Regional variation in shell utilization patterns of the hermit crab Pagurus filholi

HIROMI HASEGAWA1, SATOSHI WADA2*, MASAKAZU AOKI3 & KEIJI WADA1

1 Department of Biological Science, Faculty of Sciences, Nara Women’s University, Kitauoya-nishimachi, Nara, 630–8506, Japan
2 Laboratory of Marine Biology, Graduate School of Fisheries Sciences, Hokkaido University, 3–1–1 Minato-cho, Hakodate, 041–8611, Japan
3 Shimoda Marine Research Center, University of Tsukuba, 5–10–1 Shimoda, Shizuoka, 415–0025, Japan

Received September 10, 2008; Accepted February 3, 2009

Abstract: Shell utilization patterns of the intertidal hermit crab Pagurus filholi were compared between two distant local populations from Oura Bay, Shimoda, central Japan, and Hakodate Bay, Hakodate, northern Japan, in conjunction with the shell resource availability and shell utilization patterns of sympatric hermit crabs. Gastropod species of shells dominantly utilized by P. filholi differed between Oura Bay and Hakodate Bay, and shell utilization patterns did not correspond to the availability of shells in both study localities. Between P. filholi and other sympatric hermit crabs, there were some clear differences in shell species utilized in both localities, and values of niche overlap indices in shell and habitat utilizations between P. filholi and other crabs were higher in Hakodate Bay than in Oura Bay. The rich supply of shell resources in Hakodate Bay compared to Oura Bay is considered to be a factor responsible for the difference in the degree of niche overlapping between the two localities.

Key words: Hermit crab, Interpopulation difference, Niche overlap, Pagurus filholi, Shell resource availability, Shell utilization

Introduction

Hermit crabs generally utilize gastropod shells because their abdominal exoskeleton lacks calcification, and as such, gastropod shells are an indispensable resource for hermit crabs. Shell species and size have been known to influence various aspects of the ecological characteristics of hermit crabs, such as growth rate (Bertness 1981, Blackstone 1985), clutch size (Childress 1972), vulnerability to predators (Vance 1972b, Zisper & Vermeij 1978, Mima et al. 2003), and resistance to physical stress (Reese 1968, Bertness 1982).

Many previous studies have revealed that shell utilization by hermit crabs is influenced by local shell resource availability (e.g., Ohmori et al. 1995), interspecific competition among sympatric hermit crabs (Vance 1972a, Bach et al. 1976), predation pressure (Bertness et al. 1981, Bertness 1982) and preferences for specific shell characteristics (Bertness 1980, 1982, Imazu & Asakura 1994, Ohmori et al. 1995, Turra & Leite 2001, Oba & Goshima 2004). Shell preference by hermit crabs has also been shown to be affected by environmental conditions such as oxygen level (Cote et al. 1998), water flow (Hahn 1998), and predation risk (Mima et al. 2003). Therefore, it is expected that the shell utilization pattern varies among populations occurring in different regions that have different environmental conditions. However, there have been few studies exploring such regional variation of shell utilization pattern within the same hermit crab species (Brown 1992).

Pagurus filholi (de Man) commonly inhabits intertidal rocky shores from southern Hokkaido to Kyushu, Japan. Although the shell utilization pattern of this species has been elucidated for each local population (Imazu & Asakura 1994, Ohmori et al. 1995), no studies have compared the shell utilization pattern among different local populations, in relation to the shell availability. In this study, we compare the shell utilization pattern of P. filholi between two distant populations, one of Oura Bay, Shimoda, central Japan and the other in Hakodate Bay, Hakodate, northern Japan in conjunction with shell utilization patterns of other co-occurring hermit crab species and the availability of shell resources. We then discuss some ecological causes of regional difference in shell utilization pat-
terns of \textit{P. filholi}.

**Materials and Methods**

The study was conducted on the intertidal rocky shores in Oura Bay, Shimoda, central Japan (34°40′N, 138°57′E), from 28 February to 14 March, 2005, and in Hakodate Bay, Hakodate, northern Japan (41°44′N, 140°36′E), between 22 and 29 of July, 2006 (Fig. 1). Latitudinal variation in reproductive season has been reported in \textit{Pagurus filholi} (Wada et al. 2005), and the main reproductive seasons of Oura population and Hakodate population are considered as winter and spring. New settlements have been found from March to May in Kominato (35°0′N, 140°0′E) (Imazu & Asakura 1994), geographically close to Oura Bay (Fig. 1), and from August to November in Hakodate Bay (Oba & Goshima 2004), and shell utilization pattern of settlements differed from that of adults (Ohmori et al. 1995, Oba & Goshima 2004). Our sampling dates were determined to reduce the differences in seasonality of life cycle between the two populations.

In order to assess shell utilization patterns of hermit crabs and abundance of shell resources (live gastropods and empty shells), line transect sampling was carried out at both sites. On an intertidal rocky shore inhabited by \textit{P. filholi}, four transects perpendicular to the shoreline were established in Oura Bay, and two transects established in Hakodate Bay. Three to five sampling points (4–20 m intervals) with eight quadrats (25×25 cm) were placed along each transect, totaling 17 points (136 quadrats) in Oura Bay and 8 points (64 quadrats) in Hakodate Bay. At each sampling point, hermit crabs, live gastropods and empty shells (not used by hermit crabs) were collected from the eight quadrats. The collected hermit crabs, after being fixed in 10% formalin, were identified to the species level and examined under a stereoscopic microscope for sex (gonopore on coxa of third pereopod in females and that of fifth pereopod in males), shield length (calcified anterior portion of the cephalothorax) with an ocular micrometer, and ovigerous condition for females. We also identified the species of live gastropods, empty shells and shells occupied by hermit crabs, and measured their shell widths with calipers.

To quantify the niche overlap of habitat and shell utilization pattern between \textit{P. filholi} and all other hermit crab species, we calculated Morisita’s index (Morisita 1959), given by \( C_{ij} = \frac{2P_{ij}}{N_i} \left(\frac{N_i - 1}{N_j} + \frac{N_j - 1}{N_i} - 1\right) \), where \( P_{ij} \) and \( P_k \) are the frequencies that species \( j \) (\textit{P. filholi}) and \( k \) (all other hermit crab species) are found in the habitat category \( i \) (sampling point) or in the utilized shell category \( i \) (shell species), respectively, \( N_i \) and \( N_j \) the numbers of individuals of each species that use the resource category \( i \), and \( N_i \) and \( N_j \) the total numbers of individuals of each species. The index ranges from 0 (no resources used in common between two species) to 1.0 (complete overlap in resource use).

**Results**

In Oura Bay, five hermit crab species were collected during the line transect sampling (Table 1), and among them, \textit{Pagurus filholi} was predominant (Table 1), with the crab size ranging 0.80 to 6.75 mm in shield length (male: mean±SD=2.49±1.16 mm, \( n=704 \), female: 3.17±0.94, \( n=878 \)). In Hakodate Bay, six hermit crab species were collected: \textit{P. filholi}, \textit{Pagurus middendorffii} Brand, \textit{Pagurus lanuginosus} de Haan, \textit{Pagurus minutus} Hess, \textit{Paguristes ormanni} Miyake, \textit{Pagurus proximus} Komai. As in Oura Bay, \textit{P. filholi} was predominant (Table 1), with the crab size ranging from 1.48 to 5.90 mm in shield length (male: mean±SD=2.64±0.96 mm, \( n=436 \), female: 2.26±0.27, \( n=547 \)). The density of total hermit crabs per quadrat in Hakodate Bay (mean±SD=31.8±32.7, range=0–131, \( n=64 \) quadrats) was significantly higher than that in Oura Bay (mean±SD=14.6±11.7, range=0–63, \( n=136 \) quadrats) (Mann-Whitney U test, \( z=-2.55, P<0.05 \)).

The numbers of species of live gastropods collected through the transect sampling were 32 in Oura Bay and 10 in Hakodate Bay. The density of gastropods per quadrat in Hakodate Bay (mean±SD=21.7±16.5, range=0–84, \( n=64 \) quadrats) was significantly higher than that in Oura Bay (mean±SD=10.1±12.6, range=0–65, \( n=136 \) quadrats) (Mann-Whitney U test, \( z=-5.76, p<0.001 \)). In
Oura Bay, *Nerita albicilla* Linnaeus (52.5%) and *Monodonta labio* (Linnaeus) form *confusa* (19.6%) were common, while in Hakodate Bay *Chlorostoma lischkei* Tapparone-Canefri (72.0%) was predominant (Fig. 2).

The density of empty gastropod shells per quadrat was significantly higher in Hakodate Bay (mean±SD=23.8±43.2, range=0–305, n=64 quadrats) than in Oura Bay (mean±SD=0.4±0.8, range=0–5, n=136 quadrats) (Mann-Whitney U test, z=-10.71, p<0.0001). The availability of empty shells per hermit crab showed a marked difference in frequency between the two populations, being 0.75 in Hakodate Bay and 0.03 in Oura Bay.

Fifty-nine species of gastropod shells were used by *P. filholi* in Oura Bay, with *M. labio* form *confusa* being commonest (19.6%) (Fig. 2). Utilization frequency of the most dominant gastropod *N. albicilla* was significantly lower than its availability (χ²-test, χ²=668.34, p<0.001), while the utilization frequency of *M. labio* form *confusa* was not significantly different from its availability (χ²-test, χ²=0.12, p>0.05). As shown in Fig. 2, the second commonest hermit crab species co-existing with *P. filholi* in Oura Bay, *Clibanarius virescens* (Krauss) (shield length; male: mean±SD=2.07±1.11 mm, n=202, female: 2.40±0.78, n=90), used 37 species of gastropod shells, with *Euplica scripta* Lamarck (35.3%) being most frequently utilized.

In Hakodate Bay, *P. filholi* used 10 species of gastropod shells, with *Batillaria cumingi* (Crosse) (74.0%) being commonest (Fig. 2). The utilization frequency of *B. cumingi* was significantly higher than its availability (χ²-test, χ²=1504.81, p<0.001), whereas the most dominant gastropod *C. lischkei* was utilized significantly less frequently than its availability (χ²-test, χ²=359.16, p<0.001). *Pagurus mddendorffii* (shield length; male: mean±SD=1.99±0.65 mm, n=525, female: 2.04±0.41, n=302) that occurred commonly with *P. filholi* in Hakodate Bay used 11 species of gastropod shells, with *Homalopoma sangarense* (Schrenck) (32.0%) and *B. cumingi* (23.2%) being common (Fig. 2). *Pagurus lanuginosus* (shield length; male: mean±SD=5.59±1.65 mm, n=76, female: 5.56±1.26, n=136) that also occurred commonly with *P. filholi* in Hakodate Bay used 7 species of gastropod shells, with *C. lischkei* (89.6%) being predominant (Fig. 2).

Values of niche overlap indices of habitat and shell utilization patterns between *P. filholi* and all other hermit crab species were higher in Hakodate Bay (habitat: 0.89, shell utilization: 0.51) than in Oura Bay (habitat: 0.29, shell utilization: 0.19).

**Discussion**

Shell species utilized by *Pagurus filholi* differed between Oura Bay and Hakodate Bay. The gastropod species that was mainly utilized by *P. filholi* was *Monodonta labio* form *confusa* in Oura Bay, and *P. filholi* utilized mainly *Batillaria cumingi* in Hakodate Bay. This difference may be caused by differences in the species composition and abundance of gastropods between the two localities. However, shell utilization frequency in *P. filholi* did not necessarily correspond to the availability of gastropods in both localities, suggesting preferential utilization of gastropod shells in both localities.

Shell utilizations in both localities seem to reflect the preference for gastropod species by *P. filholi*. In Oura Bay, *Nerita albicilla* appeared to be less preferred by *P. filholi*. Imafuku (1985) showed in laboratory experiments that *P. filholi* in Tanabe Bay, Wakayama Prefecture (33°43′N, 135°22′E), preferred gastropod shells in the order of *Thais clavigera*, *Turbo cornutus coreensis* or *M. labio* form *confusa*, and *N. albicilla*. Our laboratory experiments (Hasegawa, unpublished) revealed that *P. filholi* in Oura Bay preferred gastropod shells in the order of *T. clavigera*, *M. labio* form *confusa* and *N. albicilla*. Thus, the less frequent use of *N. albicilla* by *P. filholi* in Oura Bay reflects the lack of preference for this gastropod species. Our results have also revealed that *P. filholi* in Hakodate Bay utilized gastropod shells of *B. cumingi* most commonly among the gastropod species occurring in the bay and did so more frequently compared to the availability of *B. cumingi*. Hermit crabs of *P. filholi* in Hakodate Bay preferred *B. cumingi* under chemical stimulus of the sympatric predatory crab *Gaetice depressus* (Mima et al. 2003) although they did not choose *B. cumingi* shells under a predatory threat (Ohmori et al. 1995). Since *G. depressus* is a dominant species in our study site of Hakodate Bay, *P. filholi* would appear to prefer shells of *B. cumingi* in the field.

Niche overlap indices of shell and habitat utilization patterns between *P. filholi* and other sympatric hermit crab species were higher in Hakodate Bay than in Oura Bay. This may be attributable to regional differences in shell resource abundance. Empty shells in Oura Bay were very

- Table 1. Species and the number of individuals of hermit crabs collected during the survey in Oura Bay and Hakodate Bay.

| Locality | Hermit crab species | N  | Proportion (%) |
|----------|---------------------|----|----------------|
| Shimoda  | *Pagurus filholi*    | 1612 | 81.2          |
|          | *Clibanarius virescens* | 292 | 14.7          |
|          | *Pagurus nigrivittatus* | 65  | 3.3           |
|          | *Pagurus maculosus*   | 15  | 0.8           |
|          | *Paguristes japonicus* | 2   | 0.1           |
| Total    |                      | 1986 | 100           |
| Hakodate | *Pagurus filholi*    | 983  | 48.3          |
|          | *Pagurus mddendorffii* | 827 | 40.6          |
|          | *Pagurus lanuginosus* | 212 | 10.4          |
|          | *Pagurus minutus*     | 5   | 0.2           |
|          | *Pagurus proximus*    | 5   | 0.2           |
|          | *Paguristes ortmanni* | 3   | 0.1           |
| Total    |                      | 2035 | 100           |
Regional variation in shell utilization patterns of the hermit crab *Pagurus filholi*

Figure 2. Shell utilization patterns of the hermit crabs and shell availability in Oura Bay and Hakone Bay. Shell availability is the relative abundance of live snails and empty snail shells.
limited, whereas in Hakodate Bay they were more abundant. Therefore, competition over shells between *P. filholi* and other hermit crabs in Oura Bay would be more intense than in Hakodate Bay, leading to lower niche overlap indices. Regional differences in other environmental factors, such as food resource and habitat diversity, might also be responsible for the regional difference in niche overlapping among sympatric hermit crab species. Future studies that incorporate these factors are needed to clarify the reason for the difference in niche overlapping among sympatric hermit crab species between Oura Bay and Hakodate Bay.

**Acknowledgments**

We express our gratitude to Drs. Yoichi Yusa and Hiroaki Sato of Nara Women’s University for their valuable advice and suggestions. We also thank Takuma Kawaminami, Takashi Oba and other members of the Benthos Research Group, the laboratory of Marine Biology and Diversity, Faculty of Fisheries, Hokkaido University, for their support with the field study. Identification of gastropod species by Kohichi Takenouchi is acknowledged. We also thank members of the laboratory of Animal Ecology, Nara Women’s University, and of the laboratory of Marine Ecology, Shimoda Marine Research Center, University of Tsukuba, for their valuable comments and assistance.

**References**

Bach C, Hazlett B, Rittschof D (1976) Effects of interspecific competition on fitness of the hermit crab *Clibanarius tricolor*. Ecology 57: 579–586.

Bertness MD (1980) Shell preference and utilization patterns in littoral hermit crabs of the Bay of Panama. J Exp Mar Biol Ecol 48: 1–16.

Bertness MD (1981) The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura). Crustaceana 40: 197–205.

Bertness MD (1982) Shell utilization, predation pressure, and thermal stress in Panamanian hermit crabs: an interoceanic comparison. J Exp Mar Biol Ecol 64: 159–187.

Bertness MD, Garrity SD, Levinggs SC (1981) Predation pressure and gastropod foraging: a tropical-temperate comparison. Evolution 35: 995–1007.

Blackstone NW (1985) The effects of shell size and shape on growth and form in the hermit crab *Pagurus longicarpus*. Biol Bull 168: 75–90.

Brown KM (1992) Site specific constraints on shell selection behavior in the hermit crab, *Clibanarius vittatus*. Mar Behav Physiol 21: 239–254.

Childress JR (1972) Behavioral ecology and fitness theory in a tropical hermit crab. Ecology 53: 960–964.

Cote IM, Reeverdy B, Cooke PK (1998) Less choosy or different preference? Impact of hypoxia on hermit crab shell assessment and selection. Anim Behav 56: 867–873.

Hahn DR (1998) Hermit crab shell use patterns: response to previous shell experience and to water flow. J Exp Mar Biol Ecol 228: 35–51.

Imafuku M (1983) New shell acquisition in the hermit crab, *Pagurus geminus*. J Ethol 1: 91–100.

Imafuku M (1984) Quality of shell occupied by hermit crab *Pagurus geminus*: how many hermit crabs are satisfied with their shells? J Ethol 2: 31–36.

Imafuku M (1985) Shell exchange of the hermit crab *Pagurus geminus*. Nanki Seibutu 27: 70–74.

Imazu M, Asakura A (1994) Distribution, reproduction and shell utilization patterns in three species of intertidal hermit crabs on a rocky shore on the Pacific coast of Japan. J Exp Mar Biol Ecol 184: 41–65.

Mima A, Wada S, Goshima S (2003) Antipredator defense of the hermit crab *Pagurus filholi* induced by predatory crabs. Oikos 102: 104–110.

Mori Sita M (1959) Measuring of interspecific association and similarity between communities. Memoirs of the Faculty of Science Kyushu University Series, E3: 65–80.

Oba T, Goshima S (2004) Temporal and spatial settlement patterns of sympatric hermit crabs and the influence of shell resource availability. Mar Biol 144: 871–879.

Ohmori H, Wada S, Goshima S, Nakao S (1995) Effects of body size and shell availability on the shell utilization pattern of the hermit crab *Pagurus filholi* (Anomura: Paguridae). Crustaceana 65: 13–24.

Reese ES (1968) Shell use: an adaptation for emigration from the sea by the coconut crab. Science 161: 385–386.

Turra A, Leite FPP (2001) Shell utilization patterns of a tropical rocky intertidal hermit crab assemblage: I. The case of Grande Beach. J Crust Biol 21: 393–406.

Vance RR (1972a) Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. Ecology 53: 1062–1074.

Vance RR (1972b) The role of shell adequacy in behavioral interactions involving hermit crabs. Ecology 53: 1075–1083.

Wada S, Mima A, Ito A (2005) Reproductive phenology of sympatric hermit crabs in temperate Japan. J Mar Biol Ass UK 85: 889–894.

Zisper E, Vermeij GJ (1978) Crushing behavior of tropical and temperate crabs. J Exp Mar Biol Ecol 31: 155–172.