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2 **Importance of patch size variation for the population persistence of**
3 **a decapod crustacean in seagrass beds**

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18 ABSTRACT: To understand the effects of patch attributes of seagrass beds on the persistence
19 of an animal population, we examined shifts in patch utilization that occur with the life stages
20 of a decapod crustacean, Hokkai shrimp *Pandalus latirostris*, inhabiting only eelgrass beds.
21 The abundance of juveniles did not relate to the abundance of prey, patch size, water
22 temperature, or salinity, but adult abundance decreased significantly when patches were
23 smaller. Edge effects were suggested for adults. Since patch size and shoot density were
24 inseparable structures at our study site, we conducted an experiment using artificial seagrass
25 units (ASUs) to clarify structures that were effective as shrimp habitat. This experiment
26 showed that while adults recruited mainly to the small patches regardless of shoot density,
27 juveniles, though much smaller in number, recruited to all patch types. Adults frequently
28 emerged from natural patches to bare spaces at night, while juveniles seldom used the bare
29 spaces at all. When we experimentally released shrimps between ASUs at night, adults
30 generally used the bare spaces while juveniles randomly moved to all habitat types. We
31 tethered adults in the interior of seagrass patches and bare spaces during both daytime and
32 nighttime, and found that the predation rate was high only in bare spaces during daytime. We
33 demonstrated that the habitat functions of seagrass patches can vary with the life stages of this
34 decapod crustacean, and suggest that spatial management of various sizes of patches is crucial
35 for population persistence of Hokkai shrimp.

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37 KEY WORDS: Behavioral habitat shift · Habitat structure · Diurnal behavior · Population
38 management · Eel grass · Grass shrimp · Pandalidae

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INTRODUCTION

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Understanding the functions of habitat is key to achieving effective biological conservation and management of commercially important species. Seagrass beds create ecological boundaries or transition zones in coastal ecosystems and provide temporal or permanent habitats for various animals. Studies on the ecological functions of seagrass as a habitat have increased rapidly in recent years, and spatial management of seagrass is one of the major challenges in the conservation of coastal ecosystems (recent reviews in Beck et al. 2001, Jackson et al. 2001, Duarte 2002, Heck et al. 2003, Nakaoka 2005, Boström et al. 2006, Duffy 2006, Allendorf et al. 2008).

Patch size is a crucial component of seagrass habitats, and variation in patch size provides a good opportunity to consider the relationship between the structural complexity of a habitat and species diversity or the abundance of a specific species within that habitat (Robbins & Bell 1994, Bell et al. 1995). However, patch size frequently fluctuates due to the growth and development of the seagrass itself (reviews in Hemminga & Duarte 2000, Boström et al. 2006) and to multiple disturbance processes such as natural environmental events and human activities (reviews in Orth et al. 2006, Boström et al. 2011, Short et al. 2011). If a change in patch size simply alters the ratio of the perimeter to the total area of the patch, this change can also alter the effect of the surrounding area on animals inside the patch, a phenomenon known as the edge effect (Connolly & Hindell 2006, Fletcher et al. 2007, Boström et al. 2011). Several review papers have concluded that the effects of patch size or patch edges on animal assemblages vary widely among species, because the abundance, density, and diversity of animals are influenced by multiple factors such as the life-history traits of each species, the physical structure of the seagrass, and the interactions between them (Bell et al. 2001, Nakaoka 2005, Boström et al. 2006, Connolly & Hindell 2006). Although most studies have focused on faunal assemblages in various types of patches, the attributes of patches that make them effective as a habitat may also change with the life stage of a single species. For example, many mobile animals use seagrass patches as a nursery (e.g. Gotceitas et al. 1997, Beck et al. 2001, Pittman & McAlpine 2003, Shoji et al. 2007, Mateo et al. 2011, Espino et al. 2015a), and differences in patch attributes can modify the distribution patterns of small and large individuals in a population (Almeida et al. 2008, Mizerek et al. 2011, Williams et al. 2016). However, few fine-scale studies on ontogenetic shifts in habitat utilization have been conducted, and thus we have a limited understanding of how variations in patch size or edge effects contribute to the persistence of an animal population. It is important to know what size

73 of seagrass patches should be preferentially protected when a seagrass bed is exposed to
74 various types of disturbance (Espino et al. 2015b).

75 Hokkai shrimp *Pandalus latirostris* (Rathbun, 1902), can be used as a model species
76 when examining changes in patch utilization patterns during growth. This species is a
77 relatively large decapod compared to common seagrass-dwelling decapods such as palaemonid,
78 hippolytid, and alpheid shrimps, with body lengths (the length between the eye and the end of
79 the telson) reaching up to approximately 120 mm (Bergström 2000, Chiba et al. 2013). Their
80 distribution is strictly limited to seagrass beds in northern Japan and Far East Russia (Komai
81 1999, Bergström 2000). Since this shrimp does not have a planktonic larval phase and spends
82 its whole life in seagrass (Kurata 1955, Chiba et al. 2000), it is categorized as a permanent
83 resident of seagrass beds (Kikuchi 1974). In fact, genetic analyses have suggested a restricted
84 gene flow between geographically close local populations (Kawahara-Miki et al. 2011). Each
85 seagrass bed is therefore crucially important for the persistence of local populations of Hokkai
86 shrimp. Despite the limited, regional nature of their distribution, this shrimp is one of the most
87 valuable targets of single-species fisheries in those regions (Mizushima 1981, Sitonikov et al.
88 1997). For example, annual fishing production of Hokkai shrimp by 40 fishermen in Lake
89 Notoro, a lagoon in northern Japan, had a value of over \$1 000 000 USD during the 1990s, even
90 though the fishing season was limited to less than 4 wk yr⁻¹ (Abashiri City Government 2016).
91 However, annual landings of the shrimp, at least in Japan, have been unstable and in gradual
92 decline, especially over the past decade (Chiba et al. 2013, Hokkaido Research Organization
93 2016). In addition, seagrasses in those regions have not been managed to date, in part due to a
94 lack of information on how Hokkai shrimp use seagrass beds. These seagrass habitats need to
95 be managed in accordance with the ecological characteristics of the shrimp, because the
96 responses of crustaceans to patch attributes vary widely with species (e.g. Eggleston et al. 1998,
97 Moore & Hovel 2010, Ray et al. 2014) and with situations faced by the species such as
98 predation risk, food availability, photoperiod, and season (e.g. Ochwada et al. 2009, Tait &
99 Hovel 2012, García-Sanz et al. 2014, García-Sanz et al. 2016).

100 The goal of this study was to provide a viewpoint for the management of seagrass beds
101 from the perspective of conserving an animal population by examining its habitat utilization,
102 **using** Hokkai shrimp as a model species. We focused our interests on how the suitable
103 attributes of seagrass patches changed for Hokkai shrimp with their life stage. We designed a
104 program of observations and conducted field experiments to identify major processes, such as
105 (1) the structure of seagrass patches, (2) predator–prey interactions, and (3) the rate at which

106 shrimps encounter a seagrass patch, which determines habitat utilization by mobile animals
107 (Connolly & Hindell 2006).

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MATERIALS AND METHODS

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Study site and commercial value of Hokkai shrimp

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All investigations in this study were conducted at Lake Noto, a lagoon on the island of Hokkaido in northern Japan (Fig. 1). Two eelgrasses, *Zostera marina* Linnaeus, 1753 and *Z. caespitosa* Miki, 1932, both with similar above-ground morphology (Shin & Choi 1998, Jiang et al. 2013) form a mosaic of patches on the sandy bottom of the lagoon. Prior to the surveys, we examined the size and shape of patches at water depths ranging between 50 and 80 cm in an area of approximately 40 000 m² during low spring tides at the end of July 2000. Two or more seagrass patches were often connected to each other. We defined an isolated patch as a patch that was >50 cm away from the nearest patch, because no Hokkai shrimp *Pandalus latirostris* were found even in the range of corridors between patches in our preliminary observation during daytime (see ‘Results’). We measured the long and short diameters of each patch, and tagged an identification number to each one. The shapes of the larger patches tended to be more complex. To avoid arbitrary definitions of the shape and size of patches, 4 investigators discussed the shapes of the patches, chose those that were round or elliptic, and measured the long and short diameters. This definition allowed us to assume that smaller patches had larger perimeter-to-area ratios (Connolly & Hindell 2006). Fig. 2 shows the size frequency distribution of 72 patches that were selected for the present study.

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Surveys in natural seagrass patches

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To investigate animal community structures in patches of a wide range of sizes, from the 72 tagged patches we selected 40 whose area ranged from 6.48 to 822.09 m². We used a cage (length × width × height: 80 × 80 × 80 cm) whose 4 vertical sides were covered with a net (mesh: 1 × 2 mm) to collect animals during low spring tides at the end of July 2000 (water temperature, T_w , approximately 23°C). Although the volume of water inside the cage varied slightly among patches because of differences in water depth, in this study we used 0.512 m³ as a unit for our calculation of animal abundance by assuming that water depth was 80 cm. Two

136 investigators slowly approached a seagrass patch to minimize disturbance in the patch and
137 randomly placed a cage inside it. One cage was used in each of the 18 patches whose area was
138 smaller than 5.51 m², and 2 cages were simultaneously placed in the 22 patches whose area was
139 larger than 6.48 m² (one at the edge and the other in the center), to estimate the abundance of
140 animals in each patch. Since no shrimps dashed out from any of the patches to a bare space
141 when we placed the cages, we assumed artefacts of cage sampling would be minimal. One
142 investigator held the cage in place at each sampling point, while the other used a
143 semicircle-shaped dip net (diameter: 30 cm; mesh: 1 mm) to scoop up animals from inside the
144 cage until no animals were caught 3 times in a row. All collected animals were immediately
145 fixed in bottles with buffered seawater formalin (10%) in the field. Since cage sampling made
146 it difficult to quantify gastropods on seagrass leaves, we covered above-ground seagrass near
147 the sampling point with a net (length × width × height: 25 × 25 × 80 cm; mesh: 1 mm), closed
148 the net opening, and cut it at the base. We brought the samples to a laboratory at the Abashiri
149 Fisheries Science Center (AFSC) on the shore of the lagoon, identified the species, and then
150 counted the individuals. To estimate the prey of Hokkai shrimp, we used data from analyses of
151 shrimp stomach contents by Mizushima (1981) and from our preliminary observations. In
152 addition, potential predators of the shrimp were estimated from analyses of the stomach
153 contents of fish collected at the study site (Chiba & Kawamura 2011). Water temperature and
154 salinity were also recorded at all sampling points with a portable electric conductivity meter
155 (CM-21P, TOA-DKK).

156 In early August 2000 (T_w approximately 23°C), we selected a large patch to estimate
157 the relationship between the abundance of Hokkai shrimp and their distance from the edge of
158 the patch. Although the long and short diameters were approximately 100 and 20 m,
159 respectively, the complex shape of the patch made it difficult to fit an elliptical shape inside for
160 measurement. Therefore, cage samplings were conducted along 6 straight lines that started
161 outside the patch and continued toward the center of the patch. On each line there were 4
162 sampling points spaced 3 m apart: the first was outside (−3 m), the second was at the edge (0 m),
163 the third was between the edge and the center (3 m), and the fourth was closest to the center (6
164 m). To minimize time lag between samplings at the points along each line, 2 cages were placed
165 simultaneously at 2 of the 4 sampling points on each line in the same manner used for the cage
166 samplings in the 40 patches described above. The pairs of sampling points were also irregularly
167 selected to avoid directional escapes of the shrimp from the cage.

168 We also examined whether the physical structure of seagrass changed with patch size
169 and/or distance from the edge of the patch. We cut the above-ground parts of the seagrass
170 within a 0.01 m² quadrat near each point where cage sampling was conducted, and at the
171 laboratory of the AFSC we counted the number of shoots, measured the length of all leaves,
172 and noted the wet weight of the leaves after removing the epiphytes.

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174 **Recruitment to artificial seagrass patches**

175 To clarify factors influencing the abundance of Hokkai shrimp, an experiment was
176 conducted using artificial seagrass units (ASUs). The ASUs were constructed with green
177 polypropylene tape (Rainbow-band®, Hoppou-Shouji) tied to 1 m² squares of black plastic mat
178 (Netron Sheet®, Mitsui Petrochemical Industrial Materials) with mesh size of 2 cm. One shoot
179 consisted of 4 blades, 55 cm in length and 7.5 mm in width. The number of blades and leaf
180 length were based on the mean values (4.1 blades shoot⁻¹ and 54.4 cm in length, respectively)
181 at our study site in summer, although leaf width was close to the maximum width (6.9 mm) to
182 ensure efficiency in manufacturing the ASUs. Since patch size and shoot density are
183 inseparable factors in natural seagrass beds (see 'Results'), we created 4 types of ASUs with a
184 different area (4 or 1 m²) and shoot density (1680 or 840 shoots m⁻²) for each ASU. These high
185 and low shoot densities were determined from the mean (1794 shoots m⁻²) and the lowest (850
186 shoots m⁻²) densities, respectively, in the natural seagrass patches.

187 The 4 ASUs (large/dense, large/sparse, small/dense, and small/sparse) were secured
188 with steel pegs in the bare sandy spaces between the natural seagrass patches. To confirm that
189 the black plastic mats (i.e. the material that was used for the base of the ASUs) did not affect
190 shrimp aggregation, mats of the large and small sizes but without leaves were also placed in
191 these spaces. At the experiment site, all structures (i.e. ASUs, black mats, and natural seagrass
192 patches) were spaced >3 m from each other. Two weeks later, cage sampling was conducted
193 using the same method as employed at the natural seagrass patches, i.e. 2 cages simultaneously
194 placed at the center and edge of the large patches; 1 cage in each of the small patches. This
195 experiment was repeated 4 times, twice at the end of July (T_w approximately 19°C) and again
196 in the middle of September 2001 (T_w approximately 18°C), since cage sampling at the natural
197 patches was also conducted in summer.

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Habitat utilization behavior

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200 To examine daytime and nighttime changes in habitat utilization by Hokkai shrimp, at
201 end of August 2002 (T_w approximately 18°C) we observed shrimp behavior at the sandy bare
202 corridors (>5 m width) between seagrass patches at the study site. An observer swam slowly at
203 the water surface for 30 min and counted the number of individual Hokkai shrimp estimated to
204 be 0 yr olds (carapace length [CL]: 7 to 10 mm; body length [BL]: 25 to 35 mm) and ≥ 1 yr olds
205 (CL: 15 to 36 mm; BL: 50 to 120 mm). The 0 yr old individuals that hatched in spring of that
206 year could be easily distinguished with the naked eye, because the range of their body size was
207 clearly different from that of the other age groups (and would be until September of that year;
208 Chiba & Goshima 2003). This observation was repeated twice; once during daytime and again
209 during nighttime. Although we illuminated the sea bottom with a vertically held flashlight in
210 our search during the nighttime observations, the shrimps did not show any significant
211 response to the light, such as phototactic behavior. All shrimps that were found in the corridors
212 stayed or walked, and did not aggregate to the light — possibly because we swam slowly, or
213 because they do not have a phototactic habit. It was possible to identify the shrimps at night,
214 because the water depth was shallow (approximately 1.0 m) and the body color of the shrimps
215 (dark green) made them easily visible against the color of the sandy corridor (white). In this
216 study, 0 yr old individuals are termed juveniles and those of other age groups are termed adults,
217 since Hokkai shrimp generally mature at age 1 (Chiba & Goshima 2003).

218 At the beginning of October 2002, an experiment using the ASUs was also conducted
219 to examine habitat preference of Hokkai shrimp during nighttime (T_w approximately 16°C),
220 because this was when they came out from the seagrass patches (see ‘Results’). Two sets of
221 large and small patches were placed to form a circle (radius: 9 m) on a sandy bare space
222 between natural seagrass patches (Fig. 3). These ASUs were >10 m away from the natural
223 patches. A total of 4 juvenile or 4 adult shrimps were placed in a cage (80 × 80 × 80 cm, mesh:
224 1 × 2 mm) at the center of the circle; the cage was removed 2 min later to allow the individuals
225 to move freely. This sequence was repeated 6 times each for juveniles and adults. The behavior
226 of the individuals at the center of the circle was recorded by 2 observers, and the standing
227 position of the observers relative to the cage was randomly changed with each repetition of the
228 sequence to minimize the effect of the observers. The direction in which the shrimp moved and
229 their position were recorded until they stayed at the interior or edge of the patch or went outside
230 the circle for 30 min. According to our observations, individuals that entered the patches or
231 stayed at the patch edges did not leave the patch for 30 min, while those individuals that did not

232 stop at a patch patrolled between patches and then moved away from the circle (see ‘Results’).
233 As a conclusion of this experiment, the direction in which the individuals moved clearly
234 reflected their habitat preference (Fig. 3).

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Predation risk

237 At the beginning of September 2005, a tethering experiment was conducted to
238 estimate changes in predation pressure on Hokkai shrimp with habitat type (seagrass or bare
239 sand) during daytime and nighttime (T_w approximately 19°C). Adults (CL: 18 to 24 mm; BL:
240 60 to 80 mm) were used in this experiment. In the AFSC laboratory, we attached a black
241 spangle tied with a line (60 cm length, 0.3 mm diameter) to the carapace of a shrimp with
242 cyanoacrylate glue (Konishi). Several hours later, the other end of the line was tied to a steel
243 peg. We placed 25 of these tethered shrimps in each habitat type (seagrass patch or bare sandy
244 space) during daytime and nighttime, and checked their survival 8 h later. This trial was
245 repeated 5 times. When only a broken carapace remained at the end of the line, individuals
246 were determined to have been consumed by predators, given that shrimp never mechanically
247 break their own carapace.

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Statistical analyses

250 We used simple regression analyses to examine relationships between the area of
251 patches and the abundances of each dominant animal species at the study site after performing
252 log transformation for both variables. In these analyses, mean abundance was used for the 22
253 large patches where cage sampling was conducted at both the edge and the center of each
254 patch; this was done to analyze those data together with data collected at the 18 small patches
255 where the edge and center were not distinguished because of the patch’s small size. The shrimp
256 were classified as juvenile or adult on the basis of their body size which would be the main
257 factor affecting their mobile ability. Multiple regression was used to explore factors relating to
258 the abundance of Hokkai shrimp in 40 patches that were round in shape. The response variable
259 in this analysis was the number of juveniles or adults per cage in each patch. As explanatory
260 factors in this analysis, we chose the number of prey (snails, *Lacuna decorata* and *Alvania*
261 *concinna*, and a mysid, *Neomysis mirabilis*) and the area of the seagrass patch. Although water
262 temperature and salinity were measured at each seagrass patch as potential factors affecting the

263 number of shrimp, these factors were not included in the analyses because the small variations
264 in temperature ($22.9 \pm 2.0^{\circ}\text{C}$) and salinity (33.3 ± 1.3) among patches would have had no effect
265 on physiology of Hokkai shrimp (Chiba et al. 2004). In addition, the effects of the predators
266 could not be evaluated here because our sampling methods did not collect a sufficient number
267 (see 'Results').

268 To examine edge effects on Hokkai shrimp in natural seagrass, we compared data
269 between the edge and the center of the 22 patches using a paired *t*-test for the juveniles and a
270 paired Wilcoxon test for the adults. Edge effects were also estimated from data collected at a
271 patch where the 3 cages were placed at the edge (0 m), between the edge and the center (3 m),
272 and closest to the center (6 m) of the patch. Data collected at the point outside the patch (-3 m)
273 were not included because no shrimps were collected there. These data were then tested using
274 ANOVA for the juveniles and a Kruskal-Wallis test for the adults.

275 We examined how the structure (number of shoots, leaf length, and wet weight of
276 leaves) of the seagrass samples that were collected from the 40 patches changed with the area
277 (size) of the patches. Simple regression analyses were used for these analyses after the same
278 data treatment that was used in the analyses of the relationship between area and shrimp
279 abundance was performed. ANOVA was used to compare each seagrass structure among the
280 sampling points in the patch where the effect of distance from the edge of the patch was
281 examined.

282 A *t*-test was used to compare the number of juvenile and adult Hokkai shrimp that
283 recruited to the ASUs during the 2 wk period. We also used 2-way ANOVA to examine the
284 effects of area and shoot density of each patch and their interactions on the number of juveniles
285 or adults in each ASU patch. A Tukey-Kramer test was performed if the results were
286 significant.

287 To examine habitat preference by juveniles and adults, we compared the number of
288 individuals that moved in each direction, i.e. to a small patch, a large patch, or bare sand. We
289 divided the number of individuals in the bare sand by 2 because the area of the bare sand was
290 twice that of other habitats. Kruskal-Wallis test was used for this comparison, and the
291 Steel-Dwass methods were used as a multiple comparison. Fisher's exact test was used to
292 compare the frequencies of predation among the 4 treatments (sand/day, seagrass/day,
293 sand/night, and seagrass/night), and multiple comparisons were then conducted using Tukey's
294 wholly significant difference (WSD) test, because frequency data where $n < 5$ were included in

295 the comparison (Ryan 1960). The normality of each data set that was treated as a response
296 variable was tested using a Korgomorov-Smirnov test to choose a suitable method for
297 comparison. All statistical analyses were conducted using R v.3.2.3 (R Development Core
298 Team 2015).

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RESULTS

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Community structure in seagrass beds of Lake Notoro

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We collected 22 species of animals in seagrass beds at the study site of Lake Notoro (Table 1). Collected from all patches at the study site were *Lacuna decorata* (a gastropod), *Neomysis mirabilis* (a mysid), *Eualus leptognathus* (a decapod), *Heptacarpus grebnitzkii* (a decapod), and *Pandalus latirostris* (Hokkai shrimp, a decapod). *Alvania concinna* (a gastropod) and *Gymnogobius breunigii* (a fish) were found in most of the patches. Hokkai shrimp was the fifth most dominant species in the community, and their body size was the largest with the exception of fishes (Table 1).

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Factors relating to the abundance of Hokkai shrimp

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Prey animals of Hokkai shrimp at this site were the gastropods *L. decorata* and *A. concinna* and the mysid *N. mirabilis*. Two gastropod species, *Littorina squalida* and *Homalopoma sangarense*, were also prey of Hokkai shrimp, but their abundances were low. A rockfish, *Sebastes schlegeli*, and a sculpin, *Myoxocephalus brandti*, were predators of the Hokkai shrimp, but their abundances were also low. We were not able to obtain any information regarding biological interactions between Hokkai shrimp and other animals found at the site.

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Fig. 4 shows the relationships between the area of the seagrass patches and the abundance of each dominant species. A positive relationship was found only for the gastropod *L. decorata*. Negative relationships were found for adult Hokkai shrimp, *N. mirabilis*, and *E. leptognathus*.

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Multiple regression analysis showed that the number of juvenile Hokkai shrimp did not relate to any factor considered in the analysis, whereas the abundance of adults significantly decreased with the area of the seagrass patch (Table 2, Fig. 4).

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Edge effects on Hokkai shrimp

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Neither the abundance of juveniles nor that of adults statistically varied between the edge and the center of seagrass patches (juveniles: paired t -test, $t_{21} = 1.59$, $p = 0.129$; adult: paired Wilcoxon test, $V = 150.5$, $p = 0.088$; Fig. 5). However, the number of adults at the edge deviated from a normal distribution (Fig. 5), indicating that adults aggregated in high abundance at the edge in some patches.

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We also examined the relationship between the abundance of Hokkai shrimp and the distance from the edge of each patch. No individuals were collected outside any of the patches. Data normality for the number of juveniles was detected at sampling points regardless of the distance (Fig. 6), and the distance did not relate to the number of juveniles (ANOVA, $F_{2,15} = 0.32$, $p = 0.731$). The number of adults, however, varied widely among the distances. For example, in one patch the maximum abundance of adults (56 ind. 0.512 m^{-3} ; Fig. 6) was observed at the edge (0 m), while no individuals were collected at the innermost area of this particular patch (6 m). There was a marginally significant difference among the distances for adult abundance (Kruskal-Wallis test, $\chi^2 = 6.13$, $df = 2$, $p = 0.047$; Fig. 6), although multiple comparison with the Steel-Dwass test did not detect any statistical difference between pairs of distances (0 to 3 m: $\chi^2 = 2.95$, $p = 0.229$; 0 to 6 m: $\chi^2 = 5.78$, $p = 0.056$; 3 to 6 m: $\chi^2 = 0.47$, $p = 0.790$).

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Structure of the seagrass patch

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Relationships between patch area and seagrass structure are shown in Fig. 7. Although shoot density decreased significantly with the area of patch (df adjusted $r^2 = 0.15$, $p = 0.008$), neither the length of leaves nor the wet weight of leaves were related to the area of the patch.

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Relationships between the distance and the structure of seagrass are shown in Fig. 8. Shoot density and the wet weight of leaves at the edge (0 m) were higher than at the innermost area of the patch (ANOVA, number of shoots: $F_{2,15} = 4.95$, $p = 0.028$; weight of leaves: $F_{2,15} = 7.11$, $p = 0.007$; Fig. 8). There were no significant differences in leaf length among the distances ($F_{2,15} = 1.07$, $p = 0.371$).

Recruitment of Hokkai shrimp to artificial patches

During the 2 wk of the test, more adults (mean \pm SD: 20.78 ± 9.87) than juveniles (3.28 ± 2.06) recruited to the ASUs (*t*-test; $t_{30} = 6.94$, $p < 0.001$). No relationship was observed between the abundance of juveniles and patch size or shoot density (Table 3, Fig. 9). There was a significant difference in the abundance of adults among patch sizes (Table 3), with adults more abundant in small than large patches (Fig. 9). No individuals recruited to any of the mats that contained no artificial leaves.

Habitat utilization behavior

While only 1 individual Hokkai shrimp (an adult) was found in a bare sand space between natural seagrass patches during daytime, 43 individuals (5 juveniles, 38 adults) were found there during nighttime. Some of the adults showed typical foraging behavior, moving maxillipeds and chelipeds on the surface of the sand during nighttime.

Fig. 10 shows the habitat preference of juveniles and adults released at the center of the circle during nighttime. All individuals that entered patches or stayed at patch edges did not leave the patch within 30 min. Among individuals that did not enter a patch, juveniles moved away from the circle within 30 min, and adults moved away within several minutes. While juveniles randomly selected all types of habitat (Kruskal-Wallis test; $\chi^2 = 3.82$, $df = 2$, $p = 0.148$), adults tended to patrol the bare sand ($\chi^2 = 11.61$, $df = 2$, $p = 0.003$; Fig. 10).

Predation risk on Hokkai shrimp

Broken carapaces remained on all lines where shrimps were absent in the tethering experiment, indicating that those individuals had been preyed upon. There was a significant difference among combinations of period and habitat (Fisher's exact test, $p = 0.002$), with adult shrimps being depredated more often in the bare sand spaces during daytime compared to the 3 other scenarios (bare sand spaces during nighttime, and seagrasses during both daytime and nighttime; Fig. 11).

DISCUSSION

384 This study demonstrated that the utilization of seagrass patches by *Pandalus*
385 *latirostris* (Hokkai shrimp) changed with their body size. There was no relationship between
386 the abundance of juveniles and the area of the seagrass patch or the distance from the edge of
387 each patch, suggesting that the juveniles were uniformly distributed within the seagrass patches.
388 The abundances of adults, however, decreased with patch area with no relation to biological
389 factors, and the abundances of mysids (their main prey) also decreased with patch area. This
390 result indicates that Hokkai shrimp adults and mysids were both more abundant in smaller
391 patches, although multiple regression analyses suggested no predator–prey interaction between
392 them because the abundance of the shrimp was not related to the abundance of mysids.
393 Although the relationship between the abundance of adults and their distance from the patch
394 edge was statistically marginal, extremely high abundances of adults were found at the edge.
395 This result suggests that conspecific adults of similar body size tend to congregate in the same
396 place. Grouping behavior such as shoaling in fish and size segregation is probably not
397 uncommon in mobile marine invertebrates including decapods; however, details of their
398 aggregation behaviors have not been well studied compared to fishes (Evans et al. 2007).
399 Connolly & Hindell (2006) pointed out that edge effects in species that form a group such as a
400 shoal were often masked by their variable abundances among samples because of problems
401 with the power of statistical tests, even though these effects did indeed exist. Our data was a
402 case where edge effects would have become clear if the number of sampling replications was
403 increased, because the abundances of shrimp varied widely among seagrass patches.

404 The size of the patches and the distance from the patch edge included some
405 inseparable structural attributes of natural seagrass. An increase in shoot density with a
406 decrease in patch size can be explained by the increase in shoot density at the patch edge,
407 because smaller patches had larger perimeter-to-area ratios in our study area. Although the
408 length of leaves is an important component of seagrass habitats (e.g. Bell & Westoby 1986,
409 Hori et al. 2009, Goshima & Peterson 2012, Gartner et al. 2013), it would not affect the
410 distribution of Hokkai shrimp because it did not change with patch size or distance from the
411 patch edge at our study site. The relationship between patch size and the weight of leaves was
412 unclear. While the increase in weight at the patch edge can be explained by the increase in
413 shoot density, as observed in the survey of the effect of the distance from patch edges, there
414 seemed to be an interaction between patch size and some other structures of the seagrass, such
415 as the number of leaves per shoot. These results suggest that shoot density is the most

416 important seagrass structure corresponding to patch size, and that some other structures also
417 co-vary with patch size in natural seagrass beds.

418 Our experiment using ASUs clarified the effects of seagrass structure on the patterns
419 of habitat utilization observed in the natural seagrass beds. Juveniles recruited to both small
420 and large artificial patches, while adults were more abundant in the small patches. Moreover,
421 there were no effects of shoot density and no interaction between patch size and shoot density
422 on the recruitment of both juveniles and adults. This experiment supported the uniform
423 distribution of juveniles among natural patches, and demonstrated that Hokkai shrimp adults
424 respond not to shoot density, but rather patch size.

425 Body size difference would be a fundamental factor causing behavioral differences
426 between juveniles and adults, although other factors such as physiological changes with age or
427 life stage may also have contributed to the result. Our observation of the habitat utilization
428 behavior of shrimps between natural patches suggests that juveniles strongly depend on
429 seagrass during both nighttime and daytime. When juveniles were released among the ASUs
430 during nighttime, they could not select a habitat type while they continued to depend on natural
431 seagrass patches. This result indicates that juveniles do not actively change seagrass patches by
432 crossing a corridor between patches. We therefore conclude that the low frequency in the
433 migration of juveniles between patches is related to their uniform distribution within each
434 patch. Adults, however, were collected at the ASUs in much greater numbers than juveniles in
435 the recruit experiment, suggesting that adults frequently migrated between patches. In fact,
436 adults often emerged from natural seagrass patches at night, and they tended to patrol the bare
437 sand spaces when they were released among the ASUs during nighttime. These results showed
438 that adults did not statically inhabit the interior of seagrass patches. Although it is true that the
439 distribution of Hokkai shrimp is limited to only seagrass beds (Komai 1999, Bergström 2000),
440 our fine-scale study demonstrated that while adults mainly used seagrass patches, they also
441 used bare sand spaces at night. The high abundance of adults in the small patches can therefore
442 be explained by the rate at which they encounter seagrass (Eggleston et al. 1998, 1999,
443 Arponen & Boström 2012). Body size generally affects the mobility of animals, and it may also
444 cause behavioral shifts in the selection of refuge habitats of prey species such as grass shrimps,
445 to defend themselves against predators (Davis et al. 2003). It is thus worthwhile to confirm the
446 generality of the effects of body size on changes in habitat utilization in other
447 seagrass-dwelling species.

448 Why do adults leave seagrass patches at night? This behavior may be related to both
449 diurnal changes in predation pressure and food availability. Vegetated areas are better than
450 unvegetated areas as a refuge for adults during daytime, as the tethering experiment in the
451 present study showed that predation risk in bare sand areas was higher than in the seagrass.
452 During nighttime, however, the predation rate in the bare sand areas was as low as it was in the
453 seagrass, indicating that there was no difference in predation risk between those habitats at
454 night. Seagrass would not always be a safe habitat for the shrimp, because predators employing
455 ambush tactics, such as the sculpin *Myoxocephalus brandti* at our study site (Table 1), often
456 coexist with their prey, including Hokkai shrimp inside a seagrass patch (Horinouchi et al.
457 2009). That there is no difference in predation risk between habitats at night would therefore
458 reduce the motivation of Hokkai shrimp to stay inside a patch. Moreover, food availability
459 inside patches would motivate shrimps to move to another patch. Although Hokkai shrimp
460 adults tended to use relatively smaller patches at our study site, it would be better for them to
461 change patches if they are in small patches, because their high nutritional requirement would
462 likely deplete the food resources there. We also observed that adults consumed substances such
463 as detritus on the surface of sand at night, implying that they can **obtain** different types of
464 nutrients outside the seagrass patches (Ochwada et al. 2009, Tait & Hovel 2012), although the
465 details are still unknown. The stomach contents of Hokkai shrimp reported by Mizushima
466 (1981) were generally consistent with our preliminary observations, though other methods
467 such as stable isotope analyses may clarify more details concerning their food habits. As a
468 preliminary conclusion, the decrease in predation pressure in the bare areas during nighttime
469 and their requirement for food would be plausible reasons for adults leaving seagrass patches at
470 night.

471

472

CONCLUSIONS

473 The present study showed that the habitat utilization patterns of Hokkai shrimp
474 changed with their life stage. The uniform distribution of juveniles between and within patches
475 indicates that a large, continuous patch would be effective for the conservation of juveniles
476 given that their abundance increases with the total area of seagrass patches. Although we did
477 not examine the details of the process that determined their uniform distribution, their small
478 body size would fundamentally restrict their movement between patches. In particular, small
479 grass shrimp such as Hokkai shrimp juveniles would likely not leave a seagrass patch because

480 of their low ability to escape and high risk of predation outside the patch (Bell et al. 2001).
481 Many small patches would be important for adults, however, because adults enter these patches
482 after patrolling bare spaces at night. This process is well explained by the rate at which they
483 encountered seagrass during the night due to positive edge effects. The importance of patch
484 size thus varies with their life stage, and patches of various sizes are required for their
485 population to persist. The habitat utilization pattern observed in summer may change
486 seasonally because of seasonal changes in seagrass structure and animal assemblages (e.g.
487 Eggleston et al. 1998, Hovel & Lipcius 2002, Kanamori et al. 2004, Hasegawa et al. 2008,
488 Goshima & Peterson 2012, Herrera et al. 2014). Our conclusion will not change, however, as
489 long as both large and small sizes of patches are needed in one of the seasons when the shrimp
490 are actively moving among patches. Since the pattern that we observed was an ontogenic shift,
491 our results point not to a site-specific response but an adaptive habit of the shrimp. The spatial
492 management of seagrass patches of varying size is thus of utmost importance from the
493 perspective of the persistence of this animal population.

494

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LITERATURE CITED

- 504
- 505 Abashiri City Government (2016) Annual report of fishery production in Abashiri.
506 www.city.abashiri.hokkaido.jp/030shisei/020toukei/080suisanntoukei/ (accessed 5
507 Oct 2016)
- 508 Allendorf FW, England PR, Luikart G, Ritchie PA, Ryman N (2008) Genetic effects of harvest
509 on wild animal populations. *Trends Ecol Evol* 23:327–337
- 510 Almeida MJ, Flores AAV, Queiroga H (2008) Effect of crab size and habitat type on the
511 locomotory activity of juvenile shore crabs, *Carcinus maenas*. *Estuar Coast Shelf Sci*
512 80:509–516
- 513 Arponen H, Boström C (2012) Responses of mobile epifauna to small-scale seagrass
514 patchiness: Is fragmentation important? *Hydrobiologia* 680:1–10
- 515 Beck MW, Heck KL, Able KW, Childers DL and others (2001) The identification,
516 conservation, and management of estuarine and marine nurseries for fish and
517 invertebrates. *Bioscience* 51:633–641
- 518 Bell JD, Westoby M (1986) Abundance of macrofauna in dense seagrass is due to habitat
519 preference, not predation. *Oecologia* 68:205–209
- 520 Bell SS, Hall MO, Robbins BD (1995) Toward a landscape approach in seagrass beds: using
521 macroalgal accumulation to address questions of scale. *Oecologia* 104:163–168
- 522 Bell SS, Brooks RA, Robbins BD, Fonseca MS, Hall MO (2001) Faunal response to
523 fragmentation in seagrass habitats: implications for seagrass conservation. *Biol*
524 *Conserv* 100:115–123
- 525 Bergström BI (2000) The biology of *Pandalus*. *Adv Mar Biol* 38:55–245
- 526 Boström C, Jackson EL, Simenstad CA (2006) Seagrass landscapes and their effects on
527 associated fauna: a review. *Estuar Coast Shelf Sci* 68:383–403
- 528 Boström C, Pittman SJ, Simenstad C, Kneib RT (2011) Seascape ecology of coastal biogenic
529 habitats: advances, gaps, and challenges. *Mar Ecol Prog Ser* 427:191–217
- 530 Chiba S, Goshima S (2003) Population structure and seasonal growth of the protandrous
531 pandalid shrimp *Pandalus latirostris* in Notoro Lagoon, Hokkaido. *Aquacult Sci*
532 51:375–383

- 533 Chiba S, Kawamura T (2011) Ecosystem services provided by marine invertebrates. In: Shoji J,
534 Hori M, Yamashita Y (eds) Ecosystem services of coastal waters – benefits of the sea
535 and its sustainable use. Kouseisha-Kouseikaku, Tokyo (in Japanese)
- 536 Chiba S, Goshima S, Mizushima T (2000) Factors affecting the occurrence of early maturing
537 males in the protandrous pandalid shrimp *Pandalus latirostris*. Mar Ecol Prog Ser
538 203:215–224
- 539 Chiba S, Aoki L, Ogata T (2004) Response of the pandalid shrimp *Pandalus latirostris* to
540 dissolved oxygen, salinity and turbidity. Fish Sci 70:1174–1176
- 541 Chiba S, Yoshino K, Kanaiwa M, Kawajiri T, Goshima S (2013) Maladaptive sex ratio
542 adjustment by a sex-changing shrimp in selective-fishing environments. J Anim Ecol
543 82:632–641
- 544 Connolly RM, Hindell JS (2006) Review of nekton patterns and ecological processes in
545 seagrass landscapes. Estuar Coast Shelf Sci 68:433–444
- 546 Davis JLD, Metcalfe WJ, Hines AH (2003) Implications of a fluctuating fish predator guild on
547 behavior, distribution, and abundance of a shared prey species: the grass shrimp
548 *Palaemonetes pugio*. J Exp Mar Biol Ecol 293:23–40
- 549 Duarte CM (2002) The future of seagrass meadows. Environ Conserv 29:192–206
- 550 Duffy JE (2006) Biodiversity and the functioning of seagrass ecosystems. Mar Ecol Prog Ser
551 311:233–250
- 552 Eggleston DB, Etherington LL, Elis WE (1998) Organism response to habitat patchiness:
553 species and habitat-dependent recruitment of decapod crustaceans. J Exp Mar Biol
554 Ecol 223:111–132
- 555 Eggleston DB, Elis WE, Etherington LL, Dahlgren CP, Posey MH (1999) Organism responses
556 to habitat fragmentation and diversity: habitat colonization by estuarine macrofauna. J
557 Exp Mar Biol Ecol 236:107–132
- 558 Espino F, González JA, Haroun R, Tuya F (2015a) Abundance and biomass of the parrotfish
559 *Sparisoma cretense* in seagrass meadows: temporal and spatial differences between
560 seagrass interiors and seagrass adjacent to reefs. Environ Biol Fishes 98:121–133
- 561 Espino F, Triay-Portella R, González JA, Haroun R, Tuya F (2015b) Population structure of
562 the pearly razorfish, *Xyrichtys novacula* (Actinopterygii: Labridae), in sand-seagrass

- 563 mosaics: spatial variation according to habitat features and sampling techniques. *Sci*
564 *Mar* 79:179–188
- 565 Evans SR, Finnie M, Manica A (2007) Shoaling preferences in decapod crustacea. *Anim*
566 *Behav* 74:1691–1696
- 567 Fletcher RJ Jr, Ries L, Battin J, Chalfoun AD (2007) The role of habitat area and edge in
568 fragmented landscapes: Definitely distinct or inevitably intertwined? *Can J Zool*
569 85:1017–1030
- 570 García-Sanz S, Navarro PG, Landeira JM, Tuya F (2014) Colonization patterns of decapods
571 into artificial collectors: seasonality between habitat patches. *J Crustac Biol* 34:431–
572 441
- 573 García-Sanz S, Navarro PG, Png-González L, Tuya F (2016) Contrasting patterns of amphipod
574 dispersion in a seagrass meadow between day and night: consistency through a lunar
575 cycle. *Mar Biol Res* 12:56–65
- 576 Gartner A, Tuya F, Lavery PS, McMahon K (2013) Habitat preferences of macroinvertebrate
577 fauna among seagrasses with varying structural forms. *J Exp Mar Biol Ecol* 439:143–
578 151
- 579 Goshima S, Peterson CH (2012) Both below- and aboveground shoalgrass structure influence
580 whelk predation on hard clams. *Mar Ecol Prog Ser* 451:75–92 >
- 581 Gotceitas V, Fraser S, Brown JA (1997) Use of eelgrass beds (*Zostera marina*) by juvenile
582 Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 54:1306–1319
- 583 Hasegawa N, Hori M, Mukai H (2008) Seasonal changes in eelgrass functions: current velocity
584 reduction, prevention of sediment resuspension, and control of sediment-water
585 column nutrient flux in relation to eelgrass dynamics. *Hydrobiologia* 596:387–399
- 586 Heck KL Jr, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for
587 seagrass meadows. *Mar Ecol Prog Ser* 253:123–136
- 588 Hemminga MA, Duarte CM (2000) *Seagrass ecology*. Cambridge University Press,
589 Cambridge
- 590 Herrera A, Landeira JM, Tuya F, Packard T, Espino F, Gómez M (2014) Seasonal variability of
591 suprabenthic crustaceans associated with *Cymodocea nodosa* seagrass meadows off
592 Gran Canaria (eastern Atlantic). *Cont Shelf Res* 88:1–10

593 Hokkaido Research Organization (2016) Marinenet Hokkaido database.
594 www.fishexp.hro.or.jp/marinedb/internetdb/fishdb/fish_all.asp (accessed 5 Oct 2016)

595 Hori M, Suzuki T, Monthum Y, Srisombat T, Tanaka Y, Nakaoka M, Mukai H (2009) High
596 seagrass diversity and canopy-height increase associated fish diversity and abundance.
597 *Mar Biol* 156:1447–1458

598 Horinouchi M, Mizuno N, Jo Y, Fujita M, Sano M, Suzuki Y (2009) Seagrass habitat
599 complexity does not always decrease foraging efficiencies of piscivorous fishes. *Mar*
600 *Ecol Prog Ser* 377:43–49

601 Hovel KA, Lipcius RN (2002) Effects of seagrass habitat fragmentation on juvenile blue crab
602 survival and abundance. *J Exp Mar Biol Ecol* 271:75–98

603 Jackson EL, Rowden AA, Attrill MJ, Bossey SJ, Jones MB (2001) The importance of seagrass
604 beds as a habitat for fishery species. *Oceanogr Mar Biol Annu Rev* 39:269–303

605 Jiang X, Peng J, Zhang LA, Cui CJ and others (2013) Distinguishing morphologically similar
606 *Zostera* species (*Z. caespitosa* and *Z. marina*) using microsatellite DNA markers on
607 leaf fragments. *Aquat Bot* 107:59–62

608 Kanamori M, Goshima S, Mukai H (2004) Seasonal variation in host utilization of epiphytic
609 *Lacuna* species in mixed algal and surfgrass stands in Japan. *Mar Ecol* 25:51–69

610 Kawahara-Miki R, Wada K, Azuma N, Chiba S (2011) Expression profiling without genome
611 sequence information in a non-model species, pandalid shrimp (*Pandalus latirostris*),
612 by next-generation sequencing. *PLOS ONE* 6:e26043

613 Kikuchi T (1974) Japanese contributions on consumer ecology in seagrass (*Zostera marina* L.)
614 beds, with special reference to trophic relationships and resources in inshore fisheries.
615 *Aquaculture* 4:145–160

616 Komai T (1999) A revision of the genus *Pandalus* (Crustacea: Decapoda: Caridea: Pandalidae).
617 *J Nat Hist* 33:1265–1372

618 Kurata H (1955) The post-embryonic development of the prawn, *Pandalus kessleri*. *Bull*
619 *Hokkaido Reg Fish Res Lab* 12:1–15

620 Mateo I, Durbin E, Appeldoorn R, Adams A, Juanes F, Durant D (2011) Inferred growth of
621 juvenile French grunts, *Haemulon flavolineatum*, and schoolmaster, *Lutjanus apodus*,
622 in mangrove and seagrass habitats. *Bull Mar Sci* 87:339–350

623 Mizerek T, Regan HM, Hovel KA (2011) Seagrass habitat loss and fragmentation influence
624 management strategies for a blue crab *Callinectes sapidus* fishery. *Mar Ecol Prog Ser*
625 427:247–257

626 Mizushima T (1981) Ecology and catch of the prawn, *Pandalus kessleri* in *Zostera* beds in
627 Notsuke Bay, Hokkaido, Japan. In: Japan Soc Fish Sci (ed) *Seaweed beds*.
628 Kouseisha-Kouseikaku, Tokyo p57-74 (in Japanese)

629 Moore EC, Hovel KA (2010) Relative influence of habitat complexity and proximity to patch
630 edges on seagrass epifaunal communities. *Oikos* 119:1299–131

631 Nakaoka M (2005) Plant-animal interactions in seagrass beds: ongoing and future challenges
632 for understanding population and community dynamics. *Popul Ecol* 47:167–177

633 Ochwada F, Loneragan NR, Gray CA, Suthers IM, Taylor MD (2009) Complexity affects
634 habitat preference and predation mortality in postlarval *Penaeus plebejus*:
635 implications for stock enhancement. *Mar Ecol Prog Ser* 380:161–171

636 Orth RJ, Carruthers TJB, Dennison WC, Duarte CM and others (2006) A global crisis for
637 seagrass ecosystems. *Bioscience* 56:987–996

638 R Development Core Team (2015) R: a language and environment for statistical computing. R
639 Foundation for Statistical Computing, Vienna

640 Ray BR, Johnson MW, Cammarata K, Smee DL (2014) Changes in seagrass species
641 composition in northwestern Gulf of Mexico estuaries: effects on associated seagrass
642 fauna. *PLOS ONE* 9:e107751

643 Robbins BD, Bell SS (1994) Seagrass landscapes: a terrestrial approach to the marine subtidal
644 environment. *Trends Ecol Evol* 9:301–304

645 Ryan TA (1960) Significance tests for multiple comparison of proportions, variances, and
646 other statistics. *Psychol Bull* 57:318–328

647 Shin H, Choi HK (1998) Taxonomy and distribution of *Zostera* (Zosteraceae) in eastern Asia,
648 with special reference to Korea. *Aquat Bot* 60:49–66

649 Shoji J, Sakiyama K, Hori M, Yoshida G, Hamaguchi M (2007) Seagrass habitat reduces
650 vulnerability of red sea bream *Pagrus major* juveniles to piscivorous fish predator.
651 *Fish Sci* 73:1281–1285

- 652 Short FT, Polidoro B, Livingstone SR, Carpenter KE and others (2011) Extinction risk
653 assessment of the world's seagrass species. *Biol Conserv* 144:1961–1971
- 654 Sitonikov AV, Kartavtsev YF, Nikiforov SM (1997) Estimation of the effective size of a grass
655 shrimp (*Pandalus kessleri*) population by a temporal method and direct census of
656 breeders during breeding season. *Russ J Genet* 33:1158–1164
- 657 Tait KJ, Hovel KA (2012) Do predation risk and food availability modify prey and
658 mesopredator microhabitat selection in eelgrass (*Zostera marina*) habitat? *J Exp Mar*
659 *Biol Ecol* 426-427:60–67
- 660 Williams JA, Holt GJ, Robillard MMR, Holt SA, Hensgen G, Stunz GW (2016) Seagrass
661 fragmentation impacts recruitment dynamics of estuarine-dependent fish. *J Exp Mar*
662 *Biol Ecol* 479:97–105

663 Table 1. Animals collected in seagrass beds at the study site. Body size is represented by rough ranges of body length for the mysid and decapods,
 664 total length for the fishes, and shell length for the mollusks. Number of individuals represents the mean per 0.512 m³. Proportion represents the
 665 relative proportion of the numbers of each individual of each species among all collected individuals. Prey and predator refer to animals preyed on
 666 by *Pandalus latirostris* (Hokkai shrimp) and animals that prey upon Hokkai shrimp, respectively

Taxonomy	Family	Species	Body size (mm)	No. of individuals	Proportion (%)	Prey or Predator
Mollusk	Littorinidae	<i>Lacuna decorata</i>	5–10	3009.0	84.27	Prey
		<i>Littorina squalida</i>	5–15	6.1	0.17	
	Rissoiidae	<i>Alvania concinna</i>	<5	135.9	3.81	Prey
	Turbinidae	<i>Homalopoma amussitatum</i>	5–10	6.4	0.18	
Mysid	Mysidae	<i>Neomysis mirabilis</i>	5–10	202.1	5.66	Prey
Decapod	Hippolytidae	<i>Eualus leptognathus</i>	10–15	151.1	4.23	
		<i>Heptacarpus grebnitzkii</i>	15–20	9.5	0.27	
		<i>Heptacarpus longirostris</i>	15–20	0.6	0.02	
		<i>Spirontocaris ochotensis</i>	15–20	6.4	0.18	
	Pandalidae	<i>Pandalus latirostris</i>	25–120	18.9	0.53	
		<i>Pandalus prensor</i>	15–50	0.2	0.00	
		Palaemonidae	<i>Palaemon</i> spp. ^a	20–40	0.4	0.01
	Crangonidae	<i>Crangon</i> spp. ^b	15–50	6.1	0.17	
Fish	Gobiidae	<i>Gymnogobius breunigii</i>	25–50	15.6	0.44	
	Stichaeidae	<i>Opisthocentrus dybowskii</i>	10–250	1.0	0.03	
	Zoarcodae	<i>Neozoarces steindachneri</i>	50–100	0.2	0.00	
	Pholididae	<i>Pholis picta</i>	50–250	0.0	0.00	

Pleuronectidae	<i>Pleuronectes</i> spp. ^c	50–200	0.5	0.01	Predator
Scorpaenidae	<i>Sebastes schlegeli</i>	50–150	0.2	0.01	Predator
Cottidae	<i>Myoxocephalus brandti</i>	50–200	0.1	0.00	Predator
Hemitripterae	<i>Blepsias cirrhosus</i>	50–150	0.1	0.00	
Gasterosteidae	<i>Gasterosteus aculeatus aculeatus</i>	40–50	0.1	0.00	

667 ^a*P. macrodactylus* and *P. serrifer*

668 ^b*C. propinquus* and/or *C. hakodatei*

669 ^c*P. schrenki* and *P. obscurus*

670 Table 2. Results of multiple regression analysis on the density of Hokkai shrimp *Pandalus*
 671 *latirostris* in natural seagrass patches. *LD*: *Lacuna decorata*; *AC*: *Alvania concinna*; *NM*:
 672 *Neomysis mirabilis*

Body size	Factor	Estimate	SE	<i>t</i>	p
Juvenile	Intercept	2.86	0.96	2.96	0.006
	Gastropod (<i>LD</i>)	-0.13	0.17	-0.74	0.466
	Gastropod (<i>AC</i>)	-0.08	0.12	-0.66	0.513
	Mysid (<i>NM</i>)	0.02	0.09	0.22	0.829
	Area	0.02	0.10	0.25	0.803
Adult	Intercept	5.25	1.49	3.54	0.001
	Gastropod (<i>LD</i>)	-0.34	0.26	-1.31	0.200
	Gastropod (<i>AC</i>)	0.22	0.18	1.17	0.249
	Mysid (<i>NM</i>)	-0.12	0.14	-0.87	0.391
	Area	-0.40	0.15	-2.69	0.011

673

674

675 Table 3. Results of 2-way ANOVA on the abundance of Hokkai shrimp *Pandalus latirostris* in
 676 the artificial seagrass units (ASUs)

Body size	Factor	SS	df	<i>F</i>	<i>p</i>
Juvenile	Area (A)	0.29	1	1.42	0.256
	Shoot (S)	0.09	1	0.46	0.512
	A × S	0.09	1	0.42	0.528
	Residuals	2.47	12		
Adult	Area (A)	1.26	1	7.59	0.017
	Shoot (S)	0.01	1	0.05	0.830
	A × S	0.00	1	0.03	0.868
	Residuals	1.99	12		

677

678

679 FIGURE LEGENDS

680 Fig. 1. Study site at Lake Notoro in northeastern Japan

681

682 Fig. 2. Frequency of size of round- or oval-shaped patches at the study site.(a) and (b) show the
683 frequencies of all sizes of patches and those of small patches less than 50 m², respectively.

684 Curves represent the cumulative frequency of the number of patches

685

686 Fig. 3. Allocation of artificial patches for the Hokkai shrimp *Pandalus latirostris* habitat
687 preference experiment. Shaded squares: large or small artificial seagrass units (ASUs). Four
688 shrimps were released at the center of the circle in each experiment. Each area between the
689 dashed lines inside the circle was defined as a habitat type that the shrimps preferred (see
690 'Materials and methods')

691

692 Fig. 4. Relationships between the area of patches and the abundance of dominant species at the
693 study site. Areas (A) and number of individuals (N) are expressed in common logarithmic
694 values after adding 1 to each value for visualization of the relationships. Coefficient of
695 determination (r^2) adjusted for the df and p-value in each species are as follows: Hokkai shrimp
696 *Pandalus latirostris* (juvenile: $r^2 = -0.02$, $F = 0.2$, $p = 0.639$; adult: $r^2 = 0.30$, $F = 15.0$, $p <$
697 0.001 , $y = -0.44x + 1.44$); *Lacuna decorata* ($r^2 = 0.35$, $F = 13.7$, $p < 0.001$, $y = 0.31x + 1.95$);
698 *Alvania concinna* ($r^2 = -0.02$, $F = 0.21$, $p = 0.522$); *Neomysis mirabilis* ($r^2 = 0.15$, $F = 8.0$, $p =$
699 0.007 , $y = -0.38x + 2.60$); *Eualus leptognathus* ($r^2 = 0.11$, $F = 4.6$, $p = 0.024$, $y = -0.16x +$
700 2.24); *Heptacarpus grebnitzkii* ($r^2 = 0.00$, $F = 0.9$, $p = 0.363$); *Gymnogobius breunigii* ($r^2 = -$
701 0.03 , $F = 0.0$, $p = 0.985$). Linear regression lines were added in each figure where a significant
702 relationship was detected

703

704 Fig. 5. Abundance of Hokkai shrimp *Pandalus latirostris* at the edge and center of 22 patches.
705 Filled circles: means; open circles suspected outliers. Although data normality was observed in
706 juveniles at both the edge (Kolmogorov-Smirnov test, $D = 0.24$, $p = 0.149$) and the center ($D =$
707 0.19 , $p = 0.38$) and in adults at the center ($D = 0.23$, $p = 0.22$), it was not observed in adults at
708 the edge ($D = 0.34$, $p = 0.011$)

709

710 Fig. 6. Abundances of Hokkai shrimp *Pandalus latirostris* at 0, 3, and 6 m from the edge of the
711 seagrass patch. Filled circles: means; open circles: suspected outliers. The
712 Kolmogorov-Smirnov test showed data normality for juveniles at all points (0 m: $D = 0.29$, $p =$
713 0.69 ; 3 m: $D = 0.21$, $p = 0.95$; 6 m: $D = 0.19$, $p = 0.98$). Data normality for adults was not
714 performed because of the low number of samples

715

716 Fig. 7. Relationship between patch area and seagrass structure. Areas (A) are shown in
717 common logarithmic value after adding 1 to each value for visualization of the relationships.
718 Coefficient of determination (r^2) adjusted for the df and p-value in each species are as follows:
719 shoot density ($r^2 = 0.15$, $F = 7.8$, $p = 0.008$, $y = -0.10x + 1.30$); leaf length ($r^2 = 0.004$, $F = 1.7$,
720 $p = 0.287$); leaf wet weight ($r^2 = -0.12$, $F = 0.6$, $p = 0.463$). The line in the figure denotes the
721 regression line

722

723 Fig. 8. Seagrass structure at 0, 3, and 6 m from the edge of the patch. Filled circles: means; open
724 circles: suspected outliers. Different letters represent statistical differences in the
725 Tukey-Kramer method

726

727 Fig. 9. Abundances of Hokkai shrimp *Pandalus latirostris* at the 4 types of artificial patches in
728 the recruitment experiment. Horizontal axis denotes combinations of patch size and the shoot
729 density of the patch: SS: small/sparse; SD: small/dense; LS: large/sparse; LD: large/dense.
730 Filled circles: the mean of each value. Different letters denote statistical differences detected
731 by the Tukey-Kramer method

732

733 Fig. 10. Number of Hokkai shrimp *Pandalus latirostris* observed at 3 types of habitats in the
734 habitat preference experiment. Filled circles: means; open circles: suspected outliers. Different
735 letters denote statistical difference detected by the Steel-Dwass method

736

737 Fig. 11. Number of depredated Hokkai shrimp *Pandalus latirostris* in sand or seagrass habitats
738 during daytime and nighttime. Different letters denote statistical differences detected by
739 Tukey's wholly significant difference test

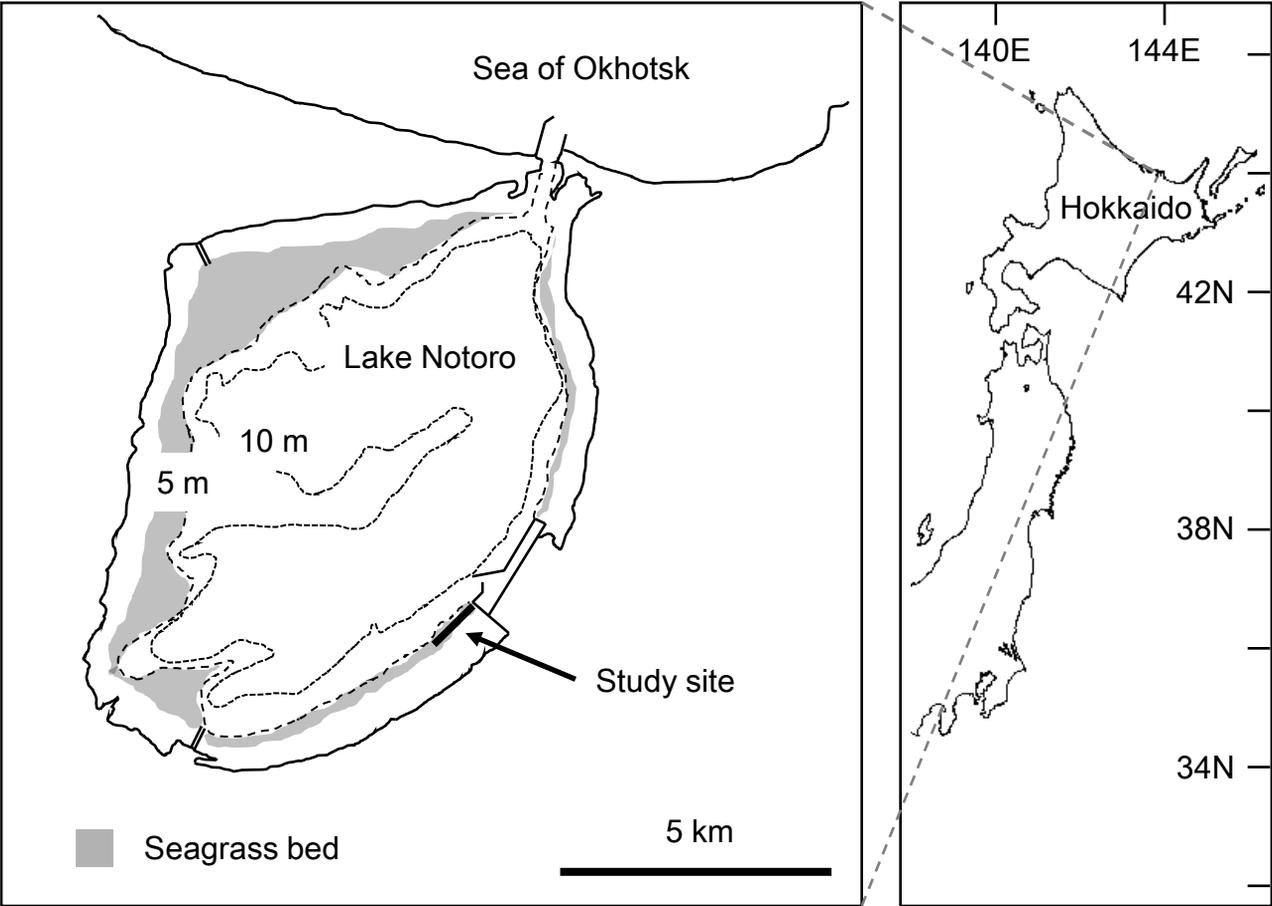


Figure 1

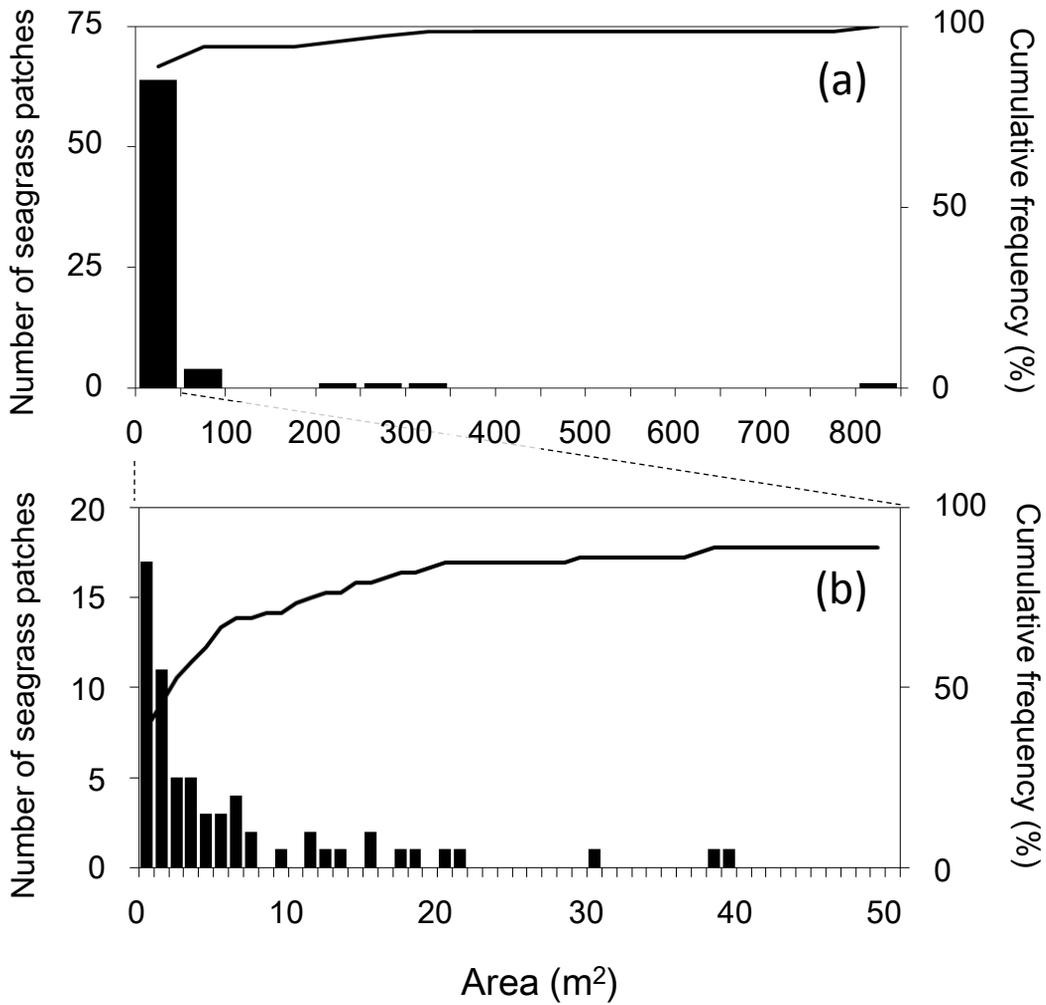


Figure 2

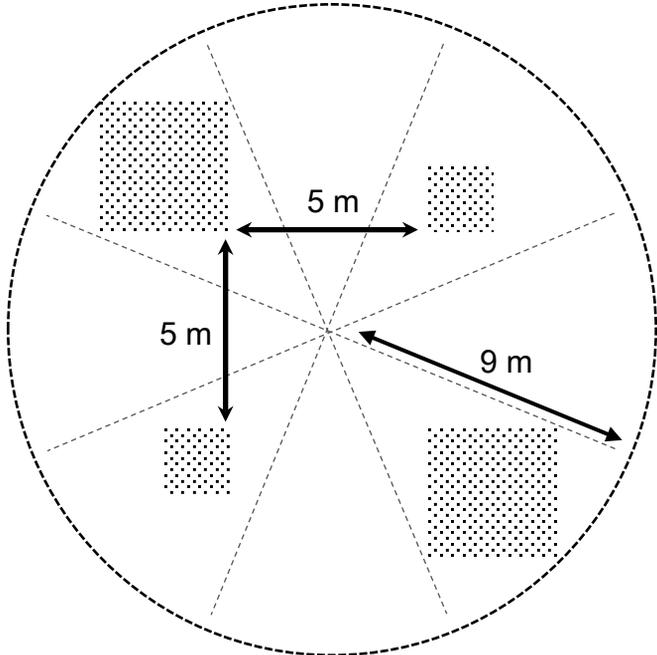


Figure 3

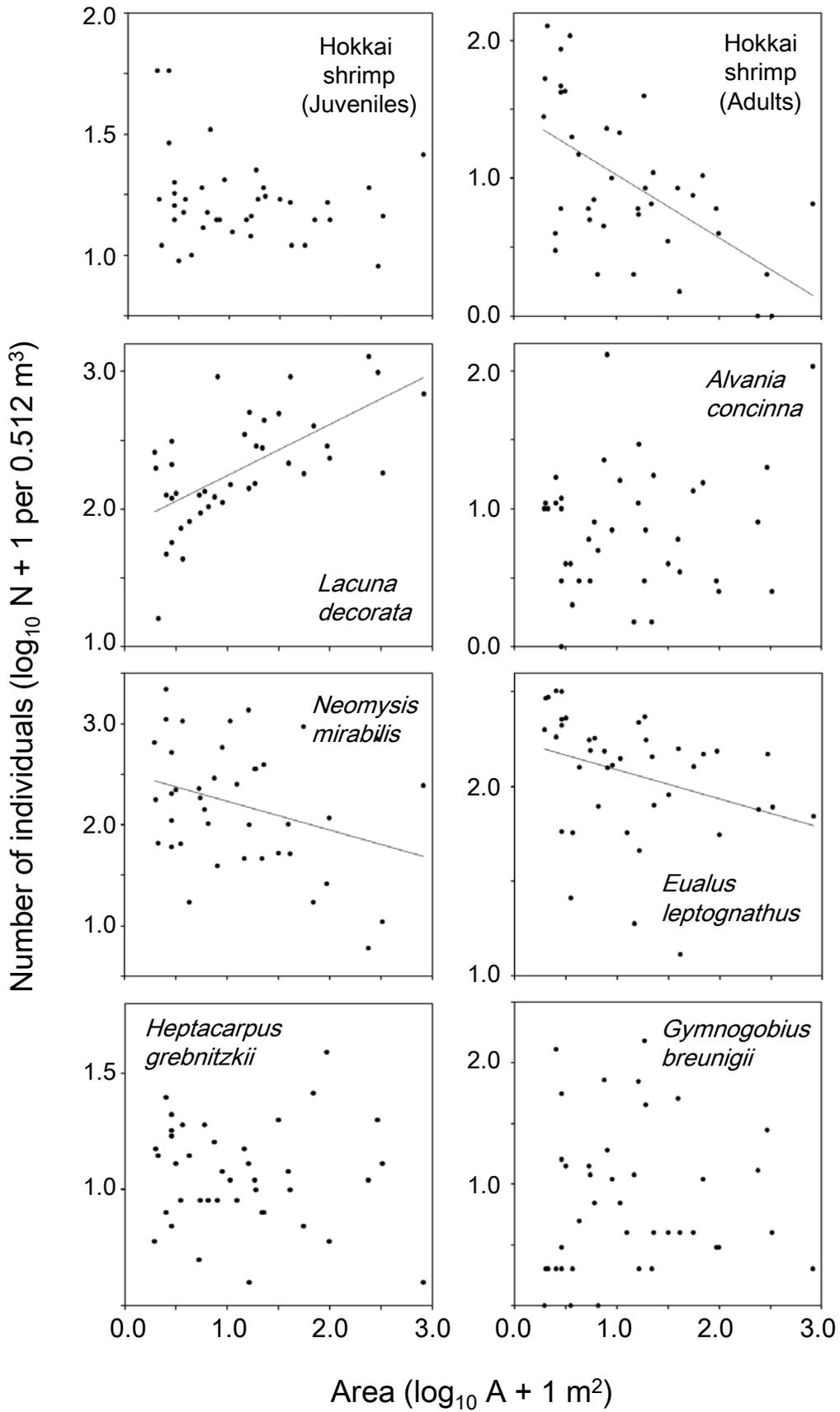


Figure 4

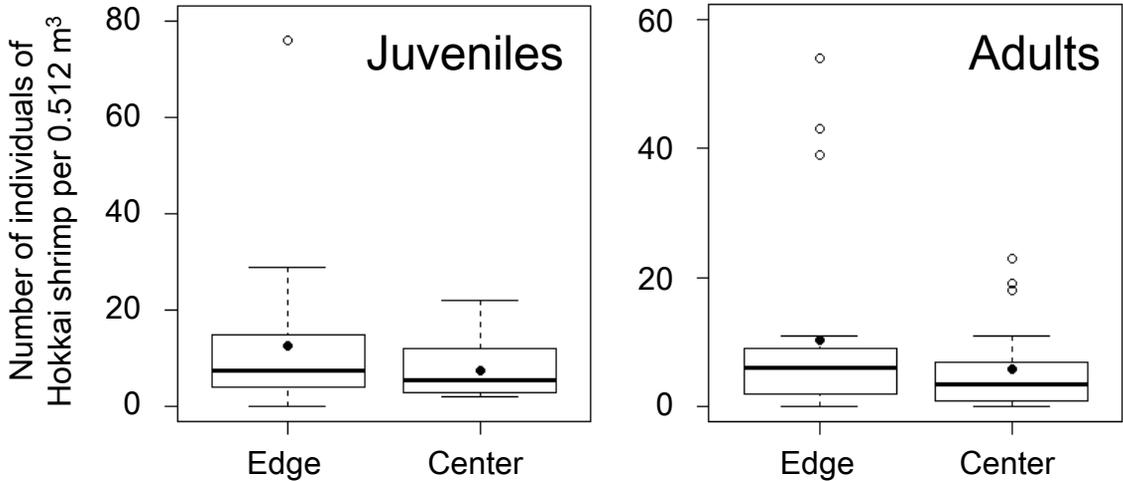


Figure 5

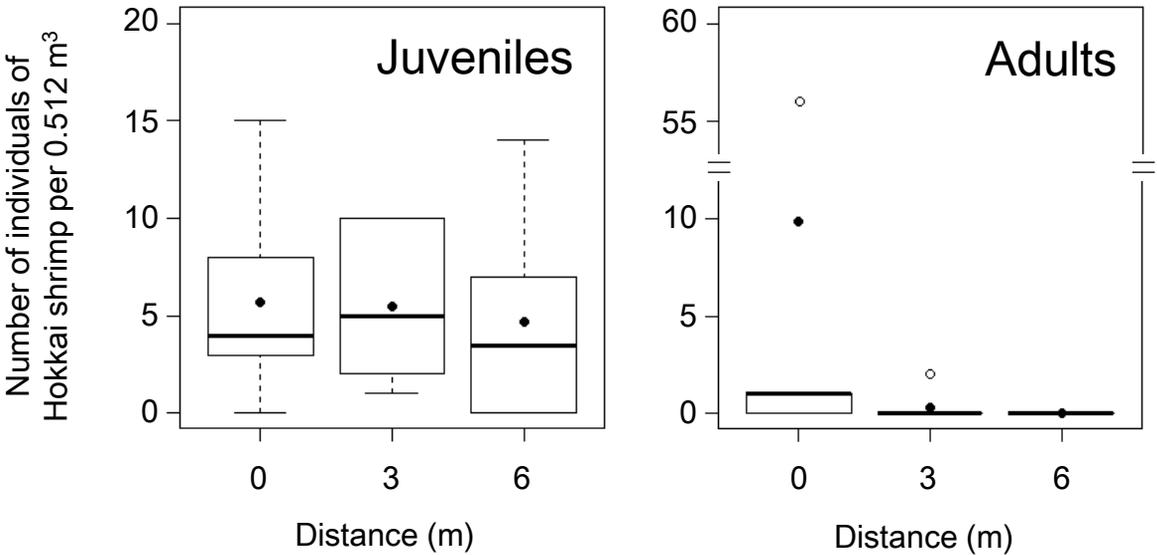


Figure 6

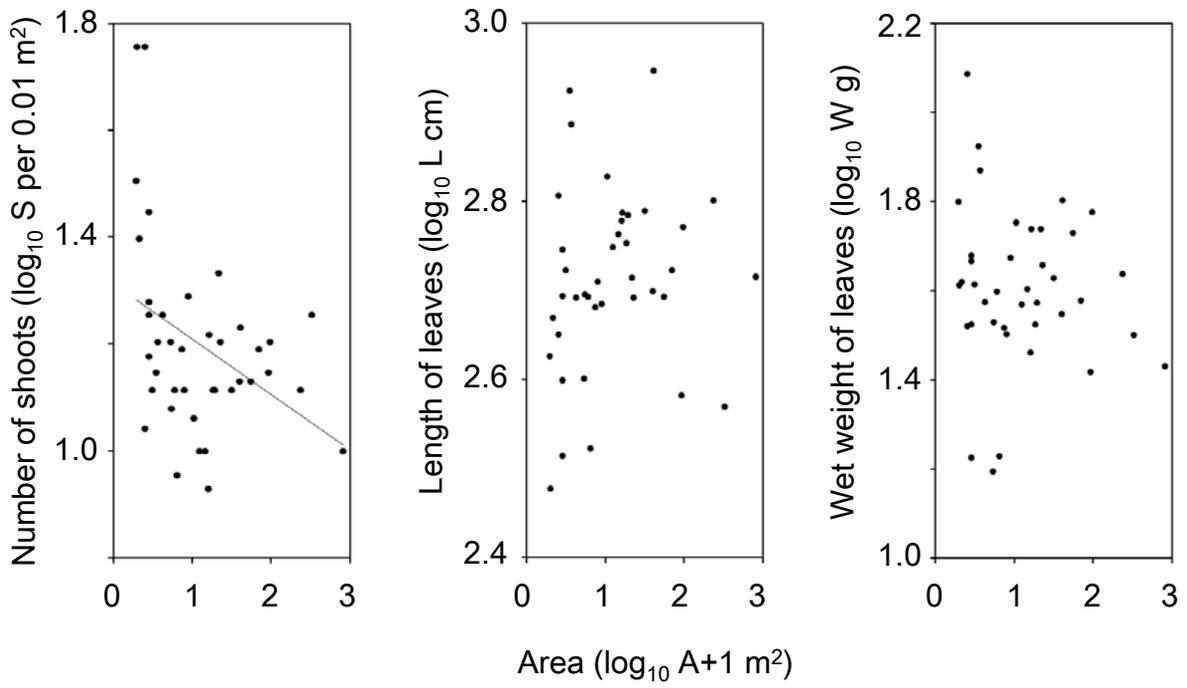


Figure 7

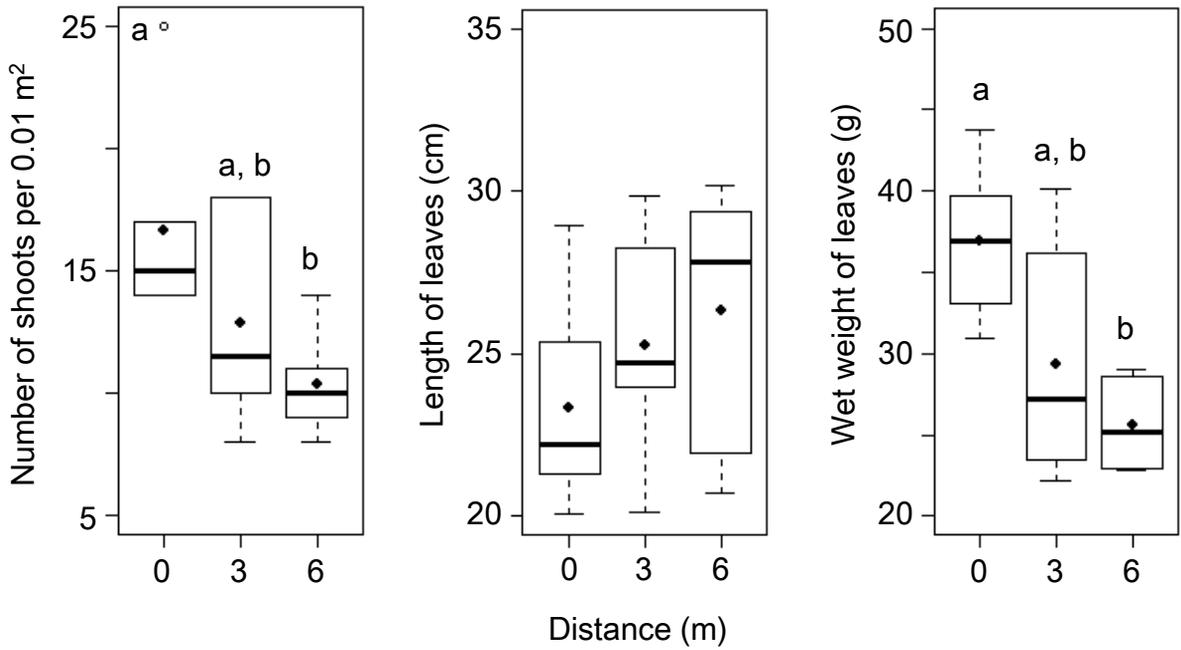


Figure 8

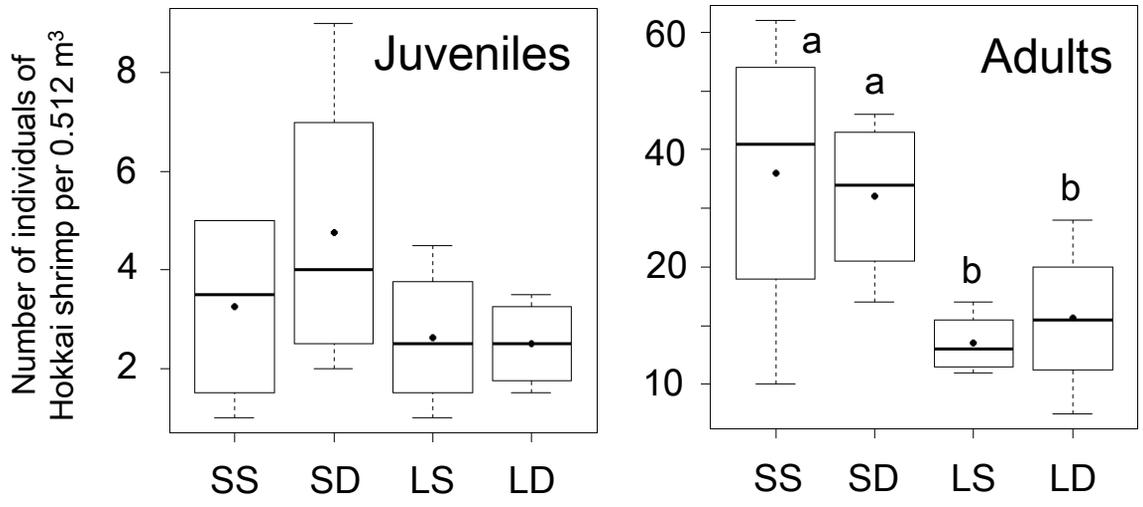


Figure 9

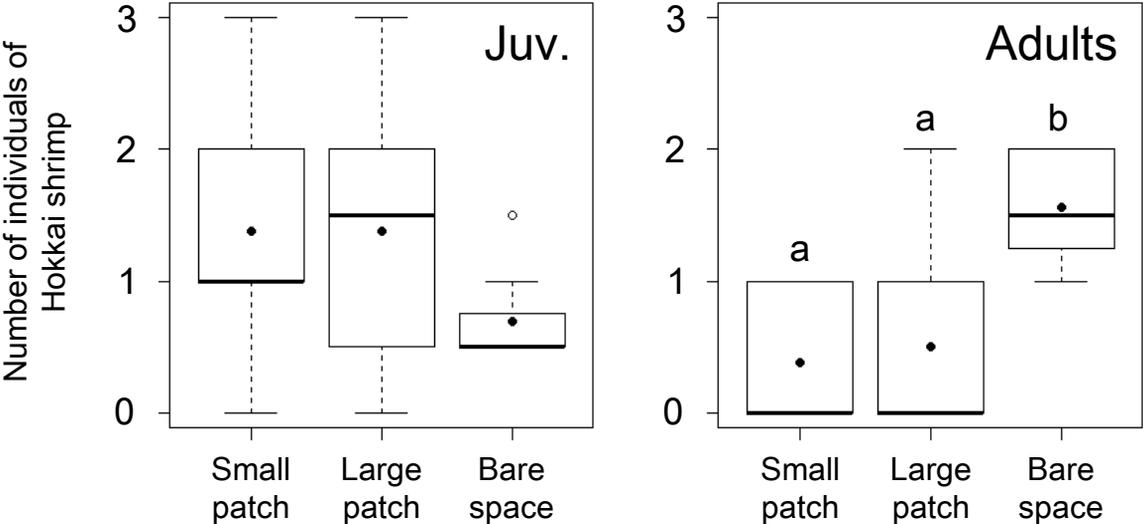


Figure 10

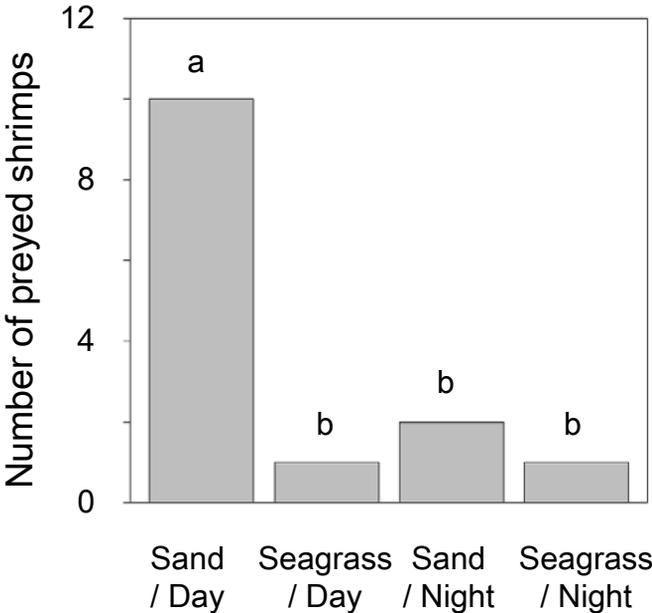


Figure 11