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Contribution of different functional groups to the diet of major predatory fishes at a seagrass meadow in northeastern Japan

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Abstract

We examined the variation in habitat use and diet of three dominant fish species (*Myoxocephalus brandti*, *Pholidapus dybowskii*, and *Pholis crassispina*) in a seagrass meadow in the Akkeshi-ko estuary in northeastern Japan, where broad and dense *Zostera marina* beds exist, using a semi-quantitative census of the fishes and analyses of their stomach contents. Differences among the three fish species in the temporal variation in abundance of each age class (mainly 1- and 2-year age classes) indicated that the temporal pattern of utilization of the seagrass meadow were different among them. In the semi-quantitative dietary analysis, two prey categories i.e., taxonomic group (order and suborder) and functional group, were used to explain the variation in prey composition with size-dependent changes. The six prey functional groups were classified based on the ecological traits of the prey, i.e., trophic level, size, and life type (habitat and behavior). Ontogenetic shifts in prey of the three fish species could be fully explained by a combination of the two prey categories, and not by the use of only-one category (taxonomic or functional group). The pattern of ontogenetic shifts in prey differed among the fish species and size (age) classes. These results indicate that segregation of habitat (seagrass meadow) and prey group (taxonomic and functional group) is performed among the three species, which may contribute to their coexistence in this estuary.

Keywords Fish · Habitat use · functional group · Predator-prey interactions · seagrass · multicategory logit model

1. Introduction

Seagrass meadows are the most diverse and productive habitats in coastal ecosystems (Hemminga and Duarte, 2000; Larkum et al., 2006) and are utilized as residence and/or transient areas by various higher-trophic-level consumers. Predatory fishes are abundant in seagrass meadows, and they affect the abundance and biomass of herbivore assemblages (Kikuchi, 1974; Bell and Pollard, 1989; Gillamders, 2006; Horinouchi, 2007; Hori et al., 2009). The prey species for these fish comprise a variety of animals with different morphologies, habitats, and life type that are closely related to seagrass vegetation (Orth et al., 1984; Jernakoff et al., 1996). The macrofaunal community, which is the most important prey (e.g., Edgar and Shaw, 1995; Gillamders, 2006), can be subdivided into "*functional groups*" according to behavioral and morphological traits such as feeding mode, mobility type, and degree of association with the seagrass vegetation (Boström et al., 2006; Yamada et al., 2007a; Halpern and Floeter, 2008) as a unit of diversity in the upper tier of species diversity (Hooper et al., 2005). Such "*functional groups*" of prey species may explain the different prey preferences of major predatory fishes, which cause differences in habitat selection resulting to facilitate their coexistence in a seagrass meadow (Bell and Westoby, 1986; Connolly, 1994; Hindell et al., 2000; Horinouchi and Sano, 2001).

In order to explain how a prey macrofaunal community is utilized by different predatory fish, the prey composition of various fish species has been evaluated by quantitative and/or semi-quantitative dietary analysis (e.g., Platell et al., 1998; Linke et al., 2001; Platell and Potter, 2001). All the studies classify prey according to higher taxonomic information (e.g., order and suborder) alone because of the difficulty of identification into species level of prey in the stomachs and the lack of knowledge on

occurrence patterns of macrofaunal species in the study area. Thus, it should be assumed in such studies that species in a higher-taxonomic group are more or less similar to prey functional traits (e.g., prey cost and benefit for fish feeding). However, variation in taxonomic diversity might not necessarily correspond to variation in prey functional diversity (traits) in an ecosystem because adaptive divergence and convergence are in conflict with this premise (Hooper et al., 2005; MacGill et al., 2006; Yamada, 2008). It is expected that prey utilization by predatory fishes can be better explained if prey communities are classified according to their ecological traits closely related to their functional traits (e.g., size, trophic level, habitat, and life type), i.e., "*functional group*" rather than taxonomic groups (Greene, 1985; DeWitt and Langerhans, 2003; MacArthur and Hyndes, 2006; Petchey and Gaston, 2006; Boström et al., 2006; Wright et al., 2006; Halpern and Floeter, 2008).

Three fish species, *Myoxocephalus brandti* (Steindachner, 1867), *Pholidapus dybowskii* (Steindachner, 1880), and *Pholis crassispina* (Temminck and Schelegel, 1845), commonly occur in the seagrass meadows of the northwestern subarctic Pacific regions, which are characterized by semi-enclosed embayments such as lagoons and estuaries (Sato, 1940; Shiogaki, 1981; 1984; Yasu, 1985; Matsuura et al., 1993; Panchenko, 2000; Panchenko and Vdovin, 2005). Predatory fishes in the Akkeshi-ko estuary, including the three above-mentioned species, are known to feed on a wide array of invertebrate macrofauna (Watanabe et al., 1996; Hori, 2006). It has been clarified that the distribution of macrofaunal assemblages in the estuary varied greatly with regard to functional groups (Yamada et al., 2007a). It is thus expected that habitat use of these three fishes associated with seagrass beds and foraging behavior related to the preference of prey species may also differ among the three predatory fish species.

In the present study, we first evaluate the differences in habitat use (seagrass meadow) among three dominant fish species and among size classes (age classes) in the Akkeshi-ko estuary, northeast Japan, where extensive seagrass meadows have developed. Second, we evaluate size-dependent changes in prey composition in order to explain its variation. In this study, prey composition was compared between two subdivided diversity categories, i.e., taxonomic group and functional group classified according to prey functional traits (Boström et al., 2006; Yamada et al., 2007a; Halpern and Floeter, 2008; Hori et al., 2009) in order to assess appropriate diversity categories in accounting for the variation in prey composition. Further, from aspect of these results, i.e., habitat and prey group differences (taxonomic and/or functional group) among fish species and size classes (age classes), we explore the mechanisms of the coexistence of three fish species in this estuary.

2. Materials and methods

2.1. Study area

The Akkeshi-ko estuary is located in the eastern part of Hokkaido, north Japan, and belongs to the cold temperate zone. It is connected to Akkeshi Bay by a narrow channel (*ca.* 500 m wide) (Fig. 1). The southern part of Akkeshi Bay opens out into the Pacific Ocean. The surface area of the estuary is 32 km^2. The depth of the water in most parts of the Akkeshi-ko estuary is between 0.8 and 1.7 m, and the maximum water depth is 10 m near the channel (Hasegawa et al., 2007; Yamada et al., 2007a, b). Water flow in the estuary is driven mainly by tide and wind (Hasegawa et al., 2008). The spring-tide range is 1.2 m and the neap-tide range is 0.9 m. The range of the monthly average and maximum of wind speed was *ca.* 2-5 m s^{-1} and 12 m s^{-1}, respectively (Hasegawa et al.,

2008). Wind speeds were commonly higher in autumn (September-November) than in spring-summer (April-August). Three rivers (Bekanbeushi, Tokitai, and Tobai) flow into the estuary. The Bekanbeushi river has the largest catchment area, accounting for 98.8% of the total amount of inflow to the Akkeshi-ko estuary. Most parts of the estuary are usually frozen over from late December to early March. A major part of the Akkeshi-ko estuary is covered with two species of *Zostera* seagrasses: *Z. marina* covers a wide range of subtidal area and *Z. japonica* occurs at the intertidal zones of the estuary, except for the unvegetated bottoms of the channel (deepest area in the Akkeshi-ko estuary: mean 5.4 m, Yamada et al., 2007a).

In the present study, four vegetated stations were established for the collection of 3 fish species in the Akkeshi-ko estuary (Fig. 1). At Stn. A, a few patches of *Z. marina* (1–4 shoots/patch) were commonly seen on the muddy bottom (Mukai 2006; K. Yamada and N. Hasegawa, personal observation) near the mouth of the Bekanbeushi river (with a depth of 0.8 m). Stns. B, C, and D were located in *Z. marina* beds near the river mouth (Stn. B, 0.9 m deep), in the center (Stn. C, 1.5 m), and in the southern part of the estuary (Stn. D, 1.1 m). The variation in biotic and abiotic factors (salinity, water temperature, rainfall, and shoot density, leaf height, leaf width and seagrass growth) at each site in sampling terms were summarized by Yamada et al. (2007b) and Tanaka et al. (2008).

In the Akkeshi-ko estuary, total of 32 fish species occur in the fish community (Watanabe et al., 1996; Hori, 2006). Among the 32 species, 10 species are considered resident and 22 species are considered migrant (Watanabe et al., 1996; Hori, 2006). The three fish species focused on in this study has been considered larger-size resident species (Watanabe et al., 1996). *M. brandti* is the most dominant and commercial species, and was thus represented as the principal predator in this estuarine system (Hori,

2006). The other two species (*P. dybowskii* and *P. crassispina*) are recognized as subdominant species (Watanabe et al., 1996).

Juveniles of all three species were *ca.* <20 mm and lived in the shallow areas (< 10 m). All fishes commonly mature in 2 years (2-year age class, *ca.* 50-100 mm) (Shiogaki, 1981, 1984; Yasu, 1985; Panchenko and Vdovin, 2005). The life span of *P. dybowskii* is *ca.* 2 years, while that of *P. crassispina* is longer and that of *M. brandti* is the longest (maximum 12 years, Panchenko and Vdovin, 2005). *P. dybowskii* has been considered as resident species in seagrass and/or seaweed throughout its life (Shiogaki, 1981; 1984; Yasu, 1985), while habitat preference and migration patterns of young immature and adult *M. brandti* and *P. crassispina* have not yet been well understood.

2.2. Sampling procedure

The abundance and population size distribution of the three fish species were analyzed by semi-quantitative sampling in June, September and November 2004 since environmental variation, seagrass vegetation (i.e., morphology and growth), and community structure of the macrofauna typically change significantly among the season (Hasegawa et al., 2007; Yamada et al., 2007a; Tanaka et al., 2008). We also attempted a fourth census in February 2005 but could not carry it out because the estuary was covered with ice. Three replicated samples were collected using an epibenthic sledge (height, 40 cm; width, 60 cm; and mesh size, 500 μm) at each sampling occasion and at each site. Fish sampling using the epibenthic sledge has occasionally been conducted and is recognized as the semi-quantitative. Therefore, fish density results in this study may possibly be underestimated. The sledge was towed horizontally for a distance of 40 m. The actual distance of each tow was measured using a GPS plotter (JLU-128, JRC).

Sampling was performed at mid-tide during the day in order to minimize the effect of tidal flow. Total body length (*TBL*) of all captured fish was measured to the nearest millimeter. Large fish (approximately >120 mm in *TBL*) were immediately eviscerated onboard the ship, whereas samples of the smaller fish were preserved in 10% formalin in seawater.

Because use of the epibenthic sledge makes it particularly difficult to capture larger-sized individuals, we also conducted a supplementary sampling using a box drop-trap (height, 20 cm; width, 45 cm; length, 60 cm) with more than three replicas at each study site in each sampling term for dietary content analysis using.

2.3. Dietary contents

The variation in prey composition among size classes of each species was observed via stomach content analysis. Stomach contents were examined in the laboratory under a dissecting microscope using reflected light. Each dietary item was identified to the lowest possible taxon. The percentage frequency of the occurrence of each dietary category was expressed as the percentage volume of the stomach content (%*V*) using a points method (Hynes, 1950; Hyslop, 1980; Linke et al., 2001; Platell and Potter, 2001).

Lengths of the prey individuals (mm) were measured using a graticule in the microscope eyepiece. Prey length for gastropods was calculated as shell height. The *TBL* of prey fishes and carapace length of decapods in stomachs were measured when intact; in case where fishes had been largely digested (e.g., seen only bonelike), the length of the missing sections were visually estimated. In cases of damaged macrofaunal individuals, the size of the original animal was estimated on the basis of

1 the fragments. The *TBL*s of some dominant prey species were measured from the length
2 of body parts. The *TBL* of the mysid *Neomysis* spp. was calculated from the telson
3 length using the regressions of Yamada et al. (2007b). The total length of the shrimp and
4 other mysid species (*Acanthomysis shrenckii*) was calculated from the regressions
5 between *CL* (carapace length) and *TBL* as follows. *Pandalopsis pacifica*: $TBL = 2.962\ CL + 13.293$ ($R^2 = 0.868$, $N = 113$), *Crangon* sp.: $TBL = 4.095\ CL + 4.798$ ($R^2 = 0.965$,
6 $N = 42$), and *A. shrenckii*: $Telson\ L = 0.163\ TBL + 0.0556$ ($R^2 = 0.653$, $N = 117$)
7 (Yamada 2008).
8
9
10 *2.4. Prey-faunal grouping*
11 A variety of techniques have been recently developed to classify species into
12 functional groups based on ecological traits (reviewed in Petchey and Gaston, 2006).
13 Although functional groups should ideally be defined post-hoc using experimental
14 manipulations to describe the true functional role of each species (Wright et al., 2006;
15 Halpern and Floeter, 2008), such techniques are not realistically possible for all prey
16 faunal species, and the dominant functions (functional traits) of almost all prey species
17 (especially, small-sized prey macrofauna) are not well understood. Therefore, we
18 conducted functional classification by the common *priori* method based on differences
19 of several species-traits (Wright et al., 2006; Bonström et al., 2006; Yamada et al.,
20 2007a; Halpern and Floeter, 2008; Hori et al., 2009).
21 In order to examine the variation in prey composition, prey species and taxon
22 were assigned hieratically to each functional group based on three traits, trophic level,
23 size, and habitat. Differences of these ecological traits of the prey directly coordinated
24 with prey functional traits including nutritional value and capture effort. Therefore, if a

fish species feeds on specific prey group(s), its feeding strategy is also fundamentally different from the other fish species.

For classification into prey functional group, the identified prey species were first classified into tow groups (primary producers and consumers) according to trophic level. Primary producers, consisting of plant materials and prototroph such as seagrasses, algae (macrophytes and microphytes) and epiphytes, were defined as a prey functional group, the *primary-producers* group (*PP*). Second, prey consumers were classified into three size-groups based on results of average size (see also results in Table 1), minimal-size prey fauna (0.1 < 1 mm mesh), macrofauna (1 < 20 mm mesh), and megafauna (> 20 mm mesh). Minimal-size prey fauna included meiofauna (e.g., Calanoida) and microfauna (e.g., juveniles of *Ruditapes philippinarum* and *Munna* spp.). Prey functional traits (e.g., low nutritional value of an individual with less capture effort) may be similar among species in this faunal group; therefore, this group was defined as a prey functional group, i.e., the *minimal-fauna* group (*MF*). Megafauna consisted of shrimp and pisces. To feed on these large-size megafauna, fish commonly have larger gape size, and particular ability (i.e., function) for capture and ingestion. Therefore, we defined this group as a prey functional group, i.e., the *large-faunal* group (*LF*).

Prey macrofauna, which have been considered as main prey (Watanabe et al., 1995; Hori, 2006), were further classified into three groups based on their life type (e.g., behavior and mobile type) and habitat requirement, such as the degree of association with seagrass and benthic substrates. The first macrofaunal group was the *seagrass-associated* group (*SA*), which consisted of epifauna that were firmly attached to seagrass substrates. The second macrofaunal group was the *benthic-faunal* group

(*BF*), which was comprised of fauna that were firmly attached to benthic substrates. Mobility categories of the macrofaunal species included mobile, semi-mobile, or sessile. Species belonging to the *SA* and *BF* groups were either sessile or semi-mobile type (Bonström et al., 2006), while the other species of macrofauna were mobile. These species rarely attach themselves to seagrass blades and benthic substrates, and were continuously moving in water columns, like "*drift*" (Yamada et al., 2007a). Therefore, such continuous-motile species were classified as the *drift-faunal* group (*DF*) (Yamada et al., 2007a; Yamada, 2008). These macrofaunal classifications were made based on the literature and laboratory experiments summarized in Yamada et al. (2007a). For example, all mysid species were classified into the *DF* group according to references (Mauchline, 1980; Sawamura, 2000; Yamada et al., 2007a). All gammarid species were categorized according to Sawamura (2000), who investigated the microhabitat and feeding type of all faunal species captured from a surfgrass (*Phyllospadix iwatensis*) bed in northwestern Japan. Sawamura (2000) categorized the gammarid species (*ca.* 100 species) into 11 groups (borer, commensal, epi-infaunal, epifaunal, infaunal, interstitial, pelagic, phreatic, periphytic, living in streams, and terrestrial). In this study, four species belonged to the infaunal group described by Sawamura (2000), and *Corophium acherusicum* that have been reported empirically as firmly attached to benthic substrates (Yamada et al., 2007a) were classified into the *BF* group. Unidentifiable materials such as fragments of crustaceans and sediments in the stomach were not used in the analyses.

2.5. Data analyses

In order to detect differences of temporal habitat-utilization of the seagrass meadow among the three fish species, spatial and temporal variations in the density of

the three fish species (log transformed) were evaluated using two-way analysis of variance (ANOVA). When a significant difference of main effects was detected, Tukey's test was used to test for significant mean differences.

Age class structures of the three fish species were also evaluated to detect which age class primarily utilized the seagrass meadow as its habitat. Size-frequency histograms of the three fish species to evaluate year-class strength and life histories were constructed using the pooled data (standardized for density). The number of cohorts of the three species was estimated from these size-frequency histograms. Parameters in the three fish species such as growth rates in previous reports were also taken into account for cohort number estimation (Shiogaki 1981, 1984; Yasu, 1985; Panchenko, 2000; Panchenko and Vdovin, 2005).

In order to examine size-dependent changes in prey composition, a multicategory logit model and/or logistic regression model (Agresti, 2002) was applied to the prey volumes (*V*%) that were classified into taxonomic groups and functional groups. The response variable of the logit model had several possible categories (taxonomic group: 1 = Mysidacea, 2 = Gammaridea, 3 = Isopoda, 4 = Caprellidea, 5 = Gastropods, 6 = errant Polychaeta, 7 = Bivalves, 8 = Cumacea, 9 = Calanoida, 10 = Nematoda, 11 = Decapoda, 12 = Pisces, 13 = Seagrass, 14 = Algae, 15 = Epiphyte, and functional group; 1 = *SA*, 2 = *DF*, 3 = *BF*, 4 = *MF*, 5 = *LF*, 6 = *PP*). In the logit model, the probability that falls into the diet category i was denoted by $\pi_i(x)$. The 15^{th} and 6^{th} response variable class (epiphyte for taxonomic group and *PP* for functional group, respectively) was used as the base-line category. The logit model was expressed as follows:

$$\log\left(\frac{\pi_i(x)}{\pi_{15or6}(x)}\right) = \alpha_j + \beta_j x$$

where x is the *TLB* of the fish, α_j is an intercept terms, and vector β_j is a coefficient of the explaining factor. The number of response variables differed among the fish species (i.e., six for *M. brandti* and five for *P. dybowskii* and *P. crassispina* in the functional group) because species belonging to the *LA* groups (shrimp and pisces) were found only in the diet of *M. brandti*. Some taxonomic groups whose prey volumes were zero or quiet low (<0.3%) were excluded from this analysis.

Differences in deviances were used to test the significance of the independent variable (*TBL*). The parameter significance of the model (β_j for each prey group) was tested using Wald's test, which is based on the confidence limits of the odds ratio (odds ratio = $e^{parameter\ estimate}$). An odds ratio of 1 indicates no effect. If the odds ratio was significantly higher or lower than 1 (tested if the 95% confidence interval of the odds ratio was 1), the proportion of the corresponding response variable class increases (decreases) with the *TBL* compared to the proportion of the reference class (epiphyte and *PP* group). Wald's statistics were also estimated to test the significance of the independent variable (*TBL*).

3. Results

3.1. Seasonal variation in fish abundance and size distribution

A total of 351 individuals (inds.) were captured using the epibenthic sledge. The mean abundance was 0.65 inds. m^{-2} (± 1.12 SD) for *M. brandti*, 0.42 inds. m^{-2} (± 0.89 SD) for *P. dybowskii*, and 0.18 inds. m^{-2} (± 0.53 SD) for *P. crassispina* (Fig. 2). The highest density was observed at Stn. B in November for *M. brandti* and *P. dybowskii*

and at Stn. B in September for *P. crassispina.* Higher density was also observed at Stn. C in September for *M. brandti* and at Stn. C in November for *P. dybowskii.* No *P. crassispina* individuals were captured by the sledge net or by reiterant box trap samplings in November. The temporal and spatial variation in abundance and interaction between month and site were significant for the density of *M. brandti* (Month: $F_{2, 24} = 22.627$, $P < 0.001$; Site: $F_{3, 24} = 32.531$, $P < 0.001$; Month × Site; $F_{6, 24} = 11.079$, $P < 0.001$) and *P. dybowskii* (Month: $F_{2, 24} = 27.090$, $P < 0.001$; Site: $F_{3, 24} = 32.944$, $P < 0.001$; Month × Site; $F_{6, 24} = 20.159$, $P < 0.001$). However, only the temporal variation was significant for *P. crassispina* (Month: $F_{2, 24} = 3.784$, $P = 0.037$; Site: $F_{3, 24} = 0.620$, $P = 0.609$; Month × Site; $F_{6, 24} = 0.573$, $P = 0.748$). The density of *P. crassispina* in September was significant higher than that in June (Tukey's test).

Populations of the three fish species in the Akkeshi-ko estuary were mainly in the 1- and 2-year age groups (Fig. 3). Although the peak cohort for *M. brandti* in spring could not be estimated due to the small number of individuals captured, a shift in the peak cohort from 50 mm (September) to 80 mm (November) was recognized, which was considered as the 1-year age group of the spring-born. In September, 2- and >2-year age groups were seen at ca. 100-150 mm and >170 mm, respectively. In November, cohorts for the >1-year age groups were seen at >160 mm, but were not distinguished into age class. For *P. dybowskii*, the peak cohort changed from 30 mm in June to 70 mm in September and 110 mm in November, which was considered as the 1-year age group of the spring-born. Cohorts for the 2-year age group were seen in all sampling months (June, 80-130 mm; September, 130 mm; and November, 140-200 mm). In contrast, no temporal shift in the peak cohort was obvious for *P. crassispina,* although the peak cohort for *P. crassispina* in spring could not be estimated due to the small number of

individuals captured. Two cohorts for the 1-year age group of the spring-born (50–120 mm) and 2-year age groups (130–190 mm) were seen only in September.

3.2. Stomach content analysis

The stomach contents of a total of 371 individuals of three fish species (20 inds. by the box drop-trap) were examined. Among these, the guts of 72 individuals were empty. A total of 2,675 prey fauna were collected from the remaining individuals.

Small crustaceans were the most preferred prey for the three fish species (Table 1). Of the small crustaceans, gammarids and mysids were the major prey for *P. dybowskii* and *P. crassispina*, and *M. brandti* and *P. crassispina*, respectively. Isopoda was also consumed by three fish species in high proportions (5.8-17.2 %). Mollusca were consumed by all three fish species, but contributions of prey were lower (0.2-3.3 %). Polychaeta and Nematoda were consumed by *M. brandti* (1.4 %) and *P. dybowskii* (0.4 %), and *P. crassispina* (< 0.1 %). The prey contribution of Polychaeta and Nematoda was lower than Mollusca. The contribution of plant material (mainly seagrasses, epiphytes, and algae) to the diets of all 3 species was less, but higher than Mollusca, Polychaeta and Nematoda (2.7–6.8 %). Pisces and Decapoda were ingested only by *M. brandti* (7.0 % and 8.9 %, respectively). Although higher proportions of crustacean fragments were seen, these fragments may include body parts of identified species.

Dietary contents of each species changed with size classes (Fig. 4). The *LF* group, i.e., Decapoda and Pisces, were consumed less by the smaller size class (< 40 mm) of *M. brandti*, but was a major part of the diet in the larger size class (< 200 mm) (Fig. 4a and d). In *P. dybowskii*, dietary contents also changed among size classes in

both prey categories, but a clear pattern of dietary change was not evident (Fig. 4b and e). In *P. crassispina*, proportions of the *SA* group, which was consisted of part of species belonging to Gammaridea, Caprellidea, and Isopoda, gradually increased with fish size (Fig. 4c and f). Proportions of diet content in each three species were also different between prey categories, i.e., between taxonomic group and functional group (Fig. 4).

The logit model demonstrated that the proportion of some categories in the taxonomic and functional groups varied significantly with size of the three species (Table 2, 3). Wald's test indicated that the size of each three fish species was a significant factor when determining the response categories. Through taxonomic group categorization (Table 2), the prey variation in *M. brandti* with size-dependant changes was explained by Mysidacea, Gammaridea, Isopoda, Gastoropoda, Decapoda, and Pisces, which were explained > 97 % throughout size class (Fig. 5a) and *P. dybowskii* by Mysidacea, Gammaridea, Isopoda, and Caprellidea (75-85 %, Fig. 5b), and *P. crassispina* by Mysidacea, Gammaridea, and Isopoda (< 86 %, Fig. 5c). Through functional group categorization (Table 3), the prey variation in *M. brandti* was explained by the *SA*, *DF*, and *LF* groups (> 91 %, Fig. 5d), *P. dybowskii* by the *SA*, *BF*, and *MF* groups (> 19 %, Fig. 5e), and *P. crassispina* by the *SA* and *BF* groups (1-94 %, Fig. 5f).

Major prey categorized in the taxonomic and functional groups with size class (age class) changes differed among fish species (Fig. 5). Prey variation for smaller size in *M. brandti* can be explained mainly by both taxonomic (Mysidacea) and functional group (*DF* group) (Fig. 5a and d). On the other hand, functional group categorization could not explain prey composition with size-dependent changes for smaller size of *P.*

dybowskii and *P. crassispina* (Fig. 5e and f), while Mysidacea as a taxonomic group was important prey contribution for smaller sizes of these two fish species (Fig. 5b and c). Larger sizes of *M. brandti* and *P. dybowskii* can be explained by both taxonomic (Pisces and Gammaridea, respectively) (Fig. 5a and b) and functional group (*LF* and *SA* group, respectively) (Fig. 5d and e). On the other hand, taxonomic grouping could not explain prey composition with size-dependent change for smaller size in *P. crassispina* (Fig. 5c), while *SA* and *BF* as functional groups was important prey contribution for larger size in this species (Fig. 5f).

4. Discussion

4.1. Pattern of temporal and spatial utilization of seagrass bed for three fish species

Spatial and temporal occurrences of the three fish species in this study are similar to previous reports in the Akkeshi-ko estuary. For example, a few and large amount of individuals are captured at all sites in spring (April-July) and at the seagrass bed near the river mouth (around Stn. B) in autumn of 1991-1995, respectively (Watanabe et al., 1996), suggesting that spatial and temporal differences of captured individuals by the present method can reflect the temporal and spatial patterns of relative abundance in the Akkeshi-ko estuary.

Occurrence pattern and structure of temporal shift of the peak cohort of 1- age class (immature) and 2-year age class [from immature (young fish) to adult] in *M. brandti* and *P. dybowskii* revealed that these two species occurred at the seagrass bed of the Akkeshi-ko estuary at least from June to November, respectively. They also occur at the estuary in winter (Watanabe et al., 1996; Hori, 2006), suggesting that these species are resident from immature (young fish) to adult in the seagrass meadow throughout the

year. Although *P. dybowskii* is a resident of the seagrass meadow of the estuary for its life (life span is *ca.* 2 years), Adult individuals (> 2 age) of *M. brandti* (maximum life span is 15 years) may possibly migrate between the Akkeshi-ko estuary and outer areas (i.e., Akkeshi Bay) because quite large individuals (>250 mm as more than 3-year age class) have been captured occasionally in the Akkeshi-ko estuary (Watanabe et al., 1996) and the Akkeshi Bay (K. Yamada and M. Hori, personal observation). On the other hand, no *P. crassispina* individuals were captured by sledge net or additional reiterant sampling by box-traps in November. Significant higher density was observed in September, and a temporal shift of the peak cohort of 1-year age group in *P. crassispina* was not obvious. Furthermore, this species does not occur at the Akkeshi-ko estuary in winter (Watanabe et al., 1996; Hori, 2006). These suggest that immature (young fish) and adults of this species occasionally migrate between the Akkeshi-ko estuary and outer areas (Akkeshi Bay). The patterns of temporal utilization of the seagrass meadow of the Akkeshi-ko estuary are thus different among the three fish species. Similar inter-species variation in the temporal shifts in vegetated-estuarine use has been found in other vegetated coastal areas (Kikuchi, 1974; Bell and Westoby, 1986; Connolly, 1994; Horinouchi and Sano, 2001; Horinouchi, 2007). Such differences of temporal utilization of the seagrass meadow among fish species may cause habitat differentiation leading to prey-faunal differentiation, which is one of the coexistence mechanisms in fish communities with high diversity and abundance at seagrass meadow.

4.2. The prey contribution and usefulness of the functional group approach

Although many fish species in seagrass beds are considered to be opportunistic

feeders, most species feed on crustaceans as the dominant prey but are not highly specialized for feeding on a particular species of prey (Bell and Pollard, 1989; Edgar and Shaw, 1995; Platell et al., 1998; Hindell et al., 2000; Linke et al., 2001; Platell and Potter, 2001). In the qualitative results of our dietary analysis, the three dominant fish species consumed mainly crustaceans (>80%) and also fed on other animals such as polychaetes and mollusks, and even seagrass, seaweed, and detritus, all of which are consistent with previous reports.

The results of the logistic model demonstrated that both prey taxonomic and functional groups in the diet of each fish species can explain the variation in prey composition with size-dependent changes. For example, major prey and the prey variation with the size-dependent changes of *M. brandti* can be explained by taxonomic group (> 97%) as well as functional group (> 91%). On the other hand, major prey and the prey variation in smaller size *P. dybowskii* cannot be explained by the functional group alone but can be explained by the taxonomic group (Mysidacea) only. Further, major prey of smaller size and larger size in *P. crassispina* can be explained by taxonomic group (Mysidacea) and functional group (*SA* and *BF* groups), respectively. These results indicate that only one prey-category (taxonomic or functional group) cannot fully explain the prey variation, although previous studies classified prey based on only higher-taxonomic group (Platell et al., 1998; Linke et al., 2001; Platell and Potter, 2001). Trait-based functional categories (Yamada et al., 2007a; Boström et al., 2006; Halpern and Floeter, 2008; Hori et al., 2009) can be regarded as one of the effective indices of diversity to evaluate the prey variation in fish with size-dependent changes. Further, major prey of larger size (i.e., adult) in *P. crassispina* can be explained by only the *SA* group as the prey functional group but not the taxonomic

group, supporting that the prey functional group could be also regarded as effective index for prey variation by selective predation of adult fishes.

Prey functional groups which are classified by the hierarchical assignment of prey species on the basis of several given species-traits (*priori* method) correspond to variation in fish diets and brought an additional perspective in explaining the prey variation among fishes in the seagrass ecosystem. Although a variety of techniques have recently been developed to classify species into functional groups based on substantial ecological traits (Petchey and Gaston, 2006; Wright et al., 2006; Villéger et al., 2008), there may be many cases in which substantial knowledge of ecological traits (which is concerned directly with functions) in order to estimate functional diversity using these techniques has not obtained especially in aquatic fauna. Therefore, experimental studies on measurement of functional diversity based on representative and typical ecological traits concerned directly and/or indirectly with ecological functions are important for progress and generalization of concept of functional diversity in aquatic ecosystems (e.g., Bonström et al., 2006; Yamada et al., 2007a; Halpern and Floeter, 2008; Yamada 2008; Hori et al., 2009).

4.3 Dietary shifts of the fishes

Mysidacea has been known as the most important prey for small carnivorous fish (Mauchline, 1980; Takahashi et al., 1999) because of easy to be caught due to traits of its behavior (remaining stationary on the surface of seagrasses and in the water column) (Machiline, 1980; Yamada, 2008). Therefore, diet of small size fishes with less capture (swimming) ability may depend on Mysidacea. In the present study, Mysidacea was main prey for small size individuals of all three fish species, and their main prey

were shifted to other taxonomic or functional groups as they grow. Such an ontogenetic diet change has been reported for other benthic predatory fish such as *Pseudorhombus jenybsii*, *Glyptocephalus cynoglossus*, *Hippoglossoides platessoides*, *Liparis* sp., *Mallotus villosus*, and *Pleuronectes* spp. (Pepin and Penney, 1997; Schafer et al., 2002).

Main prey of the large size of *P. dybowskii* and *P. crassispina* can be explained by the *SA* group as the prey functional group. This may be concerned with development of capture ability (i.e., selective predation) with size-dependent changes. The *SA* group may be difficult to be found out to feed due to traits of its behavior (inhabit among seagrass leaves) compared with Mysidacea. Moreover, mean size and biomass of an individual in the *SA* group (i.e., nutritional value) are higher than Mysidacea (Yamada, 2008; K. Yamada, personal observation). These support that the *SA* group, with its high nutritional value, could be fed selectively by large size fishes with higher capture (swimming) ability than small size fish.

Further, main prey of the large size of *P. crassispina* can be explained by only the *SA* group, whereas that of *P. dybowskii* by the *SA* group as well as Gammaridea. This may be concerned with differences of foraging behavior between adults of the two species. *P. dybowskii* is known as a slow swimmer and bottom-oriented species (Shiogaki, 1981, 1984; K. Yamada and M. Hori, personal observation). In contrast, *P. crassispina* shows ambush behavior and can swim quite rapidly to capture prey (Shiogaki 1981, 1984; Yasu, 1985; K. Yamada and M. Hori, personal observation). This supports that *P. crassispina*, with its higher capture (swimming) ability, performs more selective predation in macrofaunal species living among seagrass leaves (*SA* group), while prey selection of *P. dybowskii* would be more opportunistic compared with *P. crassispina*. Differences of foraging behavior between *P. dybowskii* and *P. crassispina*

may cause different selection of prey groups as well as micro-habitat differentiation, which contribute to food segregation within prey functional group (*SA* group) for their coexistence.

The shift in the diet of the major predatory fishes in the estuary would partly be related to the fluctuation of abundance in prey. For example, the abundance of mysidacea as main prey of the larger size fishes decreased in summer and autumn at Stn. B (Yamada et al., 2007a, b), where larger-sized fishes abundantly occur. This decrease in the Mysidacea at Stn. B was mostly due to seasonal migrations of the dominant species in the Mysidacea (*Neomysis* spp.) to the other areas (around Stn. C) from spring to autumn (Yamada et al., 2007b). Changing the major prey group (i.e., selective predation) from Mysidacea to functional groups (e.g., *LF* or *SA* group) may be possibly promoted by such prey decrease of Mysidacea. Moreover, the *SA* group were highly abundant from summer to autumn in this estuary (Yamada et al., 2007a), when most fish grow to large sizes. This may allow a great overlap in resource use between large size *P. dybowskii* and *P. crassispina*.

5. Conclusions

The present study revealed the different patterns of habitat (seagrass meadow) use among the three dominant fish species in a seagrass meadow in the Akkeshi-ko estuary and the size-dependent variation in their prey composition. Prey variation among species and size classes was not fully explained by only one category (taxonomic or functional group), but rather a combination of the taxonomic group and functional group. The ecological traits of both prey fauna and predator species in a seagrass ecosystem, such as morphologies, behaviors, and habitats are closely related to

seagrass vegetation (Edgar and Shaw, 1995; Jernakoff et al., 1996; Yamada et al., 2007b; Hori et al., 2009). Therefore, prey taxonomic- as well as functional-group, which is classified by assigned species according to differences of habitat and life type (pattern of habitat use), is effective to evaluate variation in prey.

In this study, it was detected that inter- as well as intra-specific food segregations at prey taxonomic (e.g., Mysidacea) as well as functional group (e.g., *SA* and *LF* groups) were performed among fish species and among different size classes. Further, differences of selective predation in prey functional groups among larger sized fish species is concerned with differences of pattern of habitat (seagrass meadow) use and forging behavior among three fish species. These indicates that functional group as a prey category can offer a new understanding in coexistence mechanism in fish communities and lead to find out of the role of the seagrass bed as feeding ground for fishes.

The three dominant fish species in seagrass meadow of the Akkeshi-ko estuary had various strategies such as temporal migration, prey group partitioning, and forging and micro-habitat differentiation to avoid overlapping prey taxonomic and functional groups. Such strategies may cause species-specific and age-specific differences in the utilization of the seagrass beds and ontogenetic shift in dietary components. This is one of the reasons for the successful coexistence of these three fish species in the seagrass meadow of the estuary.

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Figure legends

Fig. 1. Study sites at Akkeshi-ko estuary (Stns. A-D). Shaded areas indicate dense vegetation covering the two *Zostera* species. Sparse and patchy *Z. marina* beds are shown near the mouth of the Bekanbeushi river (around Stn. A).

Fig. 2. Spatial and temporal variation in density of the three dominant fish species in the Akkeshi-ko estuary: (a) *Myoxocephalus brandti*, (b) *Pholidapus dybowskii*, and (c) *Pholis crassispina*. Bars indicate SD of 3 replicated samples. Descriptions indicate results of 2-way ANOVA (***, $P < 0.001$; *, $P < 0.05$; and *NS*, non-significant).

Fig. 3. Total body length (*TBL*) frequency distributions of the three fishes, *Myoxocephalus brandti*, *Pholidapus dybowskii*, and *Pholis crassispina*, in the Akkeshi-ko estuary in June, September, and November 2004. *N* indicates the number of individuals measured in length.

Fig. 4. Percentage contribution (by volume) of the higher taxonomic and functional groups in the diet of five size classes with 40-mm interval in three fish species in a seagrass meadow of the Akkeshi-ko estuary. (a)-(c) are the three fish species (*Myoxocephalus brandti*, *Pholidapus dybowskii*, and *Pholis crassispina*) and their prey taxonomic group, and (d)-(f) are the three fish species and their prey functional groups. The prey was classified into 16 taxonomic groups (order and suborder) and 6 functional groups*: primary-producers* group (*PP*),

minimal-faunal group (*MF*), *seagrass-associated* group (*SA*), *drift-faunal* group (*DF*), *benthic-faunal* group (*BF*), and *large-faunal* group (*LF*).

Fig. 5. Size-dependent changes in the proportion of the prey taxonomic and functional groups in the diet for the 3 fish species in a seagrass meadow of Akkeshi-ko estuary. (a)–(c) are the three fish species (*Myoxocephalus brandti*, *Pholidapus dybowskii*, and *Pholis crassispina*) and their prey taxonomic groups, and (d)–(f) are the three fish species and their prey functional groups. Significant prey groups analyzed by a logit model are shown. The prey was classified into 16 taxonomic groups (order and suborder) and 6 functional groups*:* *primary-producers* group (*PP*), *minimal-faunal* group (*MF*), *seagrass-associated* group (*SA*), *drift-faunal* group (*DF*), *benthic-faunal* group (*BF*), and *large-faunal* group (*LF*).

Table 1. Dietary content (in precent volume) of the three fish species (*Myoxocephalus brandti* , *Pholidapus dybowskii* and *Pholis crassispina*) and its mean size (mm) classified by taxonomic group of prey. Empty gut of 72 individuals were excluded from this analysis.

Major taxa and dietary categories	Mean prey size (mm)	Faunal type of prey	Fish species		
			Myoxocephalus brandti	*Pholidapus dybowskii*	*Pholis crassispina*
Small Crustacea (< 20mm mesh)			**81.1**	**91.8**	**95.3**
Gammaridea			**19.2**	**35.8**	**32.6**
* *Ampithoe* spp.	4.8	*SA*	4.9	6.1	8.0
* *Grandidierella* spp.	3.6	*BF*	2.6	3.2	4.3
* *Gammaropsis japonica*	3.8	*BF*	3.9	7.9	1.8
* *Pontogeneia rostrata*	2.3	*DF*	2.7	2.8	3.7
* *Corophium acherusicum*	1.5	*BF*	0.6	1.2	0.6
* *Synchelidium lenorstalum*	3.7	*DF*	0.1	0.1	0.1
* *Metopa* sp.	1.5	*SA*	<0.1	0.1	0.2
* *Allorchestes* sp.	2.6	*SA*	<0.1	0.1	-
* *Pleustes* sp.	1.6	*DF*	0.1	-	-
* *Melita* sp.	3.3	*SA*	0.3	-	0.2
* *Hyale* sp.	2.4	*SA*	-	0.6	0.3
* *Metaphoxus* sp.	3.6	*DF*	-	0.2	0.1
* *Corphium* spp.	3.4	*BF*	-	<0.1	0.8
* *Byblis japonicus*	3.6	*BF*	-	-	0.1
* *Jassa* spp.	9.0	*SA*	-	-	0.1
* *Orchomene* sp.	2.6	*DF*	-	-	<0.1
Fragment of Gammarus			4.0	13.4	12.1
Caprellidea			**0.4**	**8.3**	**12.7**
* *Caprella mutica*	10.5	*SA*	0.3	1.2	8.1
* *Caprella penantis*	4.6	*SA*	<0.1	1.7	0.4
* *Caprella scaura*	5.3	*SA*	0.1	1.9	0.1
* *Caprella polyacantha*	7.2	*SA*	-	0.1	0.5
* *Caprella laeviuscula*	4.7	*SA*	-	0.1	-
* *Caprella bispinosa*	4.8	*SA*	-	-	0.7
Fragment of *Caprella*			<0.1	3.3	2.9
Mysidacea			**48.5**	**24.0**	**34.7**
* *Neomysis awatschensis*	6.5	*DF*	17.8	4.4	17.1
* *Neomysis mirabilis*	10.1	*DF*	16.2	14.6	12.8
* *Neomysis czerniawskii*	8.4	*DF*	0.4	0.1	-
* *Acanthomysis schrencki*	6.0	*DF*	0.2	-	-
* *Exacanthomysis japonica*	9.1	*DF*	-	-	0.3
Fragment of Mysidacea			13.8	4.9	4.5
Isopods			**5.8**	**17.2**	**15.2**
* *Cymodoce japonica*	3.3	*SA*	5.4	14.7	12.0
* *Munna* spp.	0.7	*MF*	0.2	2.0	3.2
* *Paranthura japonica*	5.2	*SA*	0.2	-	-
* *Idotea ochotensis*	5.5	*SA*	-	0.4	-
* **Calanoida**	0.7	*MF*	**0.2**	**6.5**	**<0.1**
* **Cumaceans**	4.1	*BF*	**<0.1**	**<0.1**	**0.2**
Large Crustacea (> 20mm mesh)					
Decapoda			**7.0**	**-**	**-**
* *Crangon* sp.	22.7	*LF*	6.9	-	-
* *Pandalopsis pacifica*	21.6	*LF*	0.2	-	-
Mollusca					
Gastropods			**3.3**	**0.2**	**1.4**
* *Barleeia angustata*	3.1	*SA*	3.1	0.2	1.1
* *Reticunassa spurca*	2.1	*BF*	0.2	-	-
* *Lacuna decorata*	4.6	*SA*	-	-	0.3
* **Bivalves (juveniles of *Ruditapes*)**	0.6	*MF*	**-**	**0.2**	**0.3**
Annelida (Polychaeta)					
* Errant polychaeta	2.1	*DF*	**1.4**	**0.4**	**-**
Nematodes					
* Secernentea	0.8	*MF*	**-**	**-**	**<0.1**
Primary producer group					
Plant material			**4.9**	**6.8**	**2.7**
* Fragment of seagrass	-	*PP*	1.8	1.0	0.8
* Epiphyte	-	*PP*	2.4	5.4	1.5
* Algae	-	*PP*	0.5	0.5	0.4
Seagrass seed	-	-	0.2	-	-
Vertebrate (Pisces)			**8.9**	**-**	**-**
* *Myoxocephalus brandti*	30.3	*LF*	3.6	-	-
* *Chaenogobius mororanus*	22.6	*LF*	0.6	-	-
* *Chaenogobius castaneus*	25.5	*LF*	1.1	-	-
* *Pholidapus dybowskii*	43.7	*LF*	0.3	-	-
* Pleuronectiformes	49.3	*LF*	0.2	-	-
Fragment of Pisces			3.1	-	-
Other materials	-	-			
Sediment	-	-	**<0.1**	**0.1**	**0.3**
Unidentifiable material			**0.3**	**0.4**	**-**
Total number of stomachs			157	93	49

Major taxa are in boldface. Single asterisks (*) denote those dietary categories in subsequent analysis. Dashes denote zero values. Faunal types of prey indicate *SA* ; *seagrass-assciated* species, *DF* ; *drift-faunal* species, *BF* ; *benthic-faunal* species, *MF* ; *minimal-faunal* species and *LF* ; *large-faunal* spisces.

Table 2. Parameter estimates of the logit model. Estimates of the coefficients relating fish size (mm) and percentage (V%) of each prey taxonomic group per reference group (V% of epiphyte) is given with respective standard errors, odds ratios, confidence limits and Wald's statistics. Some taxonomic groups which prey volumes were zero or quiet low volumes (<0.3%, see Table 1) were excluded from this analysis. Significant parameters are denoted by asterisk, ***; P <0.001, **; P < 0.01 and *; P < 0.05.

Outcome	Parameter estimate		*S.E.*		Odds ratio	95% *c.l.* odds ratio		Wald's statistic
	α	β	α	β		Lower	Upper	
Myoxocephalus brandti								
Mysidacea	1.982	-0.0107 ***	0.250	0.0030	0.989	0.984	0.995	12.87
Gammaridea	1.021	-0.0192 ***	0.310	0.0048	0.981	0.972	0.990	16.31
Isopoda	-1.229	0.0089 **	0.303	0.0033	1.009	1.002	1.016	7.34
Caprellidea	-5.112	0.0073	1.379	0.0120	1.007	0.984	1.031	0.36
Gastropoda	1.486	-0.0680 ***	0.944	0.0201	0.934	0.898	0.972	11.51
errant Polychaeta	-4.945	0.0120	1.059	0.0080	1.012	0.996	1.028	2.28
Calanoida	-2.827	-0.0253	1.944	0.0351	0.975	0.910	1.045	0.52
Decapoda	-4.550	0.0492 ***	0.648	0.0057	1.050	1.039	1.062	73.59
Pisces	-5.178	0.0423 ***	0.508	0.0049	1.043	1.033	1.053	75.59
Seagrass	-1.625	-0.0060	0.486	0.0064	0.994	0.981	1.007	0.87
Algae	-4.001	-0.0065	1.517	0.0207	0.994	0.954	1.035	0.10
Pholidapus dybowskii								
Mysidacea	2.237	-0.0100 *	0.399	0.0045	0.990	0.981	0.999	5.00
Gammaridea	0.184	0.0181 ***	0.486	0.0056	1.018	1.007	1.029	10.44
Isopoda	-2.072	0.0202 ***	0.677	0.0059	1.020	1.009	1.032	11.76
Caprellidea	-2.739	0.0182 **	0.579	0.0064	1.018	1.006	1.031	8.00
errant Polychaeta	-4.463	-0.0089	3.287	0.0390	0.991	0.918	1.070	0.05
Calanoida	0.892	-0.0858	3.796	0.0806	0.918	0.784	1.075	1.14
Seagrass	-3.730	0.0148	0.965	0.0087	1.015	0.998	1.032	2.90
Algae	-4.550	0.0097	1.697	0.0157	1.010	0.979	1.041	0.38
Pholis crassispina								
Mysidacea	3.174	-0.0255 ***	0.744	0.0070	0.975	0.961	0.988	13.12
Gammaridea	0.631	-0.0018	0.565	0.0051	0.998	0.988	1.008	0.13
Isopoda	0.695	-0.0197 **	0.646	0.0072	0.981	0.967	0.994	7.49
Caprellidea	-1.203	-0.0166	1.479	0.0169	0.984	0.951	1.017	0.97
Gastropoda	-18.421	0.0884	24.324	0.1437	1.092	0.824	1.448	0.38
Seagrass	-4.042	0.0056	2.492	0.0209	1.006	0.965	1.048	0.07
Algae	-5.912	0.0232	2.917	0.0212	1.023	0.982	1.067	1.19

Table 3. Parameter estimates of the logit model. Estimates of the coefficients relating fish size (mm) and percentage (*V*%) of each prey functional group per reference group (*V*% of *Primary-producers* group) is given with respective standard errors, odds ratios, confidence limits and Wald's statistics. Significant parameters are denoted by asterisk, ***; P <0.001 and **; P < 0.01.

Outcome	Parameter estimate		*S.E.*		Odds ratio	95% *c.l.* odds ratio		Wald's statistic
	α	β	α	β		Lower	Upper	
Myoxocephalus brandti								
Seagrass-associated group (*SA*)	-0.426	0.0087 ***	0.221	0.0028	1.009	1.003	1.014	9.46
Drft-faunal group (*DF*)	1.103	0.0090 **	0.224	0.0031	1.009	1.003	1.015	8.30
Benthic-faunal group (*BF*)	-0.769	-0.0044	0.265	0.0037	0.996	0.988	1.003	1.42
Minimal-faunal group (*MF*)	-4.317	0.0032	0.933	0.0103	1.003	0.983	1.024	0.09
Large-faunal group (*LF*)	-6.395	0.0721 ***	0.634	0.0066	1.075	1.061	1.089	121.05
Pholidapus dybowskii								
Seagrass-associated group (*SA*)	-3.577	0.0541 ***	0.510	0.0057	1.056	1.044	1.067	89.96
Drft-faunal group (*DF*)	0.893	0.0041	0.298	0.0036	1.004	0.997	1.011	1.30
Benthic-faunal group (*BF*)	-0.349	0.0159 ***	0.379	0.0045	1.016	1.007	1.025	12.57
Minimal-faunal group (*MF*)	-3.012	0.0156 **	0.627	0.0060	1.016	1.004	1.028	6.87
Pholis crassispina								
Seagrass-associated group (*SA*)	-1.241	0.0239 ***	0.588	0.0049	1.024	1.014	1.034	24.08
Drft-faunal group (*DF*)	2.575	-0.0080	0.607	0.0050	0.992	0.982	1.002	2.48
Benthic-faunal group (*BF*)	-2.861	0.0246 ***	0.910	0.0074	1.025	1.010	1.040	11.17
Minimal-faunal group (*MF*)	-1.742	-0.0212	1.821	0.0217	0.979	0.938	1.021	0.96

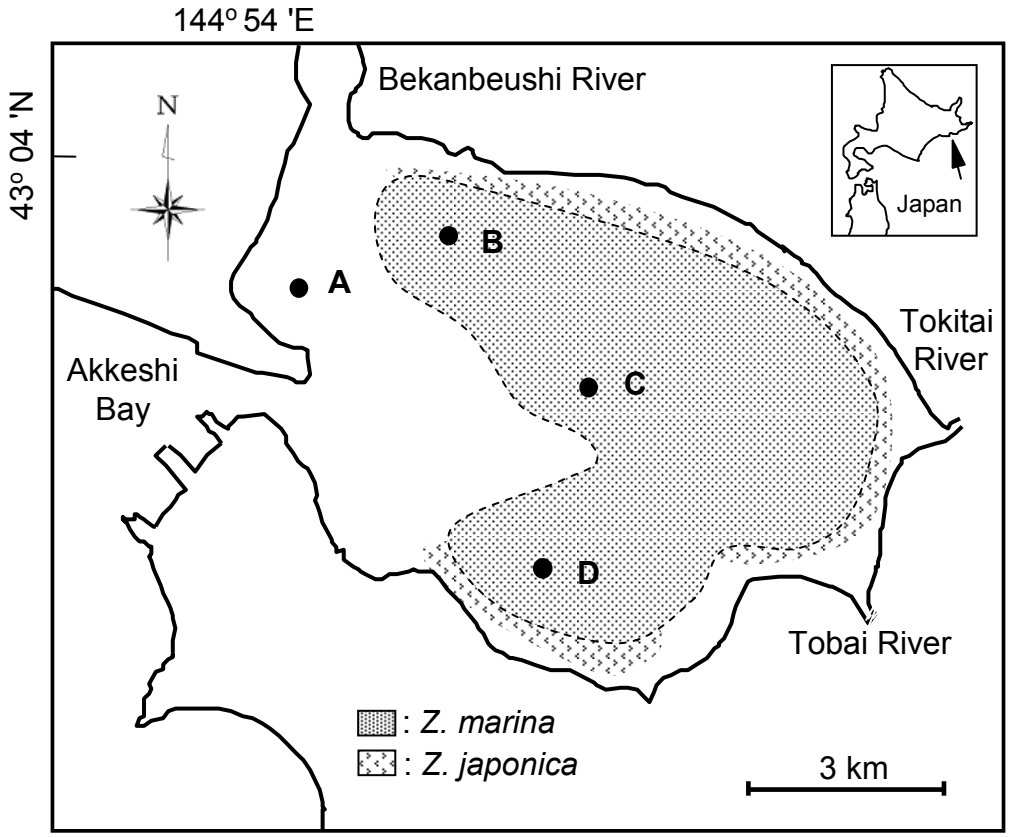
144º 54 'E
43º 04 'N
N
Bekanbeushi River
Japan
A
B
C
D
Akkeshi
Bay
Tokitai
River
Tobai River
: Z. marina
: Z. japonica
3 km

Fig. 1

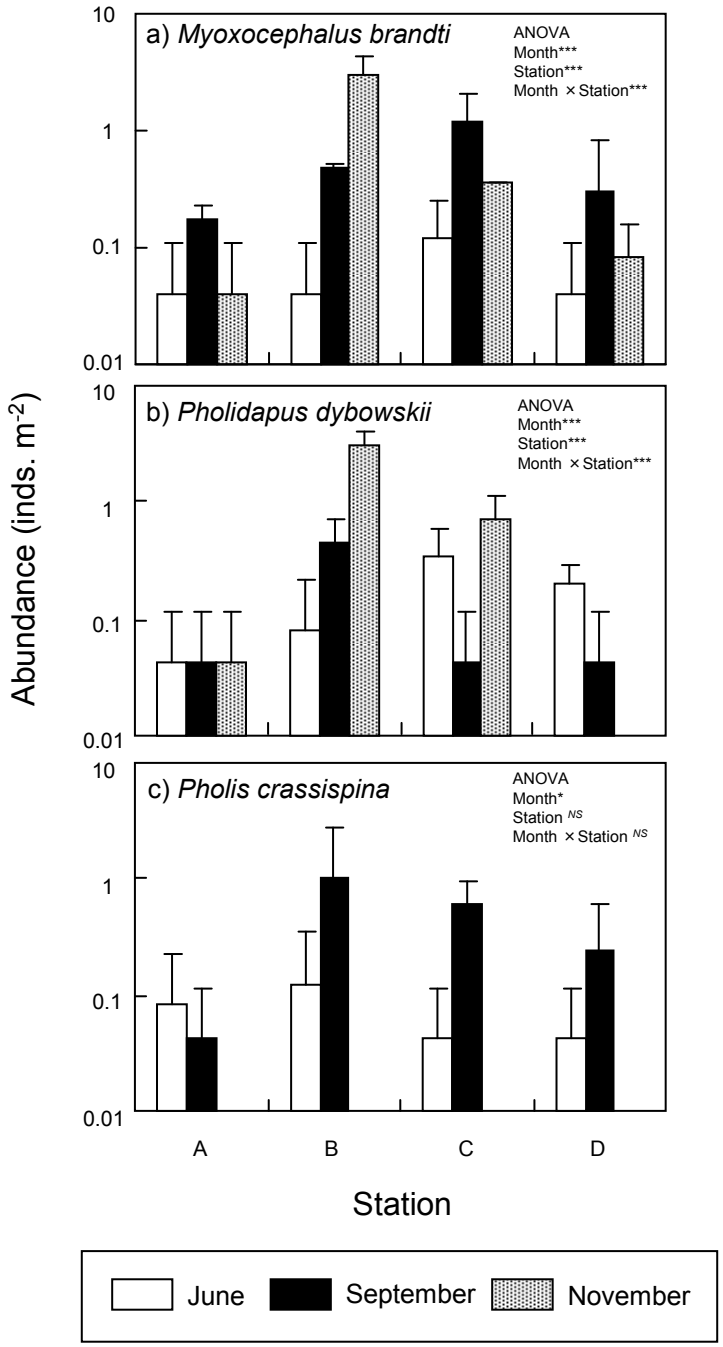
a) Myoxocephalus brandti
ANOVA
Month***
Station***
Month × Station***
b) Pholidapus dybowskii
ANOVA
Month***
Station***
Month × Station***
c) Pholis crassispina
ANOVA
Month*
Station NS
Month × Station NS
10
1
0.1
0.01
Abundance (inds. m-2)
A
B
C
D
Station
June
September
November

Fig. 2

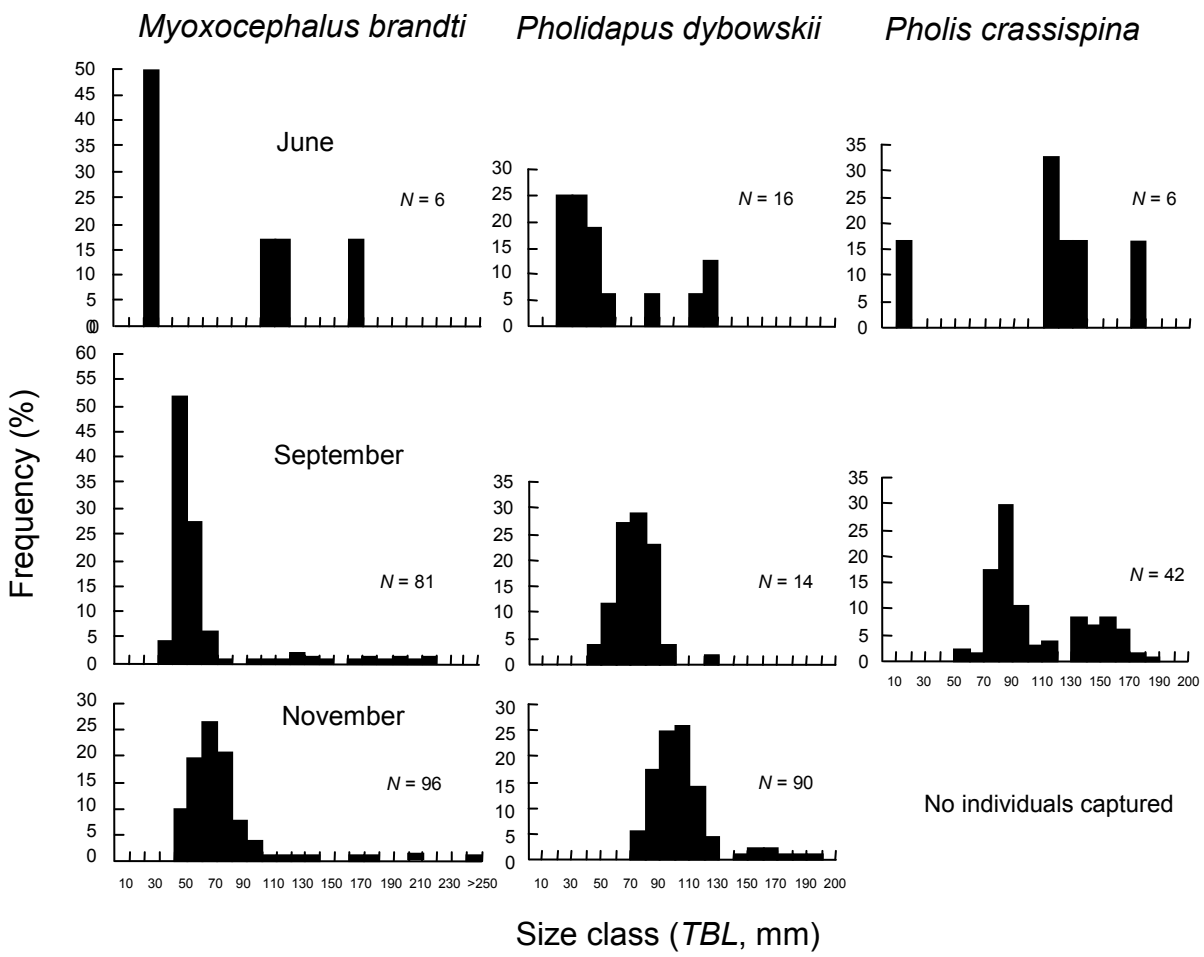
Myoxocephalus brandti
Pholidapus dybowskii
Pholis crassispina
June
September
November
N = 6
N = 16
N = 6
N = 81
N = 14
N = 42
N = 96
N = 90
No individuals captured
Frequency (%)
Size class (TBL, mm)

Fig. 3

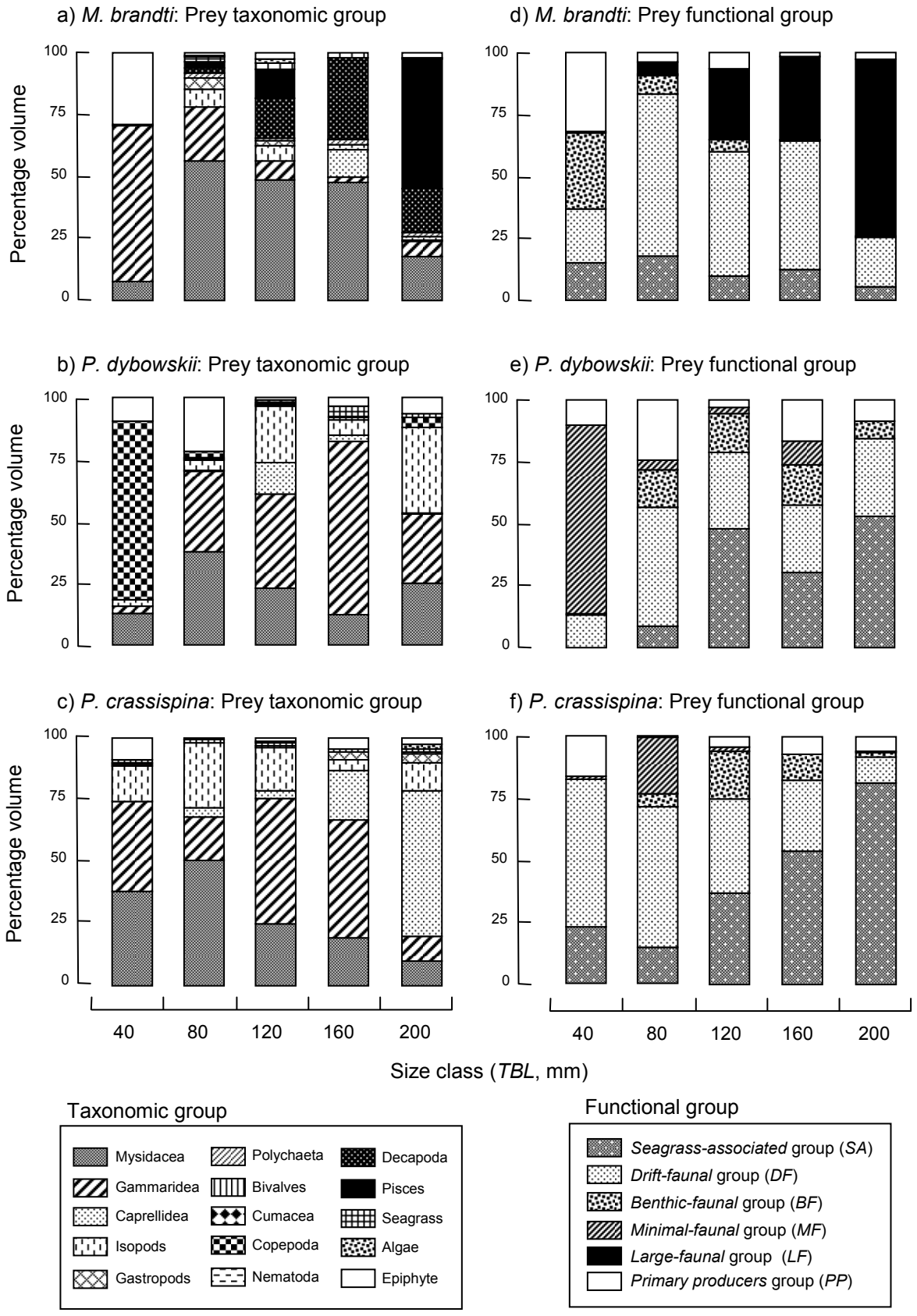
a) M. brandti: Prey taxonomic group
d) M. brandti: Prey functional group
b) P. dybowskii: Prey taxonomic group
e) P. dybowskii: Prey functional group
c) P. crassispina: Prey taxonomic group
f) P. crassispina: Prey functional group
Percentage volume
100
75
50
25
0
40
80
120
160
200
Size class (TBL, mm)
Taxonomic group
Mysidacea
Gammaridea
Caprellidea
Isopods
Gastropods
Polychaeta
Bivalves
Cumacea
Copepoda
Nematoda
Decapoda
Pisces
Seagrass
Algae
Epiphyte
Functional group
Seagrass-associated group (SA)
Drift-faunal group (DF)
Benthic-faunal group (BF)
Minimal-faunal group (MF)
Large-faunal group (LF)
Primary producers group (PP)

Fig. 4

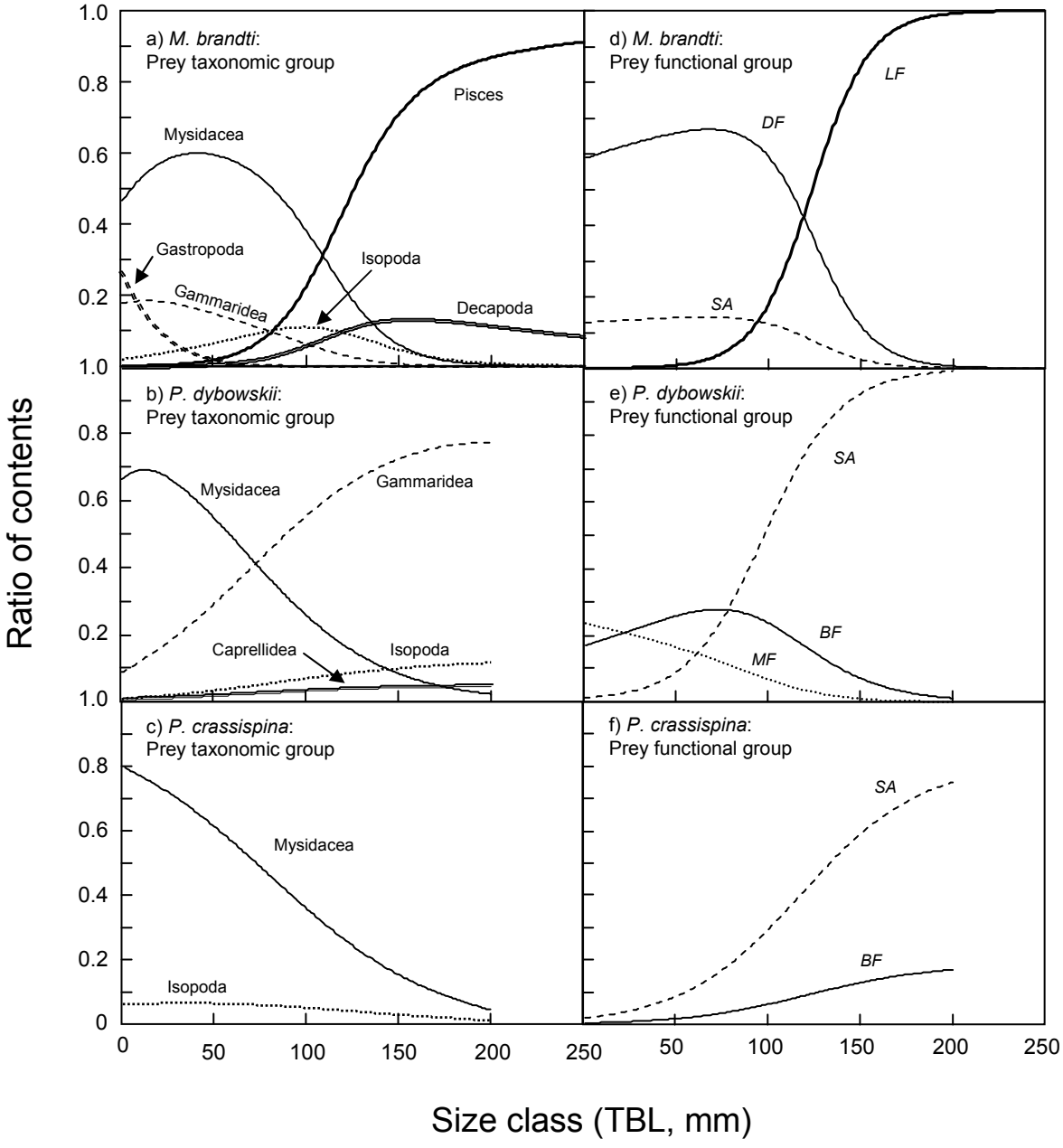
a) M. brandti:
Prey taxonomic group
Pisces
Mysidacea
Gastropoda
Isopoda
Gammaridea
Decapoda
d) M. brandti:
Prey functional group
LF
DF
SA
b) P. dybowskii:
Prey taxonomic group
Mysidacea
Gammaridea
Caprellidea
Isopoda
e) P. dybowskii:
Prey functional group
SA
BF
MF
c) P. crassispina:
Prey taxonomic group
Mysidacea
Isopoda
f) P. crassispina:
Prey functional group
SA
BF
Ratio of contents
Size class (TBL, mm)
0
0.2
0.4
0.6
0.8
1.0
50
100
150
200
250

Fig. 5