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

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1 **Abstract**

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

20

21 **Keywords** Fish · Habitat use · functional group · Predator-prey interactions · seagrass  
22 · multcategory logit model

## 1 **1. Introduction**

2           Seagrass meadows are the most diverse and productive habitats in coastal  
3 ecosystems (Hemminga and Duarte, 2000; Larkum et al., 2006) and are utilized as  
4 residence and/or transient areas by various higher-trophic-level consumers. Predatory  
5 fishes are abundant in seagrass meadows, and they affect the abundance and biomass of  
6 herbivore assemblages (Kikuchi, 1974; Bell and Pollard, 1989; Gillamders, 2006;  
7 Horinouchi, 2007; Hori et al., 2009). The prey species for these fish comprise a variety  
8 of animals with different morphologies, habitats, and life type that are closely related to  
9 seagrass vegetation (Orth et al., 1984; Jernakoff et al., 1996). The macrofaunal  
10 community, which is the most important prey (e.g., Edgar and Shaw, 1995; Gillamders,  
11 2006), can be subdivided into “*functional groups*” according to behavioral and  
12 morphological traits such as feeding mode, mobility type, and degree of association  
13 with the seagrass vegetation (Boström et al., 2006; Yamada et al., 2007a; Halpern and  
14 Floeter, 2008) as a unit of diversity in the upper tier of species diversity (Hooper et al.,  
15 2005). Such “*functional groups*” of prey species may explain the different prey  
16 preferences of major predatory fishes, which cause differences in habitat selection  
17 resulting to facilitate their coexistence in a seagrass meadow (Bell and Westoby, 1986;  
18 Connolly, 1994; Hindell et al., 2000; Horinouchi and Sano, 2001).

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

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

13         Three fish species, *Myoxocephalus brandti* (Steindachner, 1867), *Pholidapus*  
14 *dybowskii* (Steindachner, 1880), and *Pholis crassispina* (Temminck and Schelegel,  
15 1845), commonly occur in the seagrass meadows of the northwestern subarctic Pacific  
16 regions, which are characterized by semi-enclosed embayments such as lagoons and  
17 estuaries (Sato, 1940; Shiogaki, 1981; 1984; Yasu, 1985; Matsuura et al., 1993;  
18 Panchenko, 2000; Panchenko and Vdovin, 2005). Predatory fishes in the Akkeshi-ko  
19 estuary, including the three above-mentioned species, are known to feed on a wide array  
20 of invertebrate macrofauna (Watanabe et al., 1996; Hori, 2006). It has been clarified that  
21 the distribution of macrofaunal assemblages in the estuary varied greatly with regard to  
22 functional groups (Yamada et al., 2007a). It is thus expected that habitat use of these  
23 three fishes associated with seagrass beds and foraging behavior related to the  
24 preference of prey species may also differ among the three predatory fish species.

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

13

## 14 **2. Materials and methods**

### 15 *2.1. Study area*

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

1 2008). Wind speeds were commonly higher in autumn (September-November) than in  
2 spring-summer (April-August). Three rivers (Bekanbeushi, Tokitai, and Tobai) flow into  
3 the estuary. The Bekanbeushi river has the largest catchment area, accounting for 98.8%  
4 of the total amount of inflow to the Akkeshi-ko estuary. Most parts of the estuary are  
5 usually frozen over from late December to early March. A major part of the Akkeshi-ko  
6 estuary is covered with two species of *Zostera* seagrasses: *Z. marina* covers a wide  
7 range of subtidal area and *Z. japonica* occurs at the intertidal zones of the estuary,  
8 except for the unvegetated bottoms of the channel (deepest area in the Akkeshi-ko  
9 estuary: mean 5.4 m, Yamada et al., 2007a).

10 In the present study, four vegetated stations were established for the collection of  
11 3 fish species in the Akkeshi-ko estuary (Fig. 1). At Stn. A, a few patches of *Z. marina*  
12 (1–4 shoots/patch) were commonly seen on the muddy bottom (Mukai 2006; K. Yamada  
13 and N. Hasegawa, personal observation) near the mouth of the Bekanbeushi river (with  
14 a depth of 0.8 m). Stns. B, C, and D were located in *Z. marina* beds near the river mouth  
15 (Stn. B, 0.9 m deep), in the center (Stn. C, 1.5 m), and in the southern part of the estuary  
16 (Stn. D, 1.1 m). The variation in biotic and abiotic factors (salinity, water temperature,  
17 rainfall, and shoot density, leaf height, leaf width and seagrass growth) at each site in  
18 sampling terms were summarized by Yamada et al. (2007b) and Tanaka et al. (2008).

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

1 2006). The other two species (*P. dybowskii* and *P. crassisпина*) are recognized as  
2 subdominant species (Watanabe et al., 1996).

3 Juveniles of all three species were *ca.* <20 mm and lived in the shallow areas (<  
4 10 m). All fishes commonly mature in 2 years (2-year age class, *ca.* 50-100 mm)  
5 (Shiogaki, 1981, 1984; Yasu, 1985; Panchenko and Vdovin, 2005). The life span of *P.*  
6 *dybowskii* is *ca.* 2 years, while that of *P. crassisпина* is longer and that of *M. brandti* is  
7 the longest (maximum 12 years, Panchenko and Vdovin, 2005). *P. dybowskii* has been  
8 considered as resident species in seagrass and/or seaweed throughout its life (Shiogaki,  
9 1981; 1984; Yasu, 1985), while habitat preference and migration patterns of young  
10 immature and adult *M. brandti* and *P. crassisпина* have not yet been well understood.

11

## 12 2.2. Sampling procedure

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

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

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

10

### 11 *2.3. Dietary contents*

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

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

1 the fragments. The *TBLs* 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*:  $TBL = 2.962$   
6  $CL + 13.293$  ( $R^2 = 0.868$ ,  $N = 113$ ), *Crangon* sp.:  $TBL = 4.095 CL + 4.798$  ( $R^2 = 0.965$ ,  
7  $N = 42$ ), and *A. shrenckii*:  $Telson L = 0.163 TBL + 0.0556$  ( $R^2 = 0.653$ ,  $N = 117$ )  
8 (Yamada 2008).

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

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

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

19 Prey macrofauna, which have been considered as main prey (Watanabe et al.,  
20 1995; Hori, 2006), were further classified into three groups based on their life type (e.g.,  
21 behavior and mobile type) and habitat requirement, such as the degree of association  
22 with seagrass and benthic substrates. The first macrofaunal group was the  
23 *seagrass-associated* group (*SA*), which consisted of epifauna that were firmly attached  
24 to seagrass substrates. The second macrofaunal group was the *benthic-faunal* group

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

21

## 22 2.5. Data analyses

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

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

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

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

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

where  $x$  is the *TLB* of the fish,  $\alpha_j$  is an intercept terms, and vector  $\beta_j$  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 ( $\beta_j$  for each prey group) was tested using Wald's test, which is based on the confidence limits of the odds ratio (odds ratio =  $e^{\text{parameter estimate}}$ ). 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<sup>-2</sup> (± 1.12 SD) for *M. brandti*, 0.42 inds. m<sup>-2</sup> (± 0.89 SD) for *P. dybowskii*, and 0.18 inds. m<sup>-2</sup> (± 0.53 SD) for *P. crassispina* (Fig. 2). The highest density was observed at Stn. B in November for *M. brandti* and *P. dybowskii*

1 and at Stn. B in September for *P. crassispina*. Higher density was also observed at Stn.  
2 C in September for *M. brandti* and at Stn. C in November for *P. dybowskii*. No *P.*  
3 *crassispina* individuals were captured by the sledge net or by reiterant box trap  
4 samplings in November. The temporal and spatial variation in abundance and  
5 interaction between month and site were significant for the density of *M. brandti*  
6 (Month:  $F_{2,24} = 22.627$ ,  $P < 0.001$ ; Site:  $F_{3,24} = 32.531$ ,  $P < 0.001$ ; Month  $\times$  Site;  $F_{6,24}$   
7  $= 11.079$ ,  $P < 0.001$ ) and *P. dybowskii* (Month:  $F_{2,24} = 27.090$ ,  $P < 0.001$ ; Site:  $F_{3,24} =$   
8  $32.944$ ,  $P < 0.001$ ; Month  $\times$  Site;  $F_{6,24} = 20.159$ ,  $P < 0.001$ ). However, only the  
9 temporal variation was significant for *P. crassispina* (Month:  $F_{2,24} = 3.784$ ,  $P = 0.037$ ;  
10 Site:  $F_{3,24} = 0.620$ ,  $P = 0.609$ ; Month  $\times$  Site;  $F_{6,24} = 0.573$ ,  $P = 0.748$ ). The density of *P.*  
11 *crassispina* in September was significant higher than that in June (Tukey's test).

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

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

3

### 4 3.2. Stomach content analysis

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

8 Small crustaceans were the most preferred prey for the three fish species  
9 (Table 1). Of the small crustaceans, gammarids and mysids were the major prey for *P.*  
10 *dybowskii* and *P. crassispina*, and *M. brandti* and *P. crassispina*, respectively. Isopoda  
11 was also consumed by three fish species in high proportions (5.8-17.2 %). Mollusca  
12 were consumed by all three fish species, but contributions of prey were lower  
13 (0.2-3.3 %). Polychaeta and Nematoda were consumed by *M. brandti* (1.4 %) and *P.*  
14 *dybowskii* (0.4 %), and *P. crassispina* (< 0.1 %). The prey contribution of Polychaeta  
15 and Nematoda was lower than Mollusca. The contribution of plant material (mainly  
16 seagrasses, epiphytes, and algae) to the diets of all 3 species was less, but higher than  
17 Mollusca, Polychaeta and Nematoda (2.7–6.8 %). Pisces and Decapoda were ingested  
18 only by *M. brandti* (7.0 % and 8.9 %, respectively). Although higher proportions of  
19 crustacean fragments were seen, these fragments may include body parts of identified  
20 species.

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

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

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

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

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

9

#### 10 **4. Discussion**

##### 11 *4.1. Pattern of temporal and spatial utilization of seagrass bed for three fish species*

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

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

1 year. Although *P. dybowskii* is a resident of the seagrass meadow of the estuary for its  
2 life (life span is *ca.* 2 years), Adult individuals (> 2 age) of *M. brandti* (maximum life  
3 span is 15 years) may possibly migrate between the Akkeshi-ko estuary and outer areas  
4 (i.e., Akkeshi Bay) because quite large individuals (>250 mm as more than 3-year age  
5 class) have been captured occasionally in the Akkeshi-ko estuary (Watanabe et al.,  
6 1996) and the Akkeshi Bay (K. Yamada and M. Hori, personal observation). On the  
7 other hand, no *P. crassispina* individuals were captured by sledge net or additional  
8 reiterant sampling by box-traps in November. Significant higher density was observed  
9 in September, and a temporal shift of the peak cohort of 1-year age group in *P.*  
10 *crassispina* was not obvious. Furthermore, this species does not occur at the Akkeshi-ko  
11 estuary in winter (Watanabe et al., 1996; Hori, 2006). These suggest that immature  
12 (young fish) and adults of this species occasionally migrate between the Akkeshi-ko  
13 estuary and outer areas (Akkeshi Bay). The patterns of temporal utilization of the  
14 seagrass meadow of the Akkeshi-ko estuary are thus different among the three fish  
15 species. Similar inter-species variation in the temporal shifts in vegetated-estuarine use  
16 has been found in other vegetated coastal areas (Kikuchi, 1974; Bell and Westoby,  
17 1986; Connolly, 1994; Horinouchi and Sano, 2001; Horinouchi, 2007). Such differences  
18 of temporal utilization of the seagrass meadow among fish species may cause habitat  
19 differentiation leading to prey-faunal differentiation, which is one of the coexistence  
20 mechanisms in fish communities with high diversity and abundance at seagrass  
21 meadow.

22

#### 23 4.2. *The prey contribution and usefulness of the functional group approach*

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

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

8         The results of the logistic model demonstrated that both prey taxonomic and  
9 functional groups in the diet of each fish species can explain the variation in prey  
10 composition with size-dependent changes. For example, major prey and the prey  
11 variation with the size-dependent changes of *M. brandti* can be explained by taxonomic  
12 group (> 97%) as well as functional group (> 91%). On the other hand, major prey and  
13 the prey variation in smaller size *P. dybowskii* cannot be explained by the functional  
14 group alone but can be explained by the taxonomic group (Mysidacea) only. Further,  
15 major prey of smaller size and larger size in *P. crassispina* can be explained by  
16 taxonomic group (Mysidacea) and functional group (*SA* and *BF* groups), respectively.  
17 These results indicate that only one prey-category (taxonomic or functional group)  
18 cannot fully explain the prey variation, although previous studies classified prey based  
19 on only higher-taxonomic group (Platell et al., 1998; Linke et al., 2001; Platell and  
20 Potter, 2001). Trait-based functional categories (Yamada et al., 2007a; Boström et al.,  
21 2006; Halpern and Floeter, 2008; Hori et al., 2009) can be regarded as one of the  
22 effective indices of diversity to evaluate the prey variation in fish with size-dependent  
23 changes. Further, major prey of larger size (i.e., adult) in *P. crassispina* can be  
24 explained by only the *SA* group as the prey functional group but not the taxonomic

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

3 Prey functional groups which are classified by the hierarchical assignment of  
4 prey species on the basis of several given species-traits (*priori* method) correspond to  
5 variation in fish diets and brought an additional perspective in explaining the prey  
6 variation among fishes in the seagrass ecosystem. Although a variety of techniques have  
7 recently been developed to classify species into functional groups based on substantial  
8 ecological traits (Petchey and Gaston, 2006; Wright et al., 2006; Villéger et al., 2008),  
9 there may be many cases in which substantial knowledge of ecological traits (which is  
10 concerned directly with functions) in order to estimate functional diversity using these  
11 techniques has not obtained especially in aquatic fauna. Therefore, experimental studies  
12 on measurement of functional diversity based on representative and typical ecological  
13 traits concerned directly and/or indirectly with ecological functions are important for  
14 progress and generalization of concept of functional diversity in aquatic ecosystems  
15 (e.g., Bonström et al., 2006; Yamada et al., 2007a; Halpern and Floeter, 2008; Yamada  
16 2008; Hori et al., 2009).

#### 17 18 *4.3 Dietary shifts of the fishes*

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

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

5 Main prey of the large size of *P. dybowskii* and *P. crassispina* can be explained  
6 by the *SA* group as the prey functional group. This may be concerned with development  
7 of capture ability (i.e., selective predation) with size-dependent changes. The *SA* group  
8 may be difficult to be found out to feed due to traits of its behavior (inhabit among  
9 seagrass leaves) compared with Mysidacea. Moreover, mean size and biomass of an  
10 individual in the *SA* group (i.e., nutritional value) are higher than Mysidacea (Yamada,  
11 2008; K. Yamada, personal observation). These support that the *SA* group, with its high  
12 nutritional value, could be fed selectively by large size fishes with higher capture  
13 (swimming) ability than small size fish.

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

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

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

16

## 17 **5. Conclusions**

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

1 seagrass vegetation (Edgar and Shaw, 1995; Jernakoff et al., 1996; Yamada et al.,  
2 2007b; Hori et al., 2009). Therefore, prey taxonomic- as well as functional-group,  
3 which is classified by assigned species according to differences of habitat and life type  
4 (pattern of habitat use), is effective to evaluate variation in prey.

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

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

21

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9

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1 **Figure legends**

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

5

6

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

12

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

17

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

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

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

Table 1. Dietary content (in percent 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		
			<i>Myoxocephalus brandti</i>	<i>Pholidapus dybowskii</i>	<i>Pholis crassispina</i>
<b>Small Crustacea (&lt; 20mm mesh)</b>			<b>81.1</b>	<b>91.8</b>	<b>95.3</b>
<b>Gammaridea</b>			<b>19.2</b>	<b>35.8</b>	<b>32.6</b>
* <i>Ampithoe</i> spp.	4.8	SA	4.9	6.1	8.0
* <i>Grandidierella</i> spp.	3.6	BF	2.6	3.2	4.3
* <i>Gammaropsis japonica</i>	3.8	BF	3.9	7.9	1.8
* <i>Pontogeneia rostrata</i>	2.3	DF	2.7	2.8	3.7
* <i>Corophium acherusicum</i>	1.5	BF	0.6	1.2	0.6
* <i>Synchelidium lenorstalum</i>	3.7	DF	0.1	0.1	0.1
* <i>Metopa</i> sp.	1.5	SA	<0.1	0.1	0.2
* <i>Allorchestes</i> sp.	2.6	SA	<0.1	0.1	-
* <i>Pleustes</i> sp.	1.6	DF	0.1	-	-
* <i>Melita</i> sp.	3.3	SA	0.3	-	0.2
* <i>Hyale</i> sp.	2.4	SA	-	0.6	0.3
* <i>Metaphoxus</i> sp.	3.6	DF	-	0.2	0.1
* <i>Corphium</i> spp.	3.4	BF	-	<0.1	0.8
* <i>Byblis japonicus</i>	3.6	BF	-	-	0.1
* <i>Jassa</i> spp.	9.0	SA	-	-	0.1
* <i>Orchomene</i> sp.	2.6	DF	-	-	<0.1
Fragment of Gammarus			4.0	13.4	12.1
<b>Caprellidea</b>			<b>0.4</b>	<b>8.3</b>	<b>12.7</b>
* <i>Caprella mutica</i>	10.5	SA	0.3	1.2	8.1
* <i>Caprella penantis</i>	4.6	SA	<0.1	1.7	0.4
* <i>Caprella scaura</i>	5.3	SA	0.1	1.9	0.1
* <i>Caprella polyacantha</i>	7.2	SA	-	0.1	0.5
* <i>Caprella laeviuscula</i>	4.7	SA	-	0.1	-
* <i>Caprella bispinosa</i>	4.8	SA	-	-	0.7
Fragment of <i>Caprella</i>			<0.1	3.3	2.9
<b>Mysidacea</b>			<b>48.5</b>	<b>24.0</b>	<b>34.7</b>
* <i>Neomysis avatschensis</i>	6.5	DF	17.8	4.4	17.1
* <i>Neomysis mirabilis</i>	10.1	DF	16.2	14.6	12.8
* <i>Neomysis czerniawskii</i>	8.4	DF	0.4	0.1	-
* <i>Acanthomysis schrencki</i>	6.0	DF	0.2	-	-
* <i>Exacanthomysis japonica</i>	9.1	DF	-	-	0.3
Fragment of Mysidacea			13.8	4.9	4.5
<b>Isopods</b>			<b>5.8</b>	<b>17.2</b>	<b>15.2</b>
* <i>Cymodoce japonica</i>	3.3	SA	5.4	14.7	12.0
* <i>Munna</i> spp.	0.7	MF	0.2	2.0	3.2
* <i>Paranthurus japonica</i>	5.2	SA	0.2	-	-
* <i>Idotea ochotensis</i>	5.5	SA	-	0.4	-
* <b>Calanoida</b>	0.7	MF	<b>0.2</b>	<b>6.5</b>	<b>&lt;0.1</b>
* <b>Cumaceans</b>	4.1	BF	<b>&lt;0.1</b>	<b>&lt;0.1</b>	<b>0.2</b>
<b>Large Crustacea (&gt; 20mm mesh)</b>					
<b>Decapoda</b>			<b>7.0</b>	-	-
* <i>Crangon</i> sp.	22.7	LF	6.9	-	-
* <i>Pandalopsis pacifica</i>	21.6	LF	0.2	-	-
<b>Mollusca</b>					
<b>Gastropods</b>			<b>3.3</b>	<b>0.2</b>	<b>1.4</b>
* <i>Barleeia angustata</i>	3.1	SA	3.1	0.2	1.1
* <i>Reticunassa spurca</i>	2.1	BF	0.2	-	-
* <i>Lacuna decorata</i>	4.6	SA	-	-	0.3
* <b>Bivalves (juveniles of <i>Ruditapes</i>)</b>	0.6	MF	-	<b>0.2</b>	<b>0.3</b>
<b>Annelida (Polychaeta)</b>					
* Errant polychaeta	2.1	DF	<b>1.4</b>	<b>0.4</b>	-
<b>Nematodes</b>					
* Secernentea	0.8	MF	-	-	<b>&lt;0.1</b>
<b>Primary producer group</b>					
<b>Plant material</b>			<b>4.9</b>	<b>6.8</b>	<b>2.7</b>
* 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	-	-
<b>Vertebrate (Pisces)</b>			<b>8.9</b>	-	-
* <i>Myoxocephalus brandti</i>	30.3	LF	3.6	-	-
* <i>Chaenogobius mororanus</i>	22.6	LF	0.6	-	-
* <i>Chaenogobius castaneus</i>	25.5	LF	1.1	-	-
* <i>Pholidapus dybowskii</i>	43.7	LF	0.3	-	-
* Pleuronectiformes	49.3	LF	0.2	-	-
Fragment of Pisces			3.1	-	-
<b>Other materials</b>					
Sediment	-	-	<b>&lt;0.1</b>	<b>0.1</b>	<b>0.3</b>
Unidentifiable material	-	-	<b>0.3</b>	<b>0.4</b>	-
<b>Total number of stomachs</b>			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-associated species, DF; drift-faunal species, BF; benthic-faunal species, MF; minimal-faunal species and LF; large-faunal species.

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

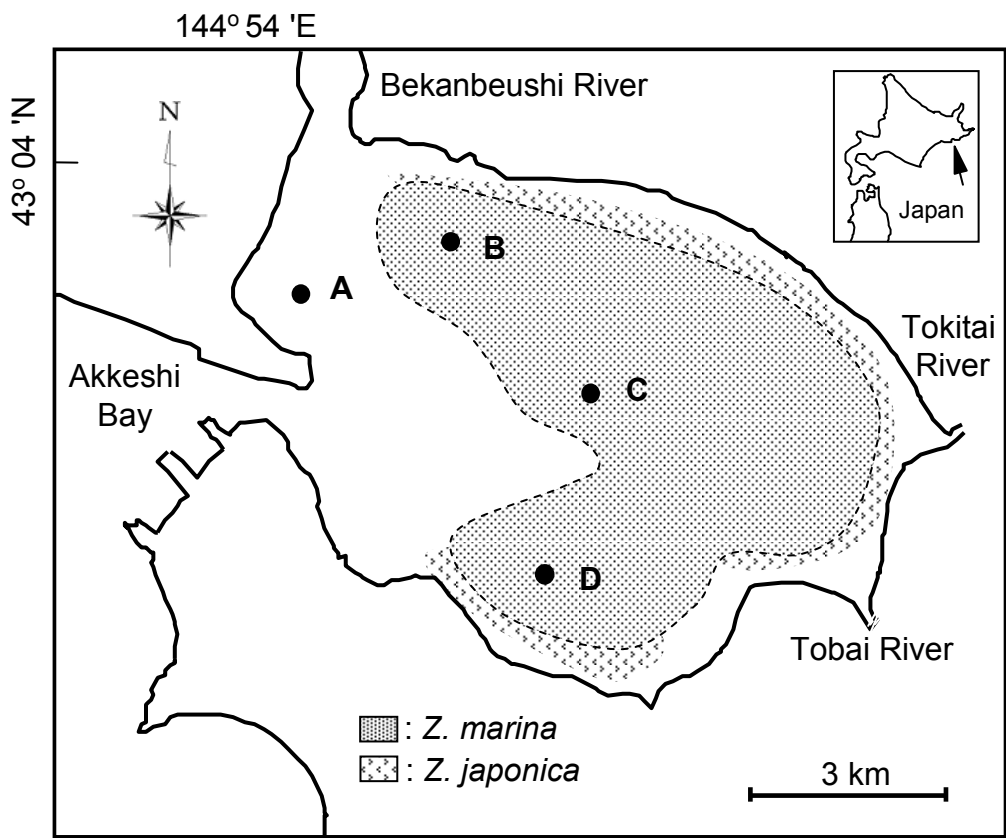


Fig. 1

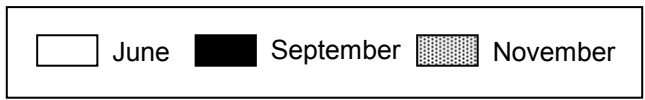
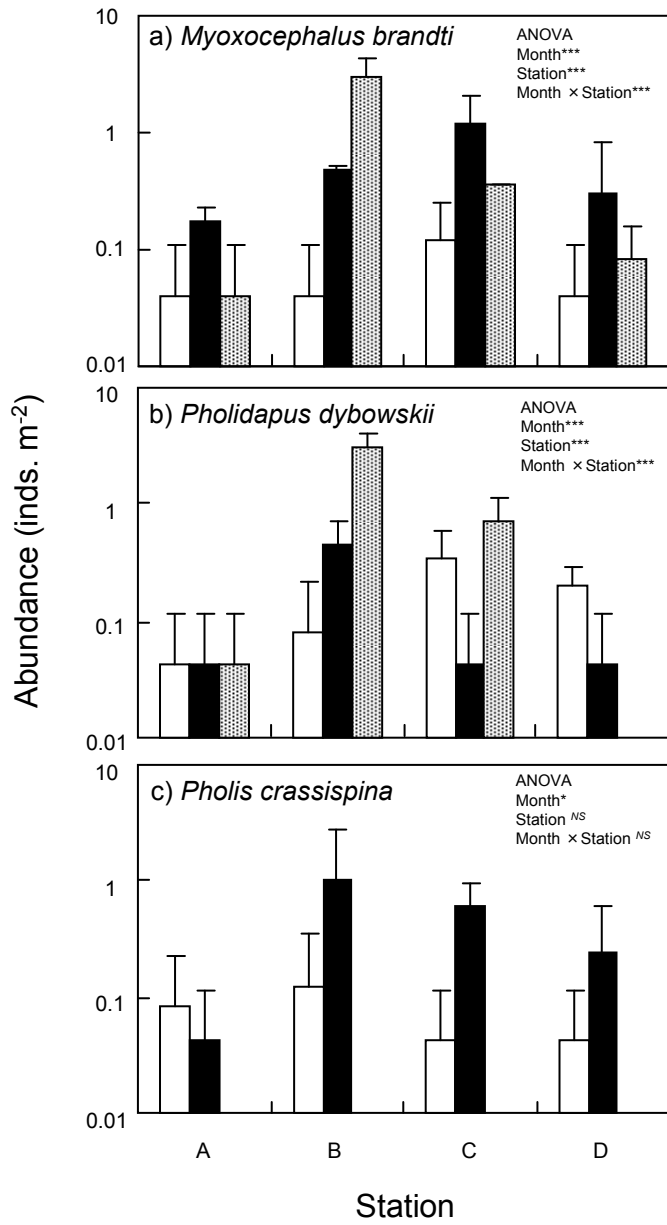


Fig. 2

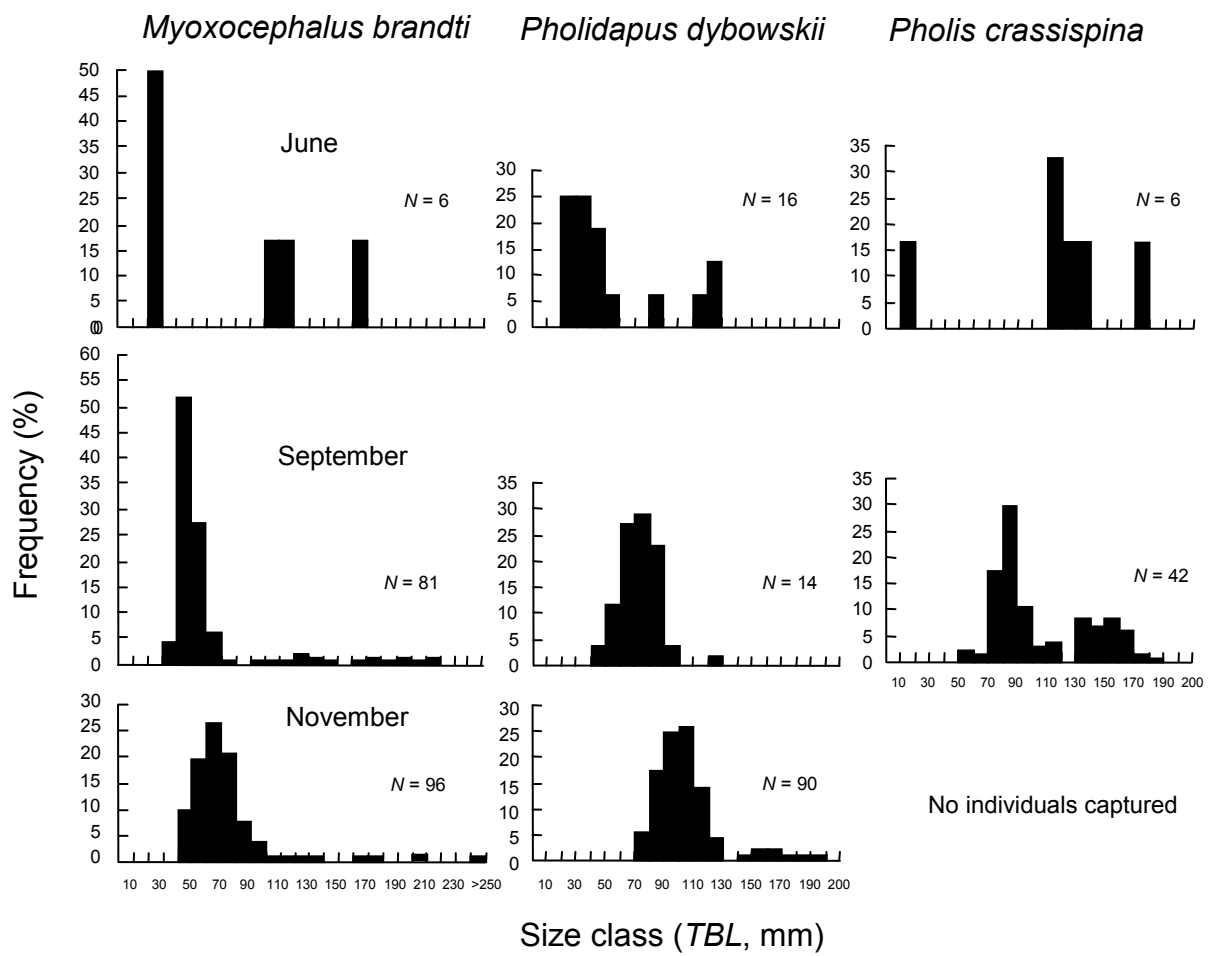


Fig. 3

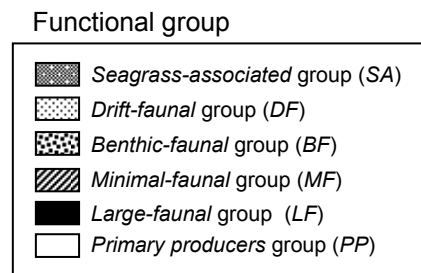
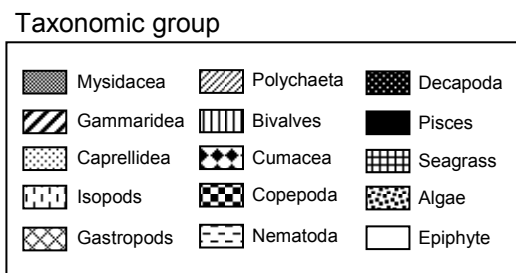
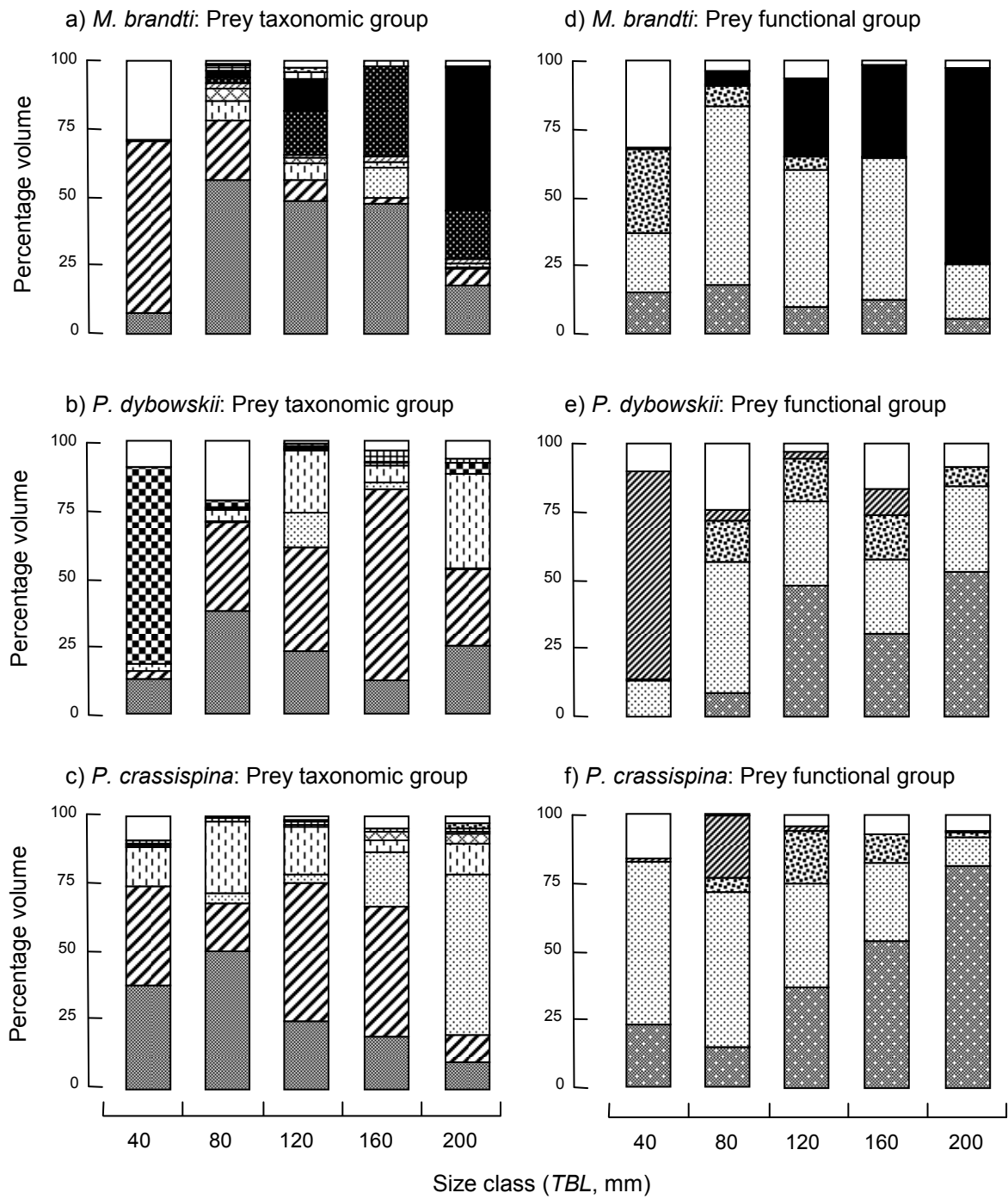


Fig. 4

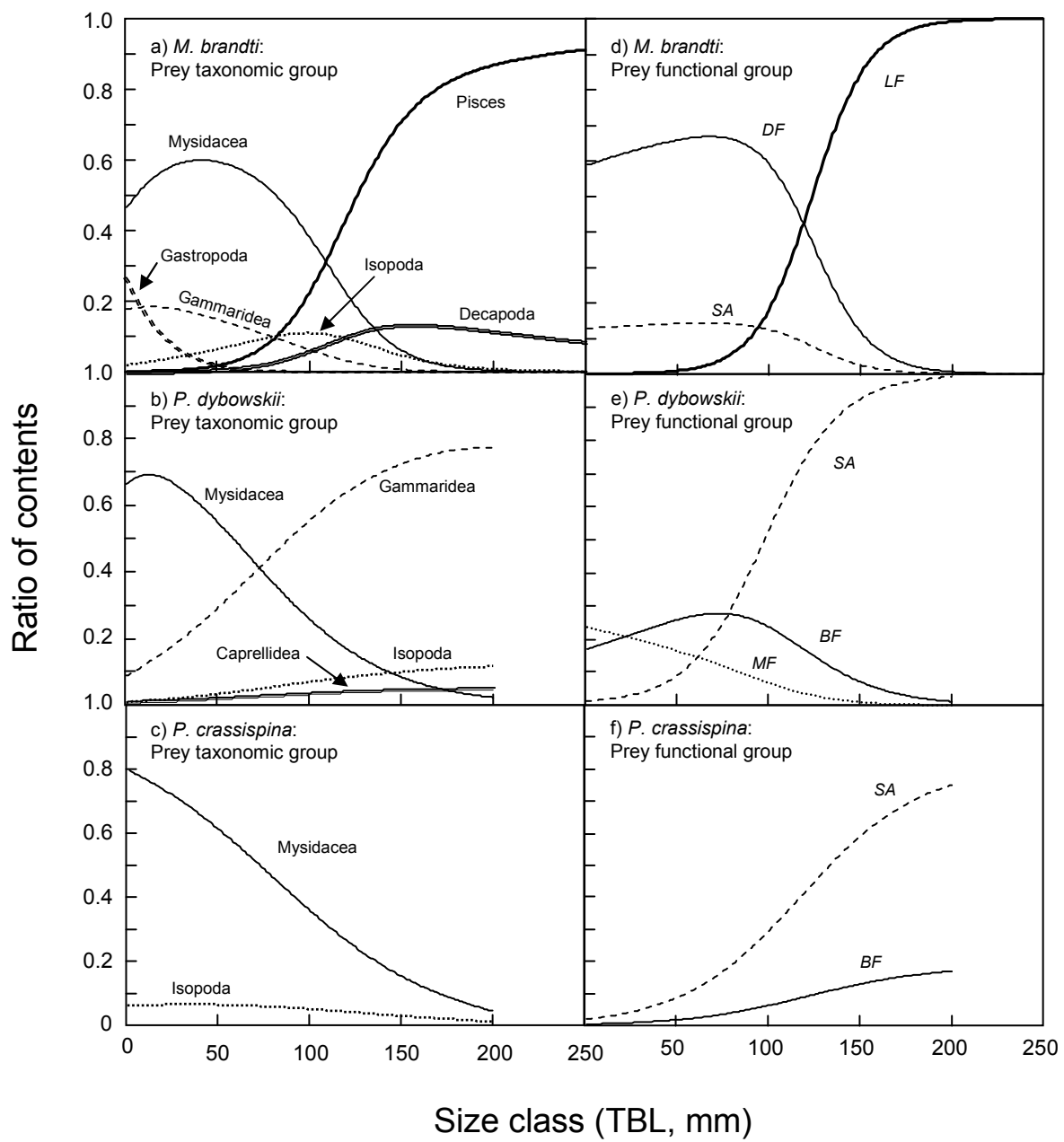


Fig. 5