論文の内容の要旨

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論文題目 Study on the ecological niches of abalone (*Haliotis* spp.) using stable isotope analyses
（安定同位体比を用いたアワビ類の生態的地位に関する研究）

1. Introduction

Abalone (*Haliotis* spp.) is one of the major members in subtidal rocky shore ecosystems and has been heavily harvested as a commercially important fishery resource in Japan. Declines in the abalone natural stocks, mainly due to the long time overfishing, have provoked the fisheries authorities to introduce hatchery-reared juveniles to the wild. This reseeding has been conducted for major abalone species on a commercial scale in Japan since the 1980s. However, the potential impacts of such long-term, large-scale harvesting and reseedings of abalone on subtidal rocky shore ecosystems have not been well studied. Despite the lasting reseedings, the abalone production has been declined since the late 1960s, which is mainly due to very low natural recruitment. Recent studies indicated the low natural recruitment could be caused by ecological problems, such as the decline of adult abalone population and high mortality of post-larvae. Especially, post-larval starvation was suggested to be one of the major causes for the low recruitment, which may be induced by the inter-specific competition for food sources with the other herbivorous gastropods. The previous laboratory studies on feeding and growth of post-larval abalone, *H. discus hannai* and *H. diversicolor*, have suggested three feeding transitions during the early growth stages. The inter-specific competition for food sources could be growth-dependent and critical in the abalone habitats. However, studies on ecological niches of abalone species including feeding habits in their natural habitats are very limited and the inter-specific relationships between abalone and other benthic organisms are left unsolved, which are important fundamental information to understand the natural recruitment mechanism of each abalone species.

Stable isotope analyses have increasingly been used to identify sources of dietary organic matter, which can be used for abalone species. Animals that show similar carbon and nitrogen stable isotope ratios are assumed to have similar food sources given that these sources are isotopically distinct. Thus, comparing $\delta^{13}C$ and $\delta^{15}N$ values may provide clues to analyses of food sources and inter-specific relationships among coexisting species in a habitat.

I examined the abundance of benthic organisms and the species composition of two latitudinally separate habitats, Tomarihama coast, Oshika Peninsula in Miyagi and Nagai coast, Miura Peninsula in Kanagawa as northern and southern habitat of abalone, respectively. *Haliotis discus hannai* is the only abalone species found at Tomarihama and four species, *H. gigantea*, *H. discus discu*s, *H. madaka* and *H. diversicolor*, inhabit Nagai coast. Stable isotope analyses were carried out to examine the major food sources of the abalone species and to identify the trophic structures of organisms inhabiting the areas.

2. Ontogenetic change in feeding habits of *H. discus hannai* and *H. diversicolor*

Feeding experiments at seven growth stages from post-larvae to juveniles of *H. discus hannai* (1, 1.5, 8, 12, 22, 27 and 35 mm in initial mean shell length, respectively) were performed to test the applicability of stable isotope analyses to study abalone feeding ecology, and find the nearest isotopic fractionation values. Benthic diatoms, macroalgal gametophyte, dried macroalgae and formulated pellets were used as food sources for each growth stage of abalone. The carbon stable isotope ratios of each food source were well differentiated with a little overlaps: dried macroalgae (-12.8 ± 2.0 ‰), benthic diatoms (-14.2 ± 1.4 ‰), formulated pellets (-21.8 ± 0.2 ‰) and macroalgal gametophyte (-31.4 ± 1.3 ‰) in enriched order. Post-larvae (SL < 2 mm), fed on diatoms or macroalgal gametophyte, showed carbon isotopic values close to their food sources after two weeks of feeding. Juveniles (5-12 mm SL) approached to the carbon isotopic value of formulated pellets after six weeks of feeding. The diet effect and the post-larval feeding transition from diatom to macroalgal gametophyte were clearly revealed by stable isotope analyses, though the fractionation values during the current experiments were different among food types.

From these feeding experiments, the diet-tissue fractionation values for various growth stages of abalone were estimated to be 1.7 ‰ and 2.9 ‰ for post-larvae (SL < 2mm) fed on benthic diatoms, 2.4 ‰ and 2.5 ‰ for juveniles (5.11-12.27 mm mean SL) fed on formulated pellets, and 3.0 ‰ and 2.5 ‰ for juveniles (7.29-17.74 mm mean SL) fed on formulated pellets, for mean $\delta^{13}C$ and mean $\delta^{15}N$, respectively. These results were considered to be bases for investigating the following feeding habits of abalone species in natural habitats.

The various growth stages of *H. discus hannai* and *H. diversicolor* were sampled from each coastal habitat to investigate the ontogenetic shift of feeding habits. In *H. discus hannai*, the carbon isotope ratio declined in the early juvenile stage from -16 ‰ (4 mm SL) to -20 ‰ (8 mm SL), indicating the diet change from benthic diatoms to juvenile macroalgae. After that, the carbon isotope ratios increased to about -17 ‰, suggesting the feeding transition from juvenile to adult macroalgae. In *H. diversicolor*, the first carbon isotopic change from -11.5 ‰ (4 mm SL) to -14.5 ‰ (9.6 mm SL) was revealed and then the following increase continued until about -11 ‰, suggesting the very similar dietary transitions to *H. discus hannai*. The similarity in feeding transitions among these two taxonomically far abalone species suggests other southern large abalone juveniles would have the similar feeding transition. However, due to a small number of juvenile samples, the ontogenetic shifts in feeding habits could not be detected for the large abalone species found at Nagai coast.

3. Community and trophic structures in the habitat of northern abalone *H. discus hannai*

The field samplings were conducted in July and December 2006 at Tomarihama coast, Oshika Peninsula. The sampling area was divided into 3 different vegetations within 100 m from land, from the shallowest *Sargassum yezoense* dominant area (Sy, < 1.5 m depth), *Eisenia bicyclis* dominant area (Eb, about 3 m depth) and then to the deepest crustose coralline algae dominant area (CCA, about 6m depth). Abalone was mainly collected from both Eb and CCA areas. Turban shells, *Omphalius rusticus* and *Chlorostoma lischkei*, and sea urchins, *Strongylocentrotus nudus* and *S. intermedius* were recognized as abundant species in Eb and CCA areas.

From stable isotope analyses, adult laminarian macroalgae showed -18 ‰ to -16 ‰ of δ^{13}C, while juvenile macroalgae did -23 ‰ to -21 ‰. *Sargassum* has very broad range of δ^{13}C, -21 ‰ to -16 ‰. Epilithic microalgae showed similar δ^{13}C values to laminarian macroalgae, but could be distinguished with relatively high δ^{15}N. The values of δ^{15}N indicated that epilithic microalgae were most likely food for juvenile abalone (4− 10 mm SL), while laminarian macroalgae for adults (SL > 55 mm). Trophic level indicated by δ^{15}N revealed that starfishes, *Asterina pectinifera* and *Aphelasterias japonica*, were dominant predators in all areas. Several gastropods as well as crabs were also recognized as predators: *Calliostoma unicum*, *C. multiliratum*, *Neptunea arthritica* and *Thais bronni*. Sea cucumber and amphipods were suggested to be competitors for foods, mainly against adult abalone (55− 98 mm SL), while chitons and limpets were considered to be much important competitors to juvenile abalone (4 mm − 25 mm SL). Several small gastropods including *Homalopoma* spp. appeared to be more important as competitors for food with post-larval and juvenile abalone (SL < 4 mm) in CCA area.

4. Community and trophic structures in the habitat of southern small abalone *H. diversicolor*.

The community and trophic structures of the abalone *H. diversicolor* were examined by collecting various species of animals and plants in *H. diversicolor* habitat (1− 5 m depth) and analyzing and comparing stable isotope ratios of the collected samples. The overall continuum of stable isotope ratios was structured into three different trophic linkages: brown algae- and red algae-dependent benthic food chains and a planktonic food chain. Brown algae and red algae are likely to play different roles with respect to carbon sources in the habitat. Conventional fractionation values indicated that the abalone *H. diversicolor* (10-65.6 mm SL; mean δ^{13}C =

-12.4 ‰ and mean δ ^{15}N = 9.3 ‰) mainly feeds on the lamina of a brown alga *Undaria pinnatifida* (mean δ ^{13}C = -13.5 ‰; mean δ ^{15}N = 6.7 ‰), while in the earlier growth stages (SL < 10 mm) they were suggested to have ontogenetic dietary shift from benthic diatoms (SL < 4 mm) to juvenile macroalgae (SL < 10 mm). Stable isotope ratios suggested that the juveniles of other abalone species as well as some amphipods and a sea cucumber species are competitors of *H. diversicolor*, whereas some Muricidae gastropods such as *T. bronni* and *E. contractus* are predators.

5. Community and trophic structures in the habitat of southern large abalone species

The habitats of southern abalone species, *H. gigantea*, *H. discus discus* and *H. madaka* were investigated in 2005 and 2006 at Nagai coast, Miura Peninsula. *H. gigantea* were most abundant among three species during the samplings. The competitors for diets of southern large abalones could not be fully investigated during the early growth stages due to the shortage of samples, but several juvenile samples (SL < 20 mm) showed very similar stable isotope values to *H. diversicolor* juveniles, suggesting diatom-diet and dietary competition with juvenile *O. pfeifferi pfeifferi* as well as amphipods and sea cucumbers. Several Muricidae gastropods were shown to be possible predator species for abalone post-larvae and juveniles. A Muricidae gastropod *Ergalatax contractus* was the most abundant species, which occupied more than 30% (17 ind/m^2) against total abundance of all samples, suggesting very high predation pressures for post-larval and juvenile abalone.

6. Discussion and Conclusion

The dietary assimilation and the dietary shift during the early growth stages of abalone were revealed for the first time by stable isotope analyses in the present study. The isotopic shift during fast-growing post-larval (SL < 2 mm) to early juvenile stages (SL < 20 mm) were proved from experimental results and were able to be applied to the field samples, showing dietary shift from benthic diatoms to juvenile macroalgae. Between juvenile and adult stages (SL > 25 mm), another significant isotopic change was observed, which indicated the dietary change from juvenile to mature macroalgae. These shifts in major diet during the life cycle of abalone may lead to the habitat change, and subsequent changes in dietary competition and predator-prey relations, indicating different ecological niches depending on growth stages.

In the northern habitat, a large population of small gastropods such as *Homalopoma amussitatum* and *H. sangarense* had severe dietary competition pressure on post-larval and juvenile *H. discus hannai.* In contrast, in the habitat of southern large abalones, both carnivorous gastropods and starfishes were dominant to produce overwhelming predatory pressure on juvenile and adult abalone. In the shallow habitat of *H. diversicolor* with relatively good reproductive production in natural population, many herbivorous organisms such as abundant turban shells and sea urchins, occupied exclusive quantity of biomass against total community. However, the stable isotope results did not show any clear evidence that these abundant herbivorous organisms could be dietary competitors to *H. diversicolor*. When the topological complexity and floral diversity of the shallow habitat were considered together, the low level of dietary competition during the life cycle could be one of the reasons to explain the relatively good status of *H. diversicolor* population in the southern shallow habitat.