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

Yuichi Shinomiya[1], Susumu Chiba[2,*], Makoto Kanamori[3], Shigeyuki Hashizume[1], Kenji Yoshino[4], Seiji Goshima[1]

[1]Laboratory of Benthology, Graduate School of Fisheries Sciences, Hokkaido University, Hakodate, Hokkaido 041-8611, Japan
[2]Department of Aquatic Bioscience, Tokyo University of Agriculture, Abashiri, Hokkaido 099-2493, Japan
[3]Hakodate Fisheries Research Institute, Fisheries Research Department, Hokkaido Research Organization, Hakodate, Hokkaido 040-0051, Japan
[4]Institute of Lowland and Marine Research, Saga University, Saga, Saga 840-8502, Japan

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

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

INTRODUCTION

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

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

The goal of this study was to provide a viewpoint for the management of seagrass beds from the perspective of conserving an animal population by examining its habitat utilization, using Hokkai shrimp as a model species. We focused our interests on how the suitable attributes of seagrass patches changed for Hokkai shrimp with their life stage. We designed a program of observations and conducted field experiments to identify major processes, such as (1) the structure of seagrass patches, (2) predator–prey interactions, and (3) the rate at which shrimps encounter a seagrass patch, which determines habitat utilization by mobile animals (Connolly & Hindell 2006).

MATERIALS AND METHODS

Study site and commercial value of Hokkai shrimp

All investigations in this study were conducted at Lake Notoro, 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 $40\,000$ m^2 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.
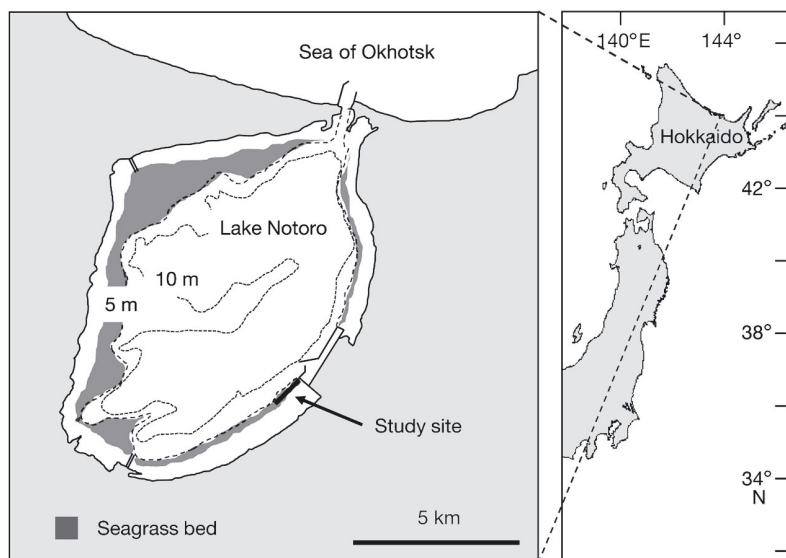
Surveys in natural seagrass patches

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

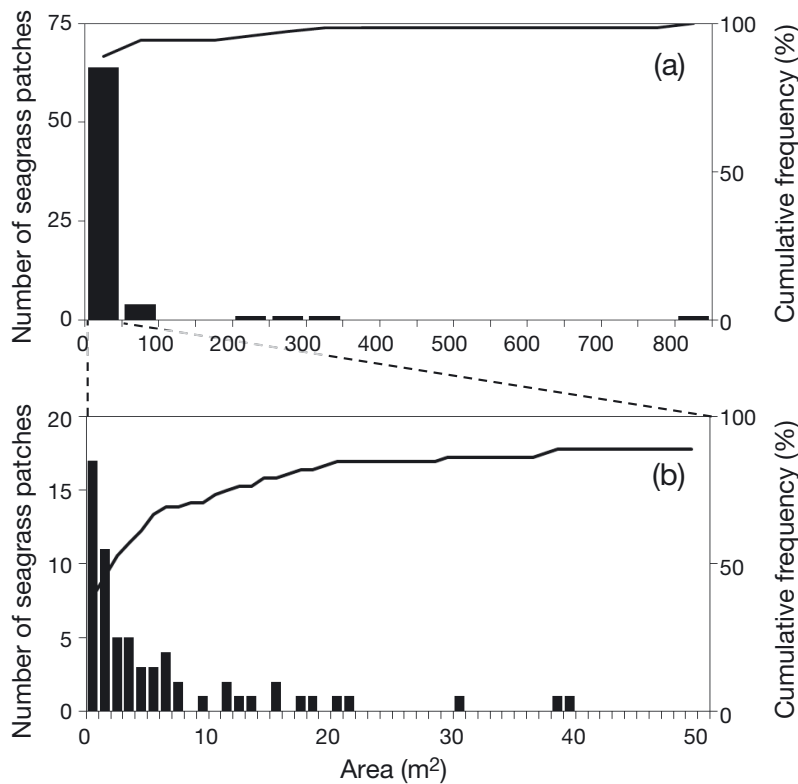Fig. 1. Study site in Lake Notoro in northeastern Japan

Fig. 2. Frequency of size of round- or oval-shaped patches at the study site. (a) and (b) show the frequencies of all sizes of patches and those of small patches less than 50 m^2, respectively. Curves represent the cumulative frequency of the number of patches

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

We also examined whether the physical structure of seagrass changed with patch size and/or distance from the edge of the patch. We cut the above-ground parts of the seagrass within a 0.01 m^2 quadrat near each point where cage sampling was conducted, and at the laboratory of the AFSC we counted the number of shoots, measured the length of all leaves, and noted the wet weight of the leaves after removing epiphytes.

Recruitment to artificial seagrass patches

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

The 4 ASUs (large/dense, large/sparse, small/dense, and small/sparse) were secured with steel pegs in the bare sandy spaces between the natural seagrass patches. To confirm that the black plastic mats (i.e. the material that was used for the base of the ASUs) did not affect shrimp aggregation, mats of the large and small sizes but without leaves were also placed in these spaces. At the experiment site, all structures (i.e. ASUs, black mats, and natural seagrass patches) were spaced >3 m from each other. Two weeks later, cage sampling was conducted using the same method as employed at the natural seagrass patches, i.e. 2 cages simultaneously placed at the center and edge of the large patches; 1 cage in each of the small

patches. This experiment was repeated 4 times, twice at the end of July (T_w approximately 19°C) and again in the middle of September 2001 (T_w approximately 18°C), since cage sampling at the natural patches was also conducted in summer.

Habitat utilization behavior

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

At the beginning of October 2002, an experiment using the ASUs was also conducted to examine habitat preference of Hokkai shrimp during nighttime (T_w approximately 16°C), because this was when they came out from the seagrass patches (see 'Results'). Two sets of large and small patches were placed to form a circle (radius: 9 m) on a sandy bare space between natural seagrass patches (Fig. 3). These ASUs were >10 m away from the natural patches. A total of 4 juvenile or 4 adult shrimps were placed in a cage (80 × 80 × 80 cm, mesh: 1 × 2 mm) at the center of the circle; the cage was removed 2 min later to
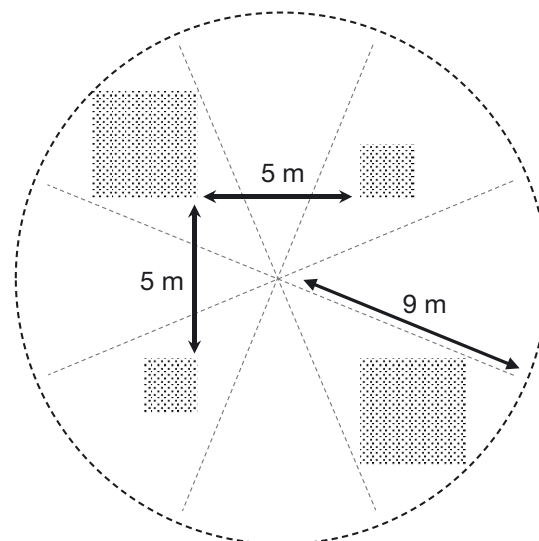

Fig. 3. Allocation of artificial patches for the Hokkai shrimp *Pandalus latirostris* habitat preference experiment. Shaded squares: large or small artificial seagrass units (ASUs). Four shrimps were released at the center of the circle in each experiment. Each area between the dashed lines inside the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

allow the individuals to move freely. This sequence was repeated 6 times each for juveniles and adults. The behavior of the individuals at the center of the circle was recorded by 2 observers, and the standing position of the observers relative to the cage was randomly changed with each repetition of the sequence to minimize the effect of the observers. The direction in which the shrimp moved and their position were recorded until they stayed in the interior or at the edge of the patch or went outside the circle for 30 min. According to our observations, individuals that entered the patches or stayed at the patch edges did not leave the patch for 30 min, while those individuals that did not stop at a patch patrolled between patches and then moved away from the circle (see 'Results'). As a conclusion of this experiment, the direction in which the individuals moved clearly reflected their habitat preference (Fig. 3).

Predation risk

At the beginning of September 2005, a tethering experiment was conducted to estimate changes in predation pressure on Hokkai shrimp with habitat type (seagrass or bare sand) during daytime and nighttime (T_w approximately 19°C). Adults (CL: 18–24 mm; BL: 60–80 mm) were used in this experiment. In the AFSC

laboratory, we attached a black spangle tied with a line (60 cm length, 0.3 mm diameter) to the carapace of a shrimp with cyanoacrylate glue (Konishi). Several hours later, the other end of the line was tied to a steel peg. We placed 25 of these tethered shrimps in each habitat type (seagrass patch or bare sandy space) during daytime and nighttime, and checked their survival 8 h later. This trial was repeated 5 times. When only a broken carapace remained at the end of the line, individuals were determined to have been consumed by predators, given that shrimp never mechanically break their own carapace.

Statistical analyses

We used simple regression analyses to examine relationships between the area of patches and the abundances of each dominant animal species at the study site after performing log transformation for both variables. In these analyses, mean abundance was used for the 22 large patches where cage sampling was conducted at both the edge and the center of each patch; this was done to analyze those data together with data collected at the 18 small patches where the edge and center were not distinguished because of the patch's small size. The shrimp were classified as juvenile or adult on the basis of their body size which would be the main factor affecting their mobile ability. Multiple regression was used to explore factors relating to the abundance of Hokkai shrimp in 40 patches that were round in shape. The response variable in this analysis was the number of juveniles or adults per cage in each patch. As explanatory factors in this analysis, we chose the number of prey (snails, *Lacuna decorata* and *Alvania concinna*, and a mysid, *Neomysis mirabilis*) and the area of the seagrass patch. Although water temperature and salinity were measured at each seagrass patch as potential factors affecting the number of shrimp, these factors were not included in the analyses because the small variations in temperature (22.9 ± 2.0°C) and salinity (33.3 ± 1.3) among patches would have had no effect on physiology of Hokkai shrimp (Chiba et al. 2004). In addition, the effects of the predators could not be evaluated here because our sampling methods did not collect a sufficient number (see 'Results').

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

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

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

To examine habitat preference by juveniles and adults, we compared the number of individuals that moved in each direction, i.e. to a small patch, a large patch, or bare sand. We divided the number of individuals in the bare sand by 2 because the area of the bare sand was twice that of other habitats. Kruskal-Wallis test was used for this comparison, and the Steel-Dwass methods were used as a multiple comparison. Fisher's exact test was used to compare the frequencies of predation among the 4 treatments (sand/day, seagrass/day, sand/night, and seagrass/night), and multiple comparisons were then conducted using Tukey's wholly significant difference (WSD) test, because frequency data where n < 5 were included in the comparison (Ryan 1960). The normality of each data set that was treated as a response variable was tested using a Korgomorov-Smirnov test to choose a suitable method for comparison. All statistical analyses were conducted using R v.3.2.3 (R Development Core Team 2015).

RESULTS

Community structure in seagrass beds of Lake Notoro

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).

Factors relating to the abundance of Hokkai shrimp

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.

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*.

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).

Edge effects on Hokkai shrimp

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; adults: paired Wilcoxon test, $V = 150.5$, p = 0.088; Fig. 5). However, the number of

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, total length for the fishes, and shell length for the mollusks. Number of individuals represents the mean per 0.512 m³. Proportion represents the relative proportion of the numbers of each individual of each species among all collected individuals. Prey and predator refer to animals preyed on by *Pandalus latirostris* (Hokkai shrimp) and animals that prey upon Hokkai shrimp, respectively

Taxon	Family	Species	Body size (mm)	No. of individuals	Proportion (%)	Prey or predator
Mollusk	Littorinidae	*Lacuna decorata*	5–10	3009.0	84.27	Prey
		Littorina squalida	5–15	6.1	0.17	
	Rissoidae	*Alvania concinna*	<5	135.9	3.81	Prey
	Turbinidae	*Homalopoma amussitatum*	5–10	6.4	0.18	
Mysid	Mysidae	*Neomysis mirabilis*	5–10	202.1	5.66	Prey
Decapod	Hippolytidae	*Eualus leptognathus*	10–15	151.1	4.23	
		Heptacarpus grebnitzkii	15–20	9.5	0.27	
		Heptacarpus longirostris	15–20	0.6	0.02	
		Spirontocaris ochotensis	15–20	6.4	0.18	
	Pandalidae	*Pandalus latirostris*	25–120	18.9	0.53	
		Pandalus prensor	15–50	0.2	0.00	
	Palaemonidae	*Palaemon* spp.[a]	20–40	0.4	0.01	
	Crangonidae	*Crangon* spp.[b]	15–50	6.1	0.17	
Fish	Gobiidae	*Gymnogobius breunigii*	25–50	15.6	0.44	
	Stichaeidae	*Opisthocentrus dybowskii*	10–250	1.0	0.03	
	Zoarcodae	*Neozoarces steindachneri*	50–100	0.2	0.00	
	Pholididae	*Pholis picta*	50–250	0.0	0.00	
	Pleuronectidae	*Pleuronectes* spp.[c]	50–200	0.5	0.01	Predator
	Scorpaenidae	*Sebastes schlegeli*	50–150	0.2	0.01	Predator
	Cottidae	*Myoxocephalus brandti*	50–200	0.1	0.00	Predator
	Hemitripteridae	*Blepsias cirrhosus*	50–150	0.1	0.00	
	Gasterosteidae	*Gasterosteus aculeatus aculeatus*	40–50	0.1	0.00	

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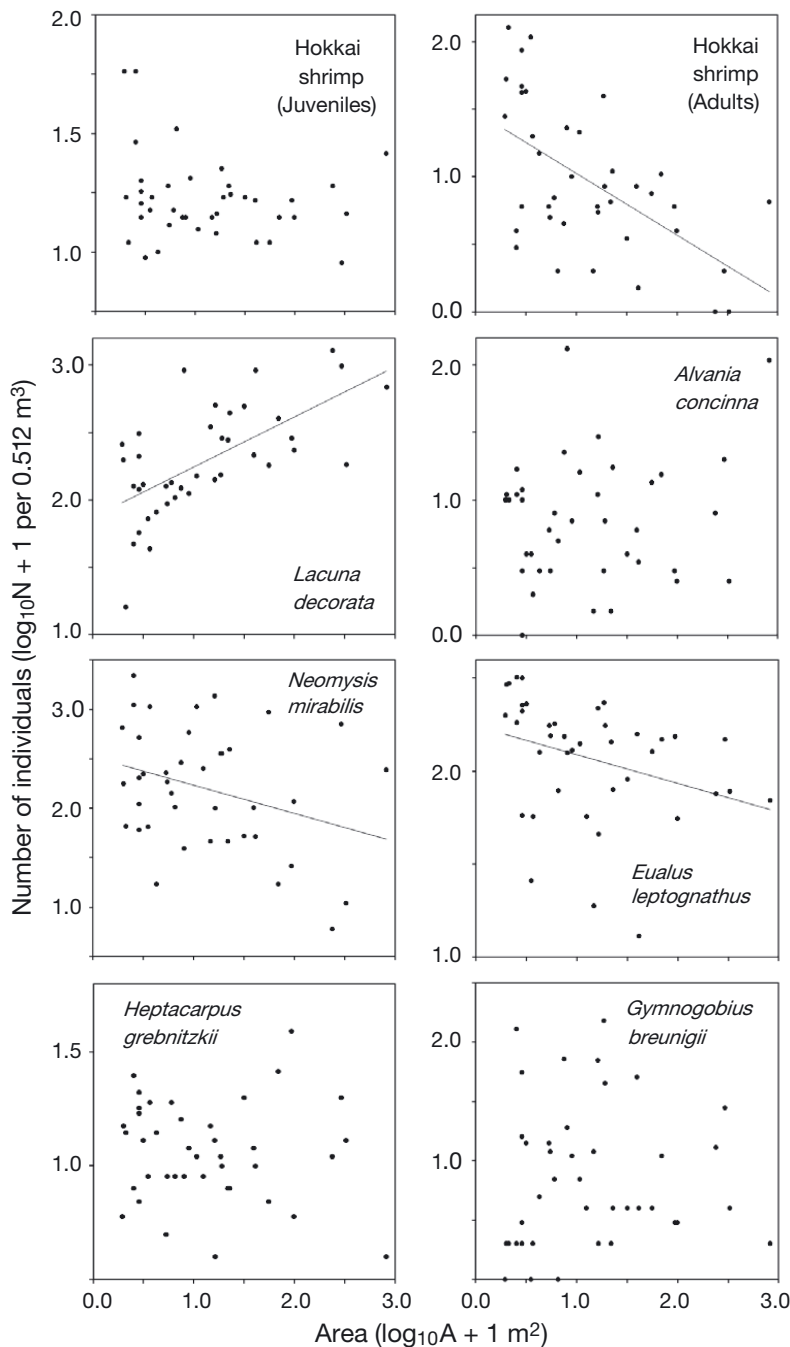
Fig. 4. Relationships between the area of patches and the abundance of dominant species at the study site. Areas (A) and number of individuals (N) are expressed in common logarithmic values after adding 1 to each value for visualization of the relationships. Coefficient of determination (r^2) adjusted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

adults at the edge deviated from a normal distribution (Fig. 5), indicating that adults aggregated in high abundance at the edge in some patches.

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 (0–3 m: $\chi^2 = 2.95$, p = 0.229; 0 to 6 m: $\chi^2 = 5.78$, p = 0.056; 3–6 m: $\chi^2 = 0.47$, p = 0.790).

Structure of the seagrass patch

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.

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

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

	Factor	Estimate	SE	*t*	p
Juvenile	Intercept	2.86	0.96	2.96	0.006
	Gastropod (*LD*)	−0.13	0.17	−0.74	0.466
	Gastropod (*AC*)	−0.08	0.12	−0.66	0.513
	Mysid (*NM*)	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 (*LD*)	−0.34	0.26	−1.31	0.200
	Gastropod (*AC*)	0.22	0.18	1.17	0.249
	Mysid (*NM*)	−0.12	0.14	−0.87	0.391
	Area	−0.40	0.15	−2.69	0.011

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 ± 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).
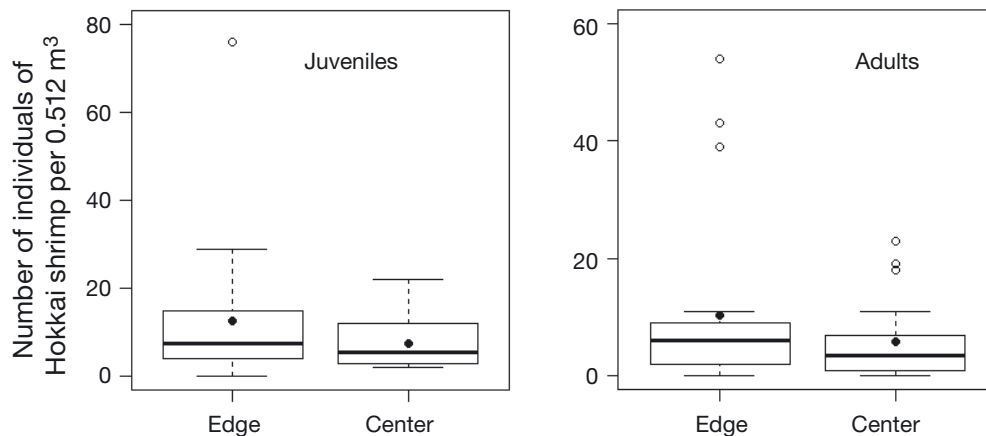

Fig. 5. Abundance of Hokkai shrimp *Pandalus latirostris* at the edge and center of 22 patches. Filled circles: means; open circles: suspected outliers. Although data normality was observed in juveniles at both the edge (Kolmogorov-Smirnov test, *D* = 0.24, p = 0.149) and the center (*D* = 0.19, p = 0.38) and in adults at the center (*D* = 0.23, p = 0.22), it was not observed in adults at the edge (*D* = 0.34, p = 0.011)
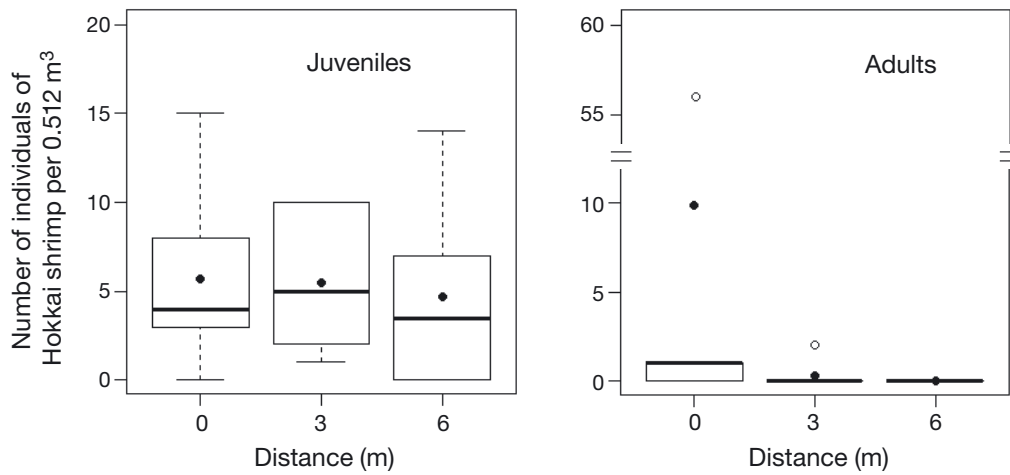
Fig. 6. Abundances of Hokkai shrimp *Pandalus latirostris* at 0, 3, and 6 m from the edge of the seagrass patch. Filled circles: means; open circles: suspected outliers. The Kolmogorov-Smirnov test showed data normality for juveniles at all points (0 m: $D = 0.29$, p = 0.69; 3 m: $D = 0.21$, p = 0.95; 6 m: $D = 0.19$, p = 0.98). Data normality for adults was not performed because of the low number of samples
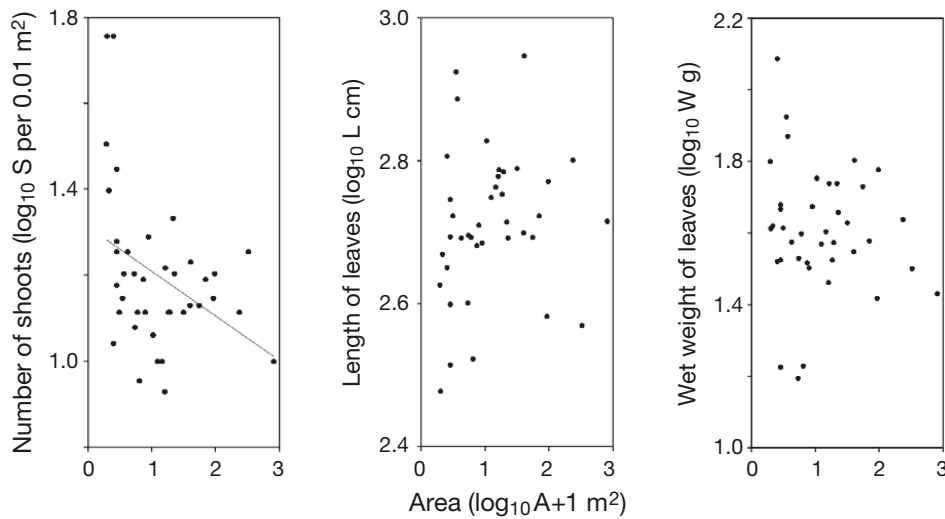

Fig. 7. Relationship between patch area and seagrass structure. Areas (A) are shown in common logarithmic value after adding 1 to each value for visualization of the relationships. Coefficient of determination (r^2) adjusted for the df and p-value in each species are as follows: shoot density ($r^2 =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

DISCUSSION

This study demonstrated that the utilization of seagrass patches by *Pandalus latirostris* (Hokkai shrimp) changed with their body size. There was no relationship between the abundance of juveniles and the area of the seagrass patch or the distance from the edge of each patch, suggesting that the juveniles were uniformly distributed within the seagrass patches. The abundances of adults, however, decreased with patch area with no relation to biological factors, and the abundances of mysids (their main prey) also decreased with patch area. This result indicates that Hokkai shrimp adults and mysids were both more abundant in smaller patches, although multiple regression analyses suggested no predator–prey interaction between them because the abundance of the shrimp was not related to the abundance of mysids. Although the relationship between the abundance of adults and their distance from the patch edge was statistically marginal, extremely high abundances of adults were found at the edge. This result suggests that conspecific adults of similar body size tend to congregate in the same place. Grouping behavior
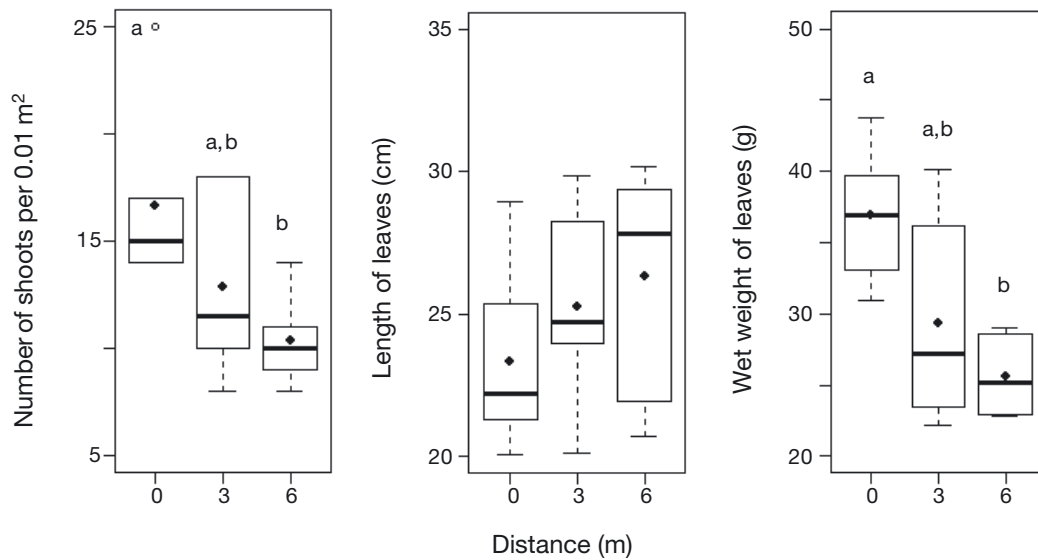
Fig. 8. Seagrass structure at 0, 3, and 6 m from the edge of the patch. Filled circles: means; open circle: suspected outlier. Different letters represent statistical differences in the Tukey-Kramer method
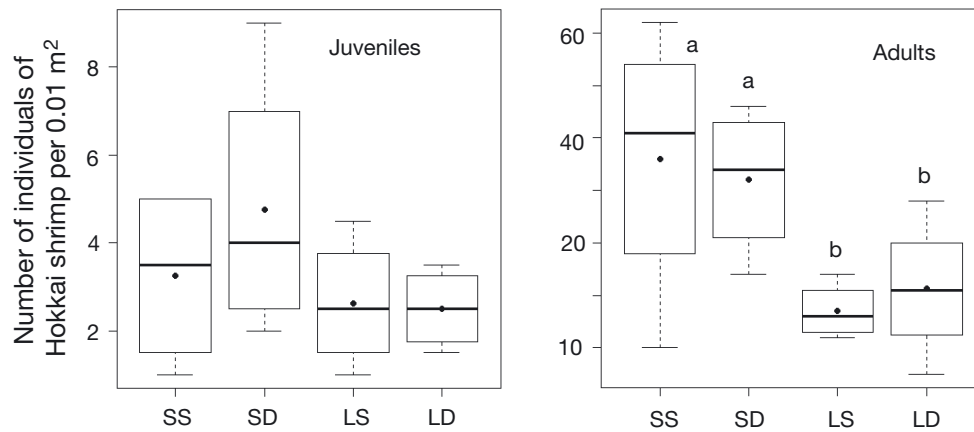

Fig. 9. Abundances of Hokkai shrimp *Pandalus latirostris* at the 4 types of artificial patches in the recruitment experiment. Horizontal axis denotes combinations of patch size and the shoot density of the patch: SS, small/sparse; SD, small/dense; LS, large/sparse; LD, large/dense. Filled circles: the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

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

Body size	Factor	SS	df	F	p
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		

such as shoaling in fish and size segregation is probably not uncommon in mobile marine invertebrates including decapods; however, details of their aggregation behaviors have not been well studied compared to fishes (Evans et al. 2007). Connolly & Hindell (2006) pointed out that edge effects in species that form a group such as a shoal were often masked by their variable abundances among samples because of problems with the power of statistical tests, even though these effects did indeed exist. Our data was a case where edge effects would have become clear if the number of sampling replications was increased, because the abundances of shrimp varied widely among seagrass patches.
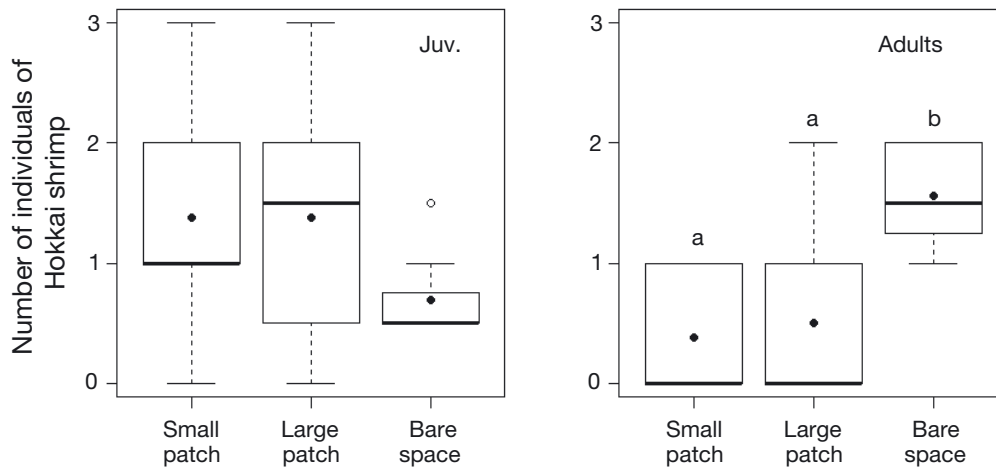
Fig. 10. Number of Hokkai shrimp *Pandalus latirostris* observed at 3 types of habitats in the habitat preference experiment. Filled circles: means; open circle: suspected outlier. Different letters denote statistical difference detected by the Steel-Dwass method
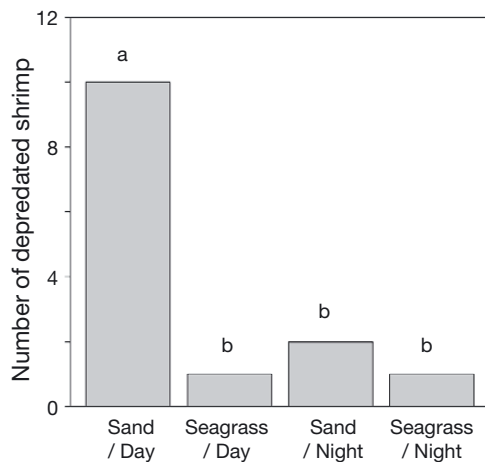

Fig. 11. Number of depredated Hokkai shrimp *Pandalus lati-rostris* in sand or seagrass habitats during daytime and night-time. Different letters denote statistical differences detected by Tukey's wholly significant difference test

The size of the patches and the distance from the patch edge included some inseparable structural attributes of natural seagrass. An increase in shoot density with a decrease in patch size can be explained by the increase in shoot density at the patch edge, because smaller patches had larger perimeter-to-area ratios in our study area. Although the length of leaves is an important component of seagrass habitats (e.g. Bell & Westoby 1986, Hori et al. 2009, Goshima & Peterson 2012, Gartner et al. 2013), it would not affect the distribution of Hokkai shrimp because it did not change with patch size or distance from the patch edge at our study site. The relationship between patch size and the weight of leaves was unclear. While the increase in weight at the patch edge can be explained by the increase in shoot den-

sity, as observed in the survey of the effect of the distance from patch edges, there seemed to be an interaction between patch size and some other structures of the seagrass, such as the number of leaves per shoot. These results suggest that shoot density is the most important seagrass structure corresponding to patch size, and that some other structures also co-vary with patch size in natural seagrass beds.

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

Body size difference would be a fundamental factor causing behavioral differences between juveniles and adults, although other factors such as physiological changes with age or life stage may also have contributed to the result. Our observation of the habitat utilization behavior of shrimps between natural patches suggests that juveniles strongly depend on seagrass during both nighttime and daytime. When juveniles were released among the ASUs during nighttime, they could not select a habitat type while they continued to depend on natural seagrass patches. This result indicates that juveniles do not actively change seagrass patches by crossing a corridor between patches. We therefore conclude that the low frequency in the migration of juveniles between

patches is related to their uniform distribution within each patch. Adults, however, were collected at the ASUs in much greater numbers than juveniles in the recruit experiment, suggesting that adults frequently migrated between patches. In fact, adults often emerged from natural seagrass patches at night, and they tended to patrol the bare sand spaces when they were released among the ASUs during nighttime. These results showed that adults did not statically inhabit the interior of seagrass patches. Although it is true that the distribution of Hokkai shrimp is limited to only seagrass beds (Komai 1999, Bergström 2000), our fine-scale study demonstrated that while adults mainly used seagrass patches, they also used bare sand spaces at night. The high abundance of adults in the small patches can therefore be explained by the rate at which they encounter seagrass (Eggleston et al. 1998, 1999, Arponen & Boström 2012). Body size generally affects the mobility of animals, and it may also cause behavioral shifts in the selection of refuge habitats of prey species such as grass shrimps, to defend themselves against predators (Davis et al. 2003). It is thus worthwhile to confirm the generality of the effects of body size on changes in habitat utilization in other seagrass-dwelling species.

Why do adults leave seagrass patches at night? This behavior may be related to both diurnal changes in predation pressure and food availability. Vegetated areas are better than unvegetated areas as a refuge for adults during daytime, as the tethering experiment in the present study showed that predation risk in bare sand areas was higher than in the seagrass. During nighttime, however, the predation rate in the bare sand areas was as low as it was in the seagrass, indicating that there was no difference in predation risk between those habitats at night. Seagrass would not always be a safe habitat for the shrimp, because predators employing ambush tactics, such as the sculpin *Myoxocephalus brandti* at our study site (Table 1), often coexist with their prey, including Hokkai shrimp inside a seagrass patch (Horinouchi et al. 2009). That there is no difference in predation risk between habitats at night would therefore reduce the motivation of Hokkai shrimp to stay inside a patch. Moreover, food availability inside patches would motivate shrimps to move to another patch. Although Hokkai shrimp adults tended to use relatively smaller patches at our study site, it would be better for them to change patches if they are in small patches, because their high nutritional requirement would likely deplete the food resources there. We also observed that adults consumed substances such as detritus on the surface of sand at night,

implying that they can obtain different types of nutrients outside the seagrass patches (Ochwada et al. 2009, Tait & Hovel 2012), although the details are still unknown. The stomach contents of Hokkai shrimp reported by Mizushima (1981) were generally consistent with our preliminary observations, though other methods such as stable isotope analyses may clarify more details concerning their food habits. As a preliminary conclusion, the decrease in predation pressure in the bare areas during nighttime and their requirement for food would be plausible reasons for adults leaving seagrass patches at night.

CONCLUSIONS

The present study showed that the habitat utilization patterns of Hokkai shrimp changed with their life stage. The uniform distribution of juveniles between and within patches indicates that a large, continuous patch would be effective for the conservation of juveniles given that their abundance increases with the total area of seagrass patches. Although we did not examine the details of the process that determined their uniform distribution, their small body size would fundamentally restrict their movement between patches. In particular, small grass shrimp such as Hokkai shrimp juveniles would likely not leave a seagrass patch because of their low ability to escape and high risk of predation outside the patch (Bell et al. 2001). Many small patches would be important for adults, however, because adults enter these patches after patrolling bare spaces at night. This process is well explained by the rate at which they encountered seagrass during the night due to positive edge effects. The importance of patch size thus varies with their life stage, and patches of various sizes are required for their population to persist. The habitat utilization pattern observed in summer may change seasonally because of seasonal changes in seagrass structure and animal assemblages (e.g. Eggleston et al. 1998, Hovel & Lipcius 2002, Kanamori et al. 2004, Hasegawa et al. 2008, Goshima & Peterson 2012, Herrera et al. 2014). Our conclusion will not change, however, as long as both large and small sizes of patches are needed in one of the seasons when the shrimp are actively moving among patches. Since the pattern that we observed was an ontogenic shift, our results point not to a site-specific response but an adaptive habit of the shrimp. The spatial management of seagrass patches of varying size is thus of utmost importance from the perspective of the persistence of this animal population.

LITERATURE CITED

Abashiri City Government (2016) Annual report of fishery production in Abashiri. www.city.abashiri.hokkaido.jp/030shisei/020toukei/080suisanntoukei/ (accessed 5 Oct 2016)

Allendorf FW, England PR, Luikart G, Ritchie PA, Ryman N (2008) Genetic effects of harvest on wild animal populations. Trends Ecol Evol 23:327–337

Almeida MJ, Flores AAV, Queiroga H (2008) Effect of crab size and habitat type on the locomotory activity of juvenile shore crabs, *Carcinus maenas.* Estuar Coast Shelf Sci 80:509–516

Arponen H, Boström C (2012) Responses of mobile epifauna to small-scale seagrass patchiness: Is fragmentation important? Hydrobiologia 680:1–10

Beck MW, Heck KL, Able KW, Childers DL and others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633–641

Bell JD, Westoby M (1986) Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. Oecologia 68:205–209

Bell SS, Hall MO, Robbins BD (1995) Toward a landscape approach in seagrass beds: using macroalgal accumulation to address questions of scale. Oecologia 104:163–168

Bell SS, Brooks RA, Robbins BD, Fonseca MS, Hall MO (2001) Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. Biol Conserv 100:115–123

Bergström BI (2000) The biology of *Pandalus.* Adv Mar Biol 38:55–245

Boström C, Jackson EL, Simenstad CA (2006) Seagrass landscapes and their effects on associated fauna: a review. Estuar Coast Shelf Sci 68:383–403

Boström C, Pittman SJ, Simenstad C, Kneib RT (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Mar Ecol Prog Ser 427:191–217

Chiba S, Goshima S (2003) Population structure and seasonal growth of the protandrous pandalid shrimp *Pandalus latirostris* in Notoro Lagoon, Hokkaido. Aquacult Sci 51:375–383

Chiba S, Kawamura T (2011) Ecosystem services provided by marine invertebrates. In: Shoji J, Hori M, Yamashita Y (eds) Ecosystem services of coastal waters—benefits of the sea and its sustainable use. Kouseisha-Kouseikaku, Tokyo (in Japanese)

Chiba S, Goshima S, Mizushima T (2000) Factors affecting the occurrence of early maturing males in the protandrous pandalid shrimp *Pandalus latirostris.* Mar Ecol Prog Ser 203:215–224

Chiba S, Aoki L, Ogata T (2004) Response of the pandalid

shrimp *Pandalus latirostris* to dissolved oxygen, salinity and turbidity. Fish Sci 70:1174–1176

Chiba S, Yoshino K, Kanaiwa M, Kawajiri T, Goshima S (2013) Maladaptive sex ratio adjustment by a sex-changing shrimp in selective-fishing environments. J Anim Ecol 82:632–641

Connolly RM, Hindell JS (2006) Review of nekton patterns and ecological processes in seagrass landscapes. Estuar Coast Shelf Sci 68:433–444

Davis JLD, Metcalfe WJ, Hines AH (2003) Implications of a fluctuating fish predator guild on behavior, distribution, and abundance of a shared prey species: the grass shrimp *Palaemonetes pugio.* J Exp Mar Biol Ecol 293:23–40

Duarte CM (2002) The future of seagrass meadows. Environ Conserv 29:192–206

Duffy JE (2006) Biodiversity and the functioning of seagrass ecosystems. Mar Ecol Prog Ser 311:233–250

Eggleston DB, Etherington LL, Elis WE (1998) Organism response to habitat patchiness: species and habitat-dependent recruitment of decapod crustaceans. J Exp Mar Biol Ecol 223:111–132

Eggleston DB, Elis WE, Etherington LL, Dahlgren CP, Posey MH (1999) Organism responses to habitat fragmentation and diversity: habitat colonization by estuarine macrofauna. J Exp Mar Biol Ecol 236:107–132

Espino F, González JA, Haroun R, Tuya F (2015a) Abundance and biomass of the parrotfish *Sparisoma cretense* in seagrass meadows: temporal and spatial differences between seagrass interiors and seagrass adjacent to reefs. Environ Biol Fishes 98:121–133

Espino F, Triay-Portella R, González JA, Haroun R, Tuya F (2015b) Population structure of the pearly razorfish, *Xyrichtys novacula* (Actinopterygii: Labridae), in sand-seagrass mosaics: spatial variation according to habitat features and sampling techniques. Sci Mar 79:179–188

Evans SR, Finnie M, Manica A (2007) Shoaling preferences in decapod crustacea. Anim Behav 74:1691–1696

Fletcher RJ Jr, Ries L, Battin J, Chalfoun AD (2007) The role of habitat area and edge in fragmented landscapes: Definitively distinct or inevitably intertwined? Can J Zool 85:1017–1030

García-Sanz S, Navarro PG, Landeira JM, Tuya F (2014) Colonization patterns of decapods into artificial collectors: seasonality between habitat patches. J Crustac Biol 34:431–441

García-Sanz S, Navarro PG, Png-González L, Tuya F (2016) Contrasting patterns of amphipod dispersion in a seagrass meadow between day and night: consistency through a lunar cycle. Mar Biol Res 12:56–65

Gartner A, Tuya F, Lavery PS, McMahon K (2013) Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms. J Exp Mar Biol Ecol 439:143–151

Goshima S, Peterson CH (2012) Both below- and above-ground shoalgrass structure influence whelk predation on hard clams. Mar Ecol Prog Ser 451:75–92

Gotceitas V, Fraser S, Brown JA (1997) Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 54:1306–1319

Hasegawa N, Hori M, Mukai H (2008) Seasonal changes in eelgrass functions: current velocity reduction, prevention of sediment resuspension, and control of sediment-water column nutrient flux in relation to eelgrass dynamics. Hydrobiologia 596:387–399

Heck KL Jr, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar Ecol Prog Ser 253:123–136

Hemminga MA, Duarte CM (2000) Seagrass ecology. Cambridge University Press, Cambridge

Herrera A, Landeira JM, Tuya F, Packard T, Espino F, Gómez M (2014) Seasonal variability of suprabenthic crustaceans associated with *Cymodocea nodosa* seagrass meadows off Gran Canaria (eastern Atlantic). Cont Shelf Res 88:1–10

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

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

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

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

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

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

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

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

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

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

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

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

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

Mizushima T (1981) Ecology and catch of the prawn, *Pandalus kessleri* in *Zostera* beds in Notsuke Bay, Hokkaido, Japan. In: Japan Soc Fish Sci (ed) Seaweed beds. Kouseisha-Kouseikaku, Tokyo, p 57–74 (in Japanese)

Moore EC, Hovel KA (2010) Relative influence of habitat complexity and proximity to patch edges on seagrass epifaunal communities. Oikos 119:1299–1311

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

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

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

Pittman SJ, McAlpine CA (2003) Movements of marine fish and decapod crustaceans: process, theory and application. Adv Mar Biol 44:205–294

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

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

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

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

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

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

Short FT, Polidoro B, Livingstone SR, Carpenter KE and others (2011) Extinction risk assessment of the world's seagrass species. Biol Conserv 144:1961–1971

Sitonikov AV, Kartavtsev YF, Nikiforov SM (1997) Estimation of the effective size of a grass shrimp (*Pandalus kessleri*) population by a temporal method and direct census of breeders during breeding season. Russ J Genet 33:1158–1164

Tait KJ, Hovel KA (2012) Do predation risk and food availability modify prey and mesopredator microhabitat selection in eelgrass (*Zostera marina*) habitat? J Exp Mar Biol Ecol 426-427:60–67

Williams JA, Holt GJ, Robillard MMR, Holt SA, Hensgen G, Stunz GW (2016) Seagrass fragmentation impacts recruitment dynamics of estuarine-dependent fish. J Exp Mar Biol Ecol 479:97–105