disturbances caused by drastic changes in the seagrass vegetation and sea bottom.
93 There is no study that analyzed the effect of drastic changes of seagrass vegetation coverage on the
94 fish community based on monitoring for longer periods.

95 In the present study, data on environmental conditions and fish community in a seagrass bed in the
96 Seto Inland Sea, Japan, affected by a disturbance of the sea bottom and sediment deposition following
97 heavy rain in 2011 was analyzed from 2007 to 2016. The hypothesis that temporal variability in

98 seagrass vegetation coverage induces change of fish community structure through a more significant
99 effect on seagrass or substrate-associated fish species was tested.

100

101 **MATERIALS AND METHODS**

102

103 **Field survey**

104 Surveys for seagrass vegetation and the fish community were conducted on a seagrass bed (ca.10 ha)
105 off the eastern Ikuno Island, central Seto Inland Sea, Japan (34°17'20"N, 132°55'32"E; Figure 1).
106 Ikuno Island has a population of approximately 17, with no human habitation on the eastern coast. The
107 vegetation of the seagrass bed is dominated by the seagrass *Z. marina*, and the mean shoot density of
108 this plant around the sampling site fluctuates between 20 and 160 m⁻² throughout the year (Mohri *et*
109 *al.*, 2013). The bottom of the seagrass area is composed of mud and sand. A heavy rain in the fall of
110 2011 induced disturbance of the sea bottom and sediment deposition on the seagrass bed on the eastern
111 shore of Ikuno Island and the area did not recover for the next five years (see the Results).

112 Fish sampling was conducted using a round seine net (2 m high, 30 m long, and 4 mm mesh
113 aperture: Kamimura & Shoji, 2013) in the day (1100–1700 h) during the spring tide period in August
114 or September from 2007 to 2016. Fish were collected from four separate locations randomly selected
115 from areas within the seagrass bed (four replicates). Tidal levels were between 50–130 cm (within two
116 hours before and after low tide), when the shore line was close to the edge of the seagrass bed. Three
117 sides of a square (10 m in side length) were surrounded using the net at a speed of ca. 1.0 m/s, with
118 another side facing into the shore (around the border of the seagrass bed). Then the net was pulled
119 landward. Each fish collection covered an area of 100 m². The collected fish were preserved in 10%
120 formalin seawater solution. The temperature and salinity of the surface water were measured at each
121 sampling. Seagrass shoot density was measured in at least four randomly placed 0.5 m square quadrats
122 in the seagrass bed. The length of seagrass leaves from at least 10 shoots was measured.

123

124 **Data analysis**

125 In the laboratory, fish were identified according to Nakabo (2013). Mean number of fish species (no.
126 fish species 100 m⁻²), abundance (no. fish 100 m⁻²) and biomass (wet weight of fish 100 m⁻²) were
127 calculated. The total length (TL, mm) of each fish was measured to the nearest 0.1 mm. To detect the
128 possible effect of the disturbance on seagrass vegetation and the fish community, the mean seagrass
129 shoot density and leaf length, number of species, abundance, and biomass were compared between the
130 periods before and after the event in 2011 using the Mann-Whitney *U* test.

131 In the previous studies conducted in northern Japan, the effects of the temporal change in seagrass

132 vegetation on fish species that were associated with the seagrass bed and substrates (rocky bottom
133 including macrophytes) were suggested to be more intensive compared to other fish species (Shoji &
134 Morimoto, 2016; Noda *et al.*, 2017). The collected fishes were divided into three groups according to
135 these previous studies: pelagic or migratory species (PM), sand or mud bottom-associated species
136 (SM) and seagrass (*Z. marina*) or substrate (rocky bottom including macrophytes)-associated species
137 (ZS). In order to examine possible effects of the environmental conditions on the fish community, a
138 linear model was constructed with the mean seagrass shoot density, water temperature and salinity as
139 explanatory variables and mean biomass of the three fish groups as response variables. The leaf length
140 was not included in the analysis due to positive correlation with seagrass shoot density ($r^2=0.680$,
141 $p<0.01$). The model selection was operated based on the Akaike information criterion. Data of *Sebastes*
142 spp. (juveniles) in 2012 was excluded from the analysis because of a significant effect of its dominance
143 (90.3% in biomass: see the Results). The Bray-Curtis dissimilarity index was calculated for each year
144 based on fish abundance and was processed for nonmetric multidimensional scaling (NMDS) to
145 visualize the differences in the fish community for each year because the index has been applied for
146 comparison of marine animal community structures (Clarke, 1993; Field *et al.*, 1982; Warwick &
147 Clarke, 2001). All statistical analyses were performed in R (3.4.0: R Development Core Team).

148

149 **Results**

150 **Physical environmental conditions and seagrass vegetation**

151 The water temperature ranged between 24.7 °C (2013) and 27.8 °C (2010) and salinity ranged between
152 27.8 (2013) and 33.0 (2015 and 2016: Table 1). The mean (\pm standard deviation: SD) seagrass shoot
153 density ranged between 0.3 ± 0.5 shoots m^{-2} (2015) and 61.8 ± 20.2 shoots m^{-2} (2007) (Figure 2a).
154 Difference in the mean seagrass shoot density between the periods before and after the disturbance
155 was significant (Mann-Whitney *U* test, $p<0.01$).

156

157 **Fish community**

158 A total of 3,024 fishes belonging to 46 taxa (22 families) were collected during the 10-year survey
159 (Table 1). The mean (\pm SD) number of fish species ranged between 4.75 ± 0.5 100 m^{-2} (2014) and
160 12.5 ± 2.9 100 m^{-2} (2011: Figure 2b). The mean number of fish species decreased after the disturbance
161 and was the lowest in 2014, with a significant difference between the two periods (Mann-Whitney *U*
162 test, $p<0.05$).

163 The mean (\pm SD) fish abundance per 100 m^2 ranged between 17.0 ± 9.3 (2014) and 220.0 ± 250.2
164 (2012: Figure 2c). The mean (\pm SD) fish biomass per 100 m^2 ranged between 18.5 ± 2.6 g (2014) and
165 504.5 ± 556.1 g (2012: Figure 2d). In 2012, one year post-disturbance, the mean fish abundance,

166 biomass and their SDs increased due to the presence of juvenile black rockfish *Sebastes* spp. at a
167 remarkably high level of abundance in one of the four collection areas within a scattered seagrass bed
168 (Table 1). The differences in fish abundance and biomass between the two periods were not significant
169 (Mann-Whitney U test, $p=0.42$ for abundance and $p=0.31$ for biomass).

170 Among the three fish groups (PM, SM and ZS, divided based on their habitats and lifestyles), year-
171 to-year variability in the biomass were larger in SM and ZS (Figure 3). The seagrass shoot density and
172 salinity were selected as explanatory variables for ZS in the model, with higher fish biomass under
173 higher seagrass shoot density and salinity ($r^2=0.75$: Table 2). For ZS, the effect of seagrass shoot
174 density was significant ($p=0.002$) and much greater than that of salinity ($p=0.077$). All initial
175 explanatory variables were not significant ($p>0.6$) and were excluded by the model for SM. For PM
176 type fish, all initial explanatory variables were adopted in the selected model ($r^2=0.28$) but were not
177 significant ($p>0.1$). Based on the fish community structures, the years were divided into three or more
178 groups (stress=0.132, Figure 4). Group 1: 2007 and 2011; group 2: 2008, 2009, 2010 and 2012; group
179 3: 2014 and 2015 and outgroup: 2013 and 2016.

180

181 **DISCUSSION**

182

183 **Effects of environmental conditions on the fish community**

184 The area of seagrass bed has been decreasing at a rate of 5% per year or more on the entire earth
185 (Waycott *et al.* 2009). The effects of human activity (e.g. low oxygenation concentrations and high
186 turbidity due to eutrophication) and natural effects are considered to affect the seagrass growth and
187 vegetation (Larkum *et al.*, 2007). As global warming progresses, fish would also be indirectly affected
188 through the effects on seagrass. Because the seagrass is vulnerable to high water temperature, the area
189 of the seagrass, which is important as a fish habitat, can decrease under the global warming (Kuwa
190 & Hori, 2019). In addition, the global warming tends to increase the frequency of heavy rains and
191 amount of single rainfall, so that can also cause disturbance to the bottom sediments of seagrass bed.
192 Mitigating the effects of human activity will reduce the rate of disappearance of the seagrass beds.
193 Furthermore, it is possible to prepare for improvement of recovery from environmental fluctuation and
194 damage in the future through maintenance of population structure/network which enables to supply
195 seagrass seeds from the surrounding area when seagrass beds disappear (Larkum *et al.*, 2007; Kuwa
196 & Hori, 2019).

197 In the present study, seagrass shoot density showed the significant effect only on seagrass- or
198 substrate-associated (ZS) fish species among the three fish groups (Table 2). In general, spatial and
199 temporal variations in habitat complexity and connectivity to adjacent habitats affect fish community

200 structures of seagrass beds and surrounding areas (Dorenbosch *et al.*, 2005; Dorenbosch *et al.*, 2006;
201 Grol *et al.*, 2011). Previous studies have shown higher number of fish species, and greater abundance
202 and biomass of fishes in areas with seagrass vegetation coverage, compared to those in surrounding
203 areas with less or without seagrass vegetation (Ferrel & Bell, 1991; Larkum *et al.*, 2007). It is likely
204 that the three-dimensional habitat complexity provided by seagrass leaves serves as predation refuge,
205 feeding ground and as a habitat for fishes. In the present study, it was demonstrated that year-to-year
206 variability of seagrass shoot density was one of the important determinants for the ZS-type fish.

207 Salinity was the important factor for ZS- and PM-type fish species although the effect was not
208 significant. Seagrass is widely distributed in estuarine waters with high tolerance to low salinity
209 condition (Nakaoka & Aioi, 2001). In a laboratory experiment conducted at salinities between 0-33
210 (0, 5, 10, 15, 20, 25 and 33), seagrass showed the highest germination rates at salinity of 0 under five
211 temperatures tested (5, 10, 15, 20 and 25°C: Yamaki *et al.*, 2006). Therefore, it is plausible that the
212 temporal variability in salinity (especially, low salinity conditions) caused by the heavy rain did not
213 have negative effect on the seagrass vegetation in the present study site. The indirect effect of salinity
214 through seagrass vegetation on fish community and direct effect of salinity on fish are also suggested
215 to be minimal because the variability of salinity recorded in the seagrass bed of the study site (27-33)
216 was relatively small (Nakaoka & Aioi, 2001; Larkum *et al.*, 2007).

217

218 **Temporal variability of seagrass vegetation**

219 Flora and fauna in coastal habitats were generally subject to high variability in environmental
220 conditions such as temperature, salinity, dissolved oxygen concentration and turbidity at a variety of
221 temporal scales affected by tide, freshwater flow and anthropogenic effects (Schubel, 1968; Valiela *et al.*,
222 1992). The succession process of the plant vegetation and the animals after a strong disturbance in
223 marine ecosystems seems to differ based on the level of disturbance. In seagrass beds, there have been
224 studies on the effects of natural disturbance such as disturbance of sea bottom and sediment deposition
225 on seagrass vegetation (Nakaoka *et al.*, 2006), benthic macrofauna (Whanpetch *et al.*, 2010) and fishes
226 (Shoji & Morimoto, 2016; Noda *et al.*, 2017). In the present survey area, the seagrass vegetation
227 drastically decreased in 2012 (46.0 shoots m⁻² in 2011 to 8.0 shoots m⁻² in 2012). The seagrass shoot
228 density has remained lower in recent years than that in the years before 2011. So far, the seagrass
229 vegetation coverage has not increased in the present survey site, although there are plenty of seagrass
230 beds with high shoot density in the surrounding waters. These seagrass beds in the surrounding waters
231 have not experienced a loss of vegetation coverage in recent years and have most likely been able to
232 provide the present survey site with seagrass seeds. Therefore, there may be other continuous factors
233 that have been preventing seagrass growth in the present survey site. Turbidity in the seagrass bed has

234 increased since the inflow of mud caused by the heavy rain in the autumn of 2011. Additionally, an
235 increase in the abundance of herbivore fishes such as *Siganus fuscescens* (Table 1) may have
236 potentially affected seagrass growth and coverage.

237

238 **Temporal change in dominant fish species**

239 The dominant fish species were replaced in the present survey area after the decrease of vegetation in
240 2011. The ZS-type fishes such as *Sebastes oblongue*, *Hypodytes rubripinnis* and *Pterogobius elapoides*
241 had been continuously collected in the seagrass bed before 2011 and were not collected in most of the
242 years after 2011. The decreases in the total fish species richness, abundance and biomass (except for
243 2012) after 2011 indicate the loss of habitat provided by seagrass vegetation, which affected ZS-type
244 fishes the most. The loss and decrease in habitat and its complexity also can alter the growth and
245 survival of young fishes by affecting feeding conditions and the seagrass' function as a predation
246 refuge (Larkum *et al.*, 2007). Therefore, temporal changes in vegetation coverage have a high potential
247 for impact on fish species richness, abundance, and biomass in seagrass beds even within the same
248 location. On the other hand, SM-type fishes such as *Pagrus major*, *Sillago japonica* and *Repomucenus*
249 *beniteguri* were more frequently collected in the seagrass bed after 2012. The seagrass beds surveyed
250 in the present study with decreased vegetation are suggested more suitable for these fish species that
251 are associated with sand or mud bottom after 2012.

252 In 2012, juveniles of *Sebastes* spp. were collected at a high mean abundance (207.8 100 m⁻²). These
253 *Sebastes* juveniles migrate into seagrass and macroalgal beds at about 20 mm in total length in the
254 central Seto Inland Sea (Kamimura & Shoji, 2009). In a previous study, occurrence of three *Sebastes*
255 juveniles (*Sebastes inermis*, *S. ventricosus* and *S. cheni*) was reported in this area (Kamimura *et al.*,
256 2013). Among the three species, juvenile *S. cheni* was most dominant accounting for 77.6 and 80.0%
257 in number of the three species in 2007 and 2008, respectively (Kamimura *et al.*, 2011). The mean
258 abundance of *S. cheni* juvenile in 2008 (451.2 individuals 100 m⁻²) was higher than that observed in
259 the present study in 2012 (207.8 individuals 100 m⁻²), indicating a large inter-annual variability of
260 juvenile recruits. In 2012, aggregation of the *Sebastes* juveniles around the scatted seagrass bed after
261 recruiting at a high abundance might have induced the high mean juvenile abundance although the
262 seagrass shoot density was low.

263 In summary, the fish community in the seagrass bed off Ikuno Island was dominated by seagrass-
264 or substrate-associated species during the pre-disturbance period with high vegetation coverage. After
265 the disappearance of vegetation caused by the heavy rain of 2011, fish species richness, abundance
266 and biomass decreased due to the absence of the species belonging to these dominant fish group.
267 During the five years after the heavy rain, there was no significant recovery of seagrass vegetation

268 coverage. The species richness increased to the same level as that before the heavy rain due to the
269 increase in that of sand or mud bottom-associated species. The seagrass- or substrate-associated
270 species, that were dominant before the seagrass vegetation loss, were replaced with sand or mud
271 bottom-associated species.

272

273

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275

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279

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285

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403

404 **FIGURE CAPTIONS**

405

406 **Fig. 1.** Map showing the location of the seagrass bed off Ikuno Island, Hiroshima Prefecture, western
407 Japan, where environmental survey and fish collection were conducted from 2007 to 2016. Depth
408 contours of 10 and 20 m are indicated as dotted lines.

409

410 **Fig. 2.** Mean shoot density of seagrass (number of shoots 100 m⁻²: a), mean number of fish species (b),
411 fish abundance (number of fish 100 m⁻²; c) and fish biomass (g 100 m⁻²; d) collected in the seagrass
412 bed off Ikuno Island from 2007 to 2016. Dotted lines and the vertical bars indicate the disturbance by
413 the heavy rain in fall 2011 and standard deviation, respectively. Photographs on top of the figure show
414 an underwater overview of the seagrass bed in 2008 and 2014.

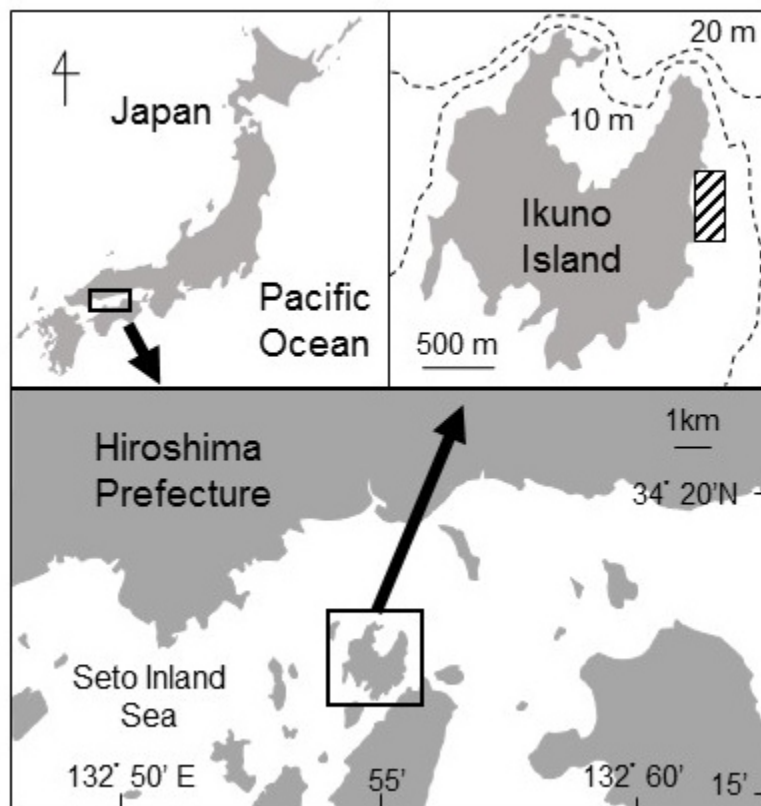
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416 **Fig. 3.** Mean biomass (wet weight 100 m⁻²) of three fish groups based on their habitat and/or life cycles
417 from 2007 to 2016. PM: pelagic and migrative group, SM: sand- or mud-bottom associated group, ZS:
418 seagrass- or substrate-associated group.

419

420 **Fig. 4.** Non-metric multidimensional scaling (NMDS) ordination using the Bray-Curtis dissimilarity
421 index to differentiate the fish species composition in the seagrass bed off Ikuno Island from 2007 to
422 2016.

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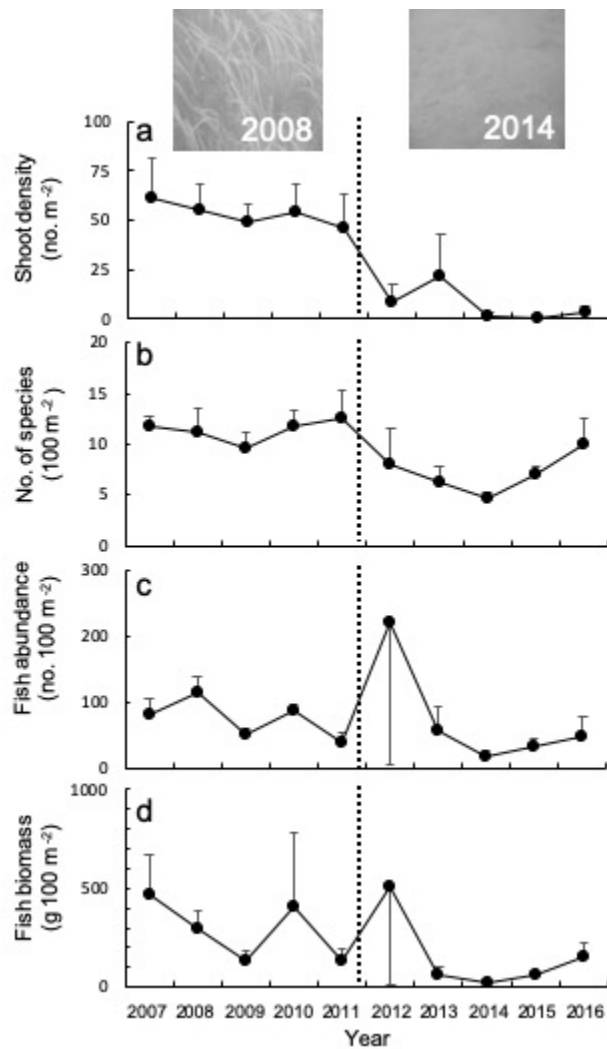
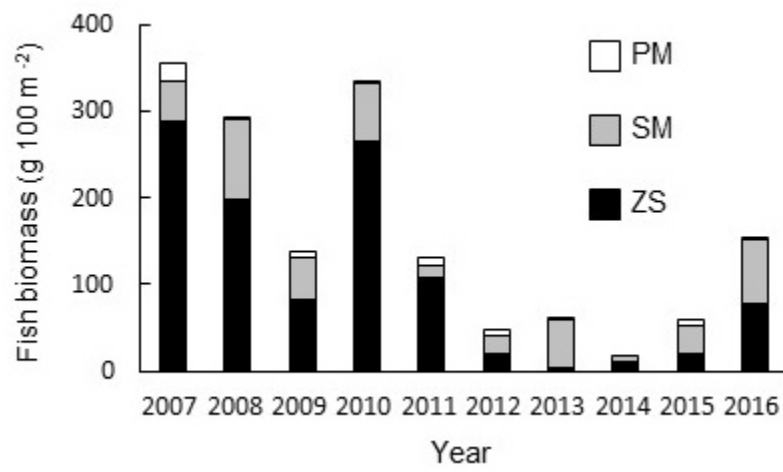


Fig. 2. Mean shoot density of seagrass (number of shoots 100^{-2} : a), mean number of fish species (b), fish abundance (number of fish 100 m^{-2} ; c) and fish biomass ($\text{g } 100\text{ m}^{-2}$; d) collected in the seagrass bed off Ikuno Island from 2007 to 2016. Dotted lines and the vertical bars indicate the disturbance by the heavy rain in fall 2011 and standard deviation, respectively. Photographs on top of the figure show an underwater overview of the seagrass bed in 2008 and 2014.

111x185mm (72 x 72 DPI)



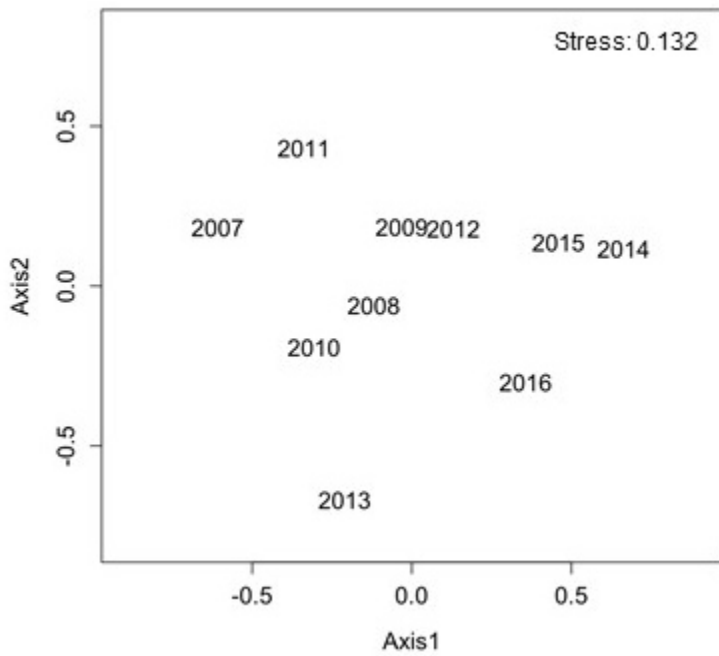


Table 1. Mean fish abundance (number 100 m⁻²), biomass (wet weight 100 m⁻²), water temperature (°C), and salinity at the seagrass bed off Ikuno Island, Seto Inland Sea, western Japan, from 2007 to 2016. Fish were divided into 3 groups driven from each habitat and/or lifestyles, PM: pelagic or migratory species, SM: sand or mud bottom-associated species, ZS: seagrass (*Z. marina*)- or substrate (rocky bottom including macrophytes)-associated species.

Family	Species	Group	No. of ind. / 100 m ²											Wet weight (g / 100 m ²)														
			2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	Total	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	Total				
Engraulidae	<i>Engraulis japonica</i>	PM					5.0								0.5	5.5								2.4			0.4	2.7
Syngnathidae	<i>Urocampus nanus</i>	ZS					0.3																					0.0
	<i>Syngnathus schlegelii</i>	ZS		1.0	0.8		0.5	0.5		0.5	1.3	1.5	6.0				1.4	1.4			0.1	0.1			0.2	0.7	1.6	5.5
	<i>Hippocampus coronatus</i>	ZS				1.5							0.3	1.8					0.5							0.1	0.6	
Mugilidae	<i>Mugil cephalus cephalus</i>	PM		2.0			3.0		0.5					5.5			2.5			6.0			0.4					8.9
	<i>Chelon haematocheilus</i>	PM	7.8		0.8	0.3								8.8		14.5		1.2	0.5									16.2
Hemiramphidae	<i>Hyporhamphus sajori</i>	PM	0.3											0.3		1.2												1.2
Sebastidae	<i>Sebastes schlegelii</i>	ZS					0.8							0.8										3.5				3.5
	<i>Sebastes oblongus</i>	ZS	0.8	0.5	1.0	0.3								2.5		2.3	1.5	3.6	0.9									8.2
	<i>Sebastes</i> spp.	ZS	36.8	41.3	11.0	14.3	3.0	207.8	0.8				12.0	326.8		205.8	166.6	43.8	136.9	15.5	471.3	3.7					33.8	1077.3
Tetrarogidae	<i>Hypodytes rubripinnis</i>	ZS	2.0	0.8	0.8	0.5	0.3	0.3						4.5		20.6	6.8	7.6	2.6	21.2	2.5							61.3
Lateolabracidae	<i>Lateolabrax japonicus</i>	PM	0.5		0.3				1.3			0.3		2.3		5.6		4.7					6.6			6.6		23.4
Haemulidae	<i>Plectorhinchus cinctus</i>	ZS					0.3				0.3			0.5						0.1			0.8					0.8
Sparidae	<i>Acanthopagrus latus</i>	SM	1.0											1.0		1.3												1.3
	<i>Acanthopagrus schlegelii</i>	SM	2.3	37.5	15.8	42.5	6.0	1.0	36.8		4.3		146.0		3.0	42.9	21.5	45.6	9.2	1.1	34.4		10.1					167.7
	<i>Pagrus major</i>	SM		0.8		1.3		0.3	3.0		0.3	8.5	14.0			1.4		2.5		0.9	6.0		1.0		55.8		67.5	
Sillaginidae	<i>Sillago japonica</i>	SM				0.3	0.5	1.0	4.5	2.8	1.0	1.0	11.0					1.2	0.03	3.7	3.4	4.2	7.2	0.3			20.0	
Embiotocidae	<i>Ditrema viride</i>	ZS												0.5	0.5											7.0	7.0	

	<i>Ditrema temminckii pacificum</i>	ZS			4.5	1.0	0.5			0.3		6.3			82.3	15.0	8.2			4.8		110.3		
	<i>Ditrema sp.</i>	ZS								0.3		0.3								5.0		5.0		
	<i>Neoditrema ransonnetii</i>	ZS	2.3	1.3							0.5	4.0	19.8	12.1								5.9	37.8	
Labridae	<i>Parajulis poecilopterus</i>	ZS	0.3									0.3	8.1										8.1	
	<i>Halichoeres tenuispinis</i>	ZS					0.5					0.5				3.9							3.9	
Hexagrammidae	<i>Hexagrammos agrammus</i>	ZS	0.8		0.5	0.5	0.8				0.3	2.8	8.9		5.4	24.4	11.9					4.6	55.2	
	<i>Hexagrammos otakii</i>	ZS	1.3					0.3				1.5	8.0							3.6			11.6	
Cottidae	<i>Pseudoblennius cottoides</i>	ZS		0.3	3.3		3.8	0.3	0.3	0.3	0.3	8.0		1.2	11.0	23.5	1.4		0.9		0.9		38.8	
Blenniidae	<i>Petroscirtes breviceps</i>	ZS		0.5	0.5			0.3				1.3		0.5	0.5				0.1				1.1	
Callionymidae	<i>Repomucenus curvicornis</i>	SM								0.3		0.3								0.0			0.0	
	<i>Repomucenus ornatipinnis</i>	SM			0.3			0.3				0.5			2.9					0.0			2.9	
	<i>Repomucenus beniteguri</i>	SM								0.8	1.0	1.8								0.8	10.7		11.5	
Gobiidae	<i>Luciogobius guttatus</i>	SM			0.3							0.3				0.0							0.0	
	<i>Pterogobius elapoides</i>	ZS	1.8	1.0	0.3	0.5	0.5			0.3		4.3	9.4	6.3	2.0	0.2	4.3				1.4		23.6	
	<i>Tridentiger trigonocephalus</i>	SM		0.5						0.3	0.3	1.0		1.4						0.0	0.3		1.7	
	<i>Acentrogobius virgatus</i>	SM	4.3	8.5	3.3	0.3	0.8	8.8	0.5	2.8	9.8	0.8	39.5	9.5	14.5	9.2	0.4	1.4	11.6	0.3	3.3	11.1	1.0	62.3
	<i>Favonigobius gymnauchen</i>	SM	2.5	16.5	11.0	10.5	1.3	2.3	7.0	1.0	3.8	4.5	60.3	5.2	26.8	18.8	10.1	1.5	2.4	8.5	0.8	2.3	3.5	79.8
	<i>Gymnogobius heptacanthus</i>	ZS		0.3						0.3		0.5		0.2						0.0			0.2	
	<i>Chaenogobius gulosus</i>	ZS	1.5			0.3						1.8	1.6			0.2							1.7	
Siganidae	<i>Siganus fuscescens</i>	ZS			0.3					0.3		2.5	3.0		0.02					0.0		10.1	10.2	
Soleidae	<i>Zebrias zebrinus</i>	SM									0.3	0.3										0.1	0.1	
Monacanthidae	<i>Rudarius ercodes</i>	ZS	0.5	0.8	0.8	4.3	8.3	1.0	2.5	9.0	12.3	6.5	45.8	0.2	1.1	3.1	5.3	7.5	0.3	0.6	3.2	5.5	2.9	29.7
	<i>Thamnaconus modestus</i>	ZS	0.8	0.5		1.8	0.3	0.5				3.8	4.0	1.6		8.0	0.4	4.4					18.2	
	<i>Stephanolepis cirrhifer</i>	ZS			1.0	1.8	0.3				6.3	9.3			4.4	3.8	0.1					16.9	25.3	
Tetraodontidae	<i>Takifugu pardalis</i>	SM	0.8			0.5		0.3				1.5	10.8				1.7		1.5				14.0	
	<i>Takifugu poecilonotus</i>	SM		0.3		0.5					0.3	1.0		0.2		4.7						0.7	5.6	
	<i>Takifugu niphobles</i>	SM	13.5	2.8		0.5	1.5	0.3			0.5	19.0	16.9	3.9		0.3	1.6	0.2				1.6	24.4	

Pleuronectidae	<i>Pleuronectes yokohamae</i>	SM											0.3	0.3							0.9	0.9		
Total			81.3	116.8	51.0	86.3	39.0	226.0	56.5	17.0	34.8	47.8			356.5	292.6	138.2	332.9	130.8	518.3	58.8	18.5	58.6	152.1
		WT (°C)	24.8	25.2	25.8	27.8	26.5	26.1	24.7	26.9	25.1	26.9												
		Salinity	32.6	32.1	31.5	31.6	31.3	31.1	27.8	30.8	33.0	33.0												

For Review Only

Table 2. Results of linear model to examine possible effect of environmental conditions (seagrass shoot density, salinity and water temperature) on fish community. Fish was divided into three groups depending on their habitats or lifestyles: pelagic or migratory species (PM), sand or mud bottom-associated species (SM) and seagrass (*Z. marina*)- or substrate (rocky bottom including macrophytes)-associated species (ZS). Response variable was the mean biomass of each group. Initial explanatory variables were seagrass shoot density, salinity, and water temperature.

Group	Analysis of variance table (Type II tests)					Summary of model			
	Source	df	SS	F	P	Parameter	Estimate	SE	P
ZS	Error	7	19771			Intercept	-761.142	370.305	0.079
	Seagrass	1	66856	23.671	0.002	Seagrass	3.387	0.696	0.002
	Salinity	1	12080	4.277	0.077	Salinity	24.356	11.777	0.077
SM						Intercept	45.970	8.592	<0.000
PM	Error	6	177.585			Intercept	26.790	54.861	0.643
	Seagrass	1	44.537	1.505	0.266	Seagrass	0.088	0.07183	0.266
	Salinity	1	60.955	2.060	0.201	Salinity	1.759	1.22562	0.201
	Water Temperature	1	87.237	2.947	0.137	Water Temperature	-3.062	1.78369	0.137

Adjusted R-squared: ZS= 0.75, SM= -0.46, PM= 0.28