

Feeding Relationships among Six Seagrass-associated Fishes in the Northeastern Gwangyang Bay, Southern Korea

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Abstract – We conducted dietary analyses of six seagrass-associated fish species inhabiting northeastern Gwangyang Bay, Korea. These six species consumed a variety of benthic invertebrates and teleosts, but their preferences for different food resources varied. Although all species consumed crustaceans, the contributions of different crustacean taxa differed among the species' diets. Caridean shrimps and crabs were a significant part of the *Hexagrammos agrammus* and *H. otakii* diets, respectively, while amphipods were consumed mainly by *Sebastes inermis*. Caridean shrimps and prawns were abundant within the *Lateolabrax japonicus* diet, but were not common prey resources for *Pseudopleuronectes yokohamae* or *S. schlegelii*. Polychaetes and ophiurids were ingested by *P. yokohamae*, and the former prey taxon also made moderate contributions to the diets of *H. agrammus* and *L. japonicus*. With the exception of *P. yokohamae*, the diets of all species included teleosts. Teleosts contributed the largest proportion of the *S. schlegelii* diet, followed by the *S. inermis* and *L. japonicus* diets; however, *H. agrammus* and *H. otakii* rarely consumed teleosts. Non-metric multidimensional scaling (nMDS) ordination plots and permutational analysis of variance (PERMANOVA) revealed the variation in dietary composition among species and the contributions of each prey taxon. These interspecific differences in diet increase the range of food resources available to these fishes, thereby reducing competition for resources within the fish community in this region.

Keywords – Gwangyang Bay, partitioning food resources, stomach contents, *Zostera marina*

1. Introduction

Knowledge about the feeding relationships among fish species is of fundamental interest in studies of trophic ecology,

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and is crucial to understand how fish share or compete for available food resources within their habitats (Grossman 1986; Mérona and Rankin-de-Mérona 2004). Sympatric fish species often exhibit resource partitioning as a strategy for reducing direct inter-specific competition (Connell 1980; Ross 1986; Platell and Potter 2001), and such partitioning of food resources is often a mechanism for niche segregation (Schoener 1974; Ross 1986). Niche segregations in direct competitive processes provide a means by which fish species can co-exist in the same geographical region.

In Korean waters, six fish species (*Hexagrammos agrammus*, *Hexagrammos otakii*, *Lateolabrax japonicus*, *Pleuronectes yokohamae*, *Sebastes inermis*, and *Sebastes schlegelii*) are coastal residents whose geographic ranges commonly overlap (Kim et al. 2005; Kwak et al. 2012). These species are commercially important components of the coastal gillnet and longline fisheries in Korean waters (Kim et al. 2004; KOSIS 2017). They often use seagrass habitats as shelter and nursery grounds, and juveniles of these species are therefore common in the seagrass beds of Southern Korea (e.g., Huh and Kwak 1997; Kwak et al. 2014). As seagrass beds provide a food resource and habitat for juvenile fishes, the distribution ranges of these juveniles are closely associated with seagrass beds and adjacent coastal habitats (Huh et al. 1998; An et al. 2010; Kwak et al. 2012). Recently, seagrass beds in Korea have been affected by human activities that have led to habitat destruction, increased nutrient and sediment runoff, and decreased water quality, causing similar declines in seagrasses in other temperate ocean regions (Lee and Lee 2003). Thus, studies on biological interactions among co-

occurring fishes may be necessary to effectively predict the effects of human activity on regional biodiversity.

The diets of these species have been studied in Korean waters (Huh and Kwak 1998; Park et al. 2007, 2016; Huh et al. 2009; Choi et al. 2017), and inter-specific resource partitioning has been reported between *H. agrammus* and *H. otakii*, as well as between *H. otakii* and *S. schlegelii* (Kwak et al. 2005; Seo and Hong 2007). Despite their economic and ecological importance, little is known about the dietary relationships among these species and how they partition food resources in Korean waters. Kwak et al. (2005) investigated the feeding ecology of two sympatric *Hexagrammos* species in the area, and reported that they shared abundant food resources. Seo and Hong (2007) compared diets of co-occurring *H. otakii* and *S. shlegeli* in the tidal flats of Western Korea, and revealed distinct resource partitioning between these two species in order to maximize the use of available food. However, these previous studies did not explore the factors that minimize competition and facilitate sympatry, nor did they examine ecological differences that might influence diet choice. Such information is crucial for defining the functional roles of species within coastal ecosystems (Wootton 1990; Brodeur and Percy 1992), and for clarifying diet-based food web structures (Bulman et al. 2001; Pasquaud et al. 2008).

In the present study, we assessed the dietary habits and interspecific dietary differences of six fish species in Southern Korean waters. Specifically, we aimed to: 1) quantify the overall diets of six co-occurring species, and 2) link differences in diet to trophic niches for these species. Comparisons of diets and trophic niches in co-occurring fish species can be used to quantify community interactions and better predict the effects of perturbations on community structure, as well as to develop management approaches for the conservation and sustainable use of biodiversity (Greenstreet and Rogers 2006).

2. Materials and Methods

Study area and sampling methods

Sampling was conducted in northeastern Gwangyang Bay, Korea (34°89'N~34°93'N, 127°82'E~127°87'E). This bay is located on the middle of the southern coast of the Korean Peninsula, and is characterized by a semi-enclosed estuarine embayment, encompassed by Yeosu and Namhae Island (Fig. 1). Large seagrass (*Zostera marina*) beds are prevalent along the eastern shoreline of the study area (Huh and Kwak 1997; Huh et al. 1998). The bay has a variety of coastal

fisheries and farming sites, as well as industrial complexes in the western inland region, which have potentially influenced the bay's marine ecosystem.

Fish samples were collected using various types of equipment, such as gillnets, longlines and pots, at depths of 5–10 m between March and June 2007. We investigated the diets of six fish species during the study period: *H. agrammus* (12.1–20.8 cm total length [TL], n = 41; Hexagrammidae), *H. otakii* (16.5–35.1 cm TL, n = 137; Hexagrammidae), *L. japonicus* (19.5–31.4 cm TL, n = 63; Lateolabracidae), *P. yokohamae* (18.5–31.7 cm TL, n = 21; Pleuronectidae), *S. inermis* (13.6–23.2 cm TL, n = 52; Sebastidae), and *S. schlegelii* (19.2–34.2 cm TL, n = 46; Sebastidae). Immediately after capture, individuals were transported to the laboratory and kept frozen at -20°C until processing, which occurred immediately after thawing in the laboratory. For each individual, the total length (TL, ± 1 mm) was measured, the stomach removed, and the contents preserved in 5% buffered formalin.

Analyses of stomach contents

Each stomach was cut open, and all prey were identified to the lowest possible taxonomic level using a dissecting microscope. The percentage weight contribution of each dietary item to the total weight of the stomach contents (%W) was estimated with the aid of an electronic balance: $%W = W_i / W_T \times 100$, where W_i is the weight of prey taxa i , and W_T is the total weight of prey taxa. Dietary niche breadth was calculated to the lowest possible taxonomic level using Levin's standardized niche breadth (B) (Krebs 1989): $B = [(\sum P_{ij})^{-1} - 1] \times (n-1)^{-1}$, where P_{ij} is the proportion of diet of predator i that is made up of prey j , and n is the number of prey items. This index ranges from 0 to 1; low values indicate a diet dominated by few prey items (specialist predator) and high values indicate a generalist diet. Diet overlap among six species was calculated using Schoener's index (C_{xy} ; Schoener 1970), as this method best estimates dietary similarities over the potential range of overlap (Wallace 1981). C_{xy} was calculated as follows: $C_{xy} = 1 - 0.5 (\sum |P_{xi} - P_{yi}|)$, where P_{xi} and P_{yi} are the proportions of prey taxa i (in terms of relative abundance by mass) in the diet of specimens or species x and y , respectively. C_{xy} ranged from 0 (diets contained no items in common) to 1 (complete overlap). An index value > 0.6 indicated high diet similarity and was considered biologically significant (Langton 1982).

Multivariate analyses of dietary data

Because gravimetric (or volumetric) data are considered

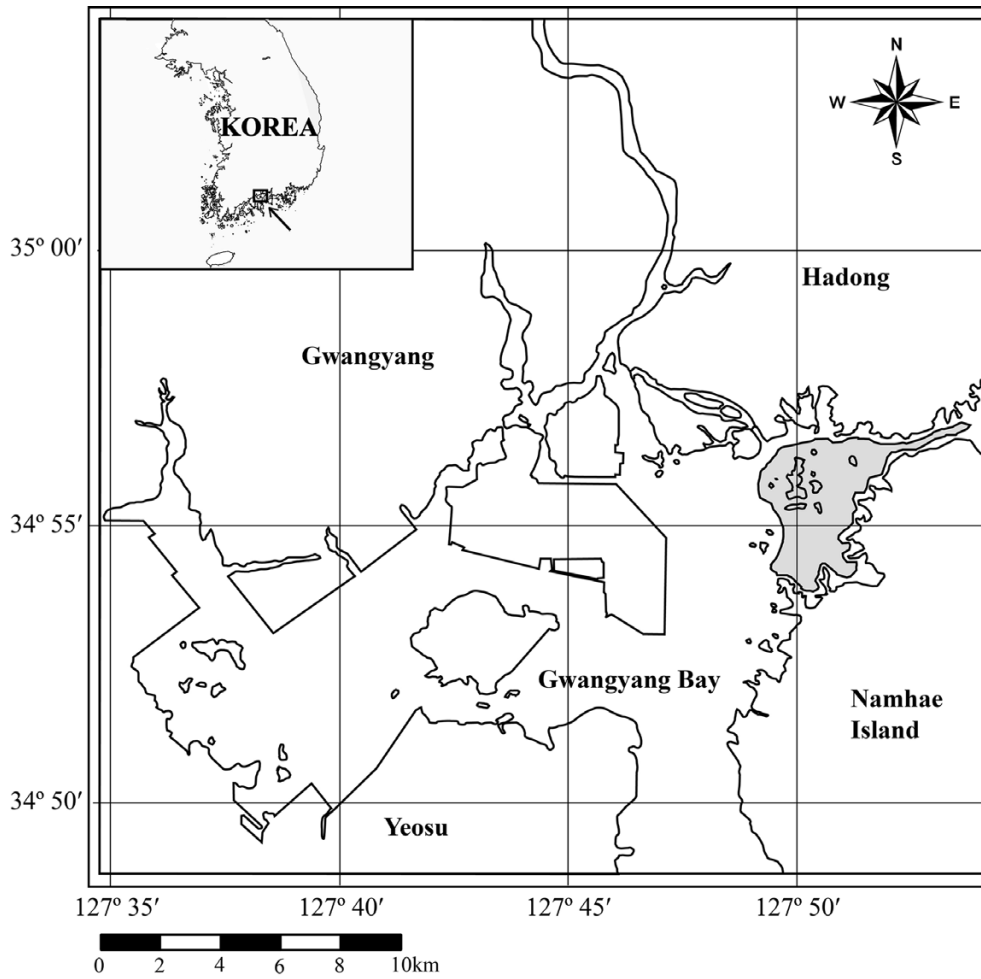


Fig. 1. Location of sampling area in northeastern Gwangyang Bay, Korea. Samples were collected within the shaded area

to best represent the relative importance of prey taxa, especially when prey items of different sizes are ingested (Hyslop 1980), subsequent analyses were performed using gravimetric data for each prey taxon. Prior to such analyses, dietary data for each of the six species were first randomly sorted into groups containing eight to ten individuals (depending on the size of the group). The averages of the percentage weight data for each prey taxa were then determined for each of the resultant groups. These averages were used for all subsequent analyses, because such randomization increases the effectiveness of multivariate analysis (De Lestang et al. 2000; Platell and Potter 2001), and because many of the stomachs examined contained only a few (mostly one to four) of the 18 dietary taxa recorded in the overall diets. Dietary data were then square root transformed to prevent the main dietary components from having an excessive influence.

Bray-Curtis similarity matrices were constructed for each of the six species and visualized via non-metric multidimensional scaling (nMDS) ordination (Platell and Potter 2001; Clarke et al. 2014). The matrices were then subjected to a series of permutational multivariate analyses of variance (PERMANOVA) using unrestricted permutations of raw data to assess whether there was significant effect on species (six levels). However, the effects of size and season were not considered, because all species had narrow length distributions and samples were collected during a single season (spring and early summer). In cases where PERMANOVA detected a significant difference, pairwise Monto Carlo (MC) tests were performed to determine which relationships between species were significant. PERMANOVA included MC tests because in some cases there were not enough possible permutations to conduct a reasonable test (generally less than 100 unique permutations) (Anderson et al. 2008).

We used canonical analysis of principal coordinates (CAP) to further investigate the significant effects obtained by PERMANOVA (Anderson et al. 2008). A permutation test was conducted, and vectors based on Spearman correlations were superimposed to determine which prey taxa characterized the differences in diet composition among species. The correlations of > 0.4 were plotted for individual species using CAP axes 1 and 2. We also used similarity percentage (SIMPER) to determine which prey taxa typified the diets of particular species and which taxa contributed most to the dietary dissimilarities identified by PERMANOVA. SIMPER analyses yielded the percentage of similarity or dissimilarity between levels of factors, and for specific levels of factors.

All analyses were performed using routines in the PRIMER v7 multivariate statistics package (www.primer-e.com) and the PERMANOVA+ add-on module (Anderson et al. 2008).

3. Results

Overall dietary compositions

The stomach contents of 360 specimens from 6 fish species were examined. Percentages of empty stomachs ranged from 14.6% for *H. otakii* to 32.6% for *S. schlegelii* (Table 1).

A total of 18 prey taxa and at least 60 prey species were identified in the diets of six species (Table S1). In terms of prey weight, three prey taxa (polychaetes, crustaceans, and teleosts) formed a large part of the diets of all six species (Table 1). For both *H. agrammus* and *H. otakii*, decapods (mostly caridean shrimps and crabs) were the most important crustacean taxa, contributing 46.3% and 48.8%, respectively, to the total dietary compositions. Meanwhile, amphipods were a significant component of the *S. inermis* diet (26.5%). Polychaetes were an important prey item for *P. yokohamae* (55.6%), as well as for *H. agrammus* (31.5%) and *L. japonicus* (27.3%). Bivalves were the next-largest dietary component for *H. otakii* (22.2%) and *P. yokohamae* (14.8%). For *L. japonicus*, *S. inermis*, and *S. schlegelii*, teleosts contributed 44.0%, 56.8% and 76.4% of the total dietary weight, respectively. Ophiurids and seaweed contributed substantially only to the diets of *P. yokohamae* and *H. agrammus*, respectively. The remaining prey taxa each accounted for $< 4\%$ of the total diet for each of the six species (Table 1).

Dietary niche breadth differed among species, being lower for *S. inermis* ($B = 0.101$) and *S. schlegelii* ($B = 0.110$), greatest for *P. yokohamae* ($B = 0.314$), and intermediate for *H. agrammus* ($B = 0.285$), *H. otakii* ($B = 0.220$), and *L. japonicus* ($B = 0.228$).

Table 1. Number of full stomachs, percentage of empty stomachs, and relative weight contributions of prey taxa in the diets of six fish species in northeastern Gwangyang Bay, Korea. Species code: HA, *Hexagrammos agrammus*; HO, *Hexagrammos otakii*; LJ, *Lateolabrax japonicus*; PY, *Pleuronectes yokohamae*; SI, *Sebastes inermis*; SS, *Sebastes schlegelii*. *Dietary categories used in multivariate analyses

| Species code | HA | HO | LJ | PY | SI | SS |
|---------------------------|----------------------------------|---------|------|------|------|---------|
| Full stomachs | 33 | 117 | 46 | 17 | 37 | 31 |
| Empty (%) | 19.5 | 14.6 | 27.0 | 19.0 | 28.8 | 32.6 |
| Taxa | Relative weight contribution (%) | | | | | |
| ANELLIDA | | | | | | |
| Polychaeta* | 31.5 | 8.9 | 27.3 | 55.6 | 0.8 | |
| MULLOSCA | | | | | | |
| Gastropoda* | | 2.9 | | | | 1.2 |
| Bivalvia* | 4.7 | 22.2 | | 14.8 | 0.2 | 0.2 |
| Cephalopoda* | | 0.7 | | | | 3.2 |
| CRUSTACEA | | | | | | |
| Copepoda* | | | | | 0.3 | |
| Cumacea* | | | | | | < 0.1 |
| Mysidacea* | | < 0.1 | 0.3 | | | |
| Amphipoda* | 0.3 | 13.0 | 1.6 | 1.2 | 26.5 | 3.0 |
| Isopoda* | 0.3 | | | | | |
| Decapoda | | | | | | |
| Penaeoidea* | | 4.6 | 14.5 | | | 5.9 |
| Caridea* | 28.8 | 13.6 | 10.7 | | 12.2 | 3.9 |
| Galatheoidea* | 0.9 | 6.7 | | | | 0.5 |
| Paguroidea* | 0.4 | | | | | 2.9 |
| Brachyura* | 16.1 | 23.9 | 1.7 | | 3.2 | 2.5 |
| ECHINODERMATA | | | | | | |
| Ophiurida* | | | | 27.0 | | |
| CHORDATA | | | | | | |
| Ascidiacea* | | | | | | 0.2 |
| Teleosts* | 5.4 | 2.7 | 44.0 | | 56.8 | 76.4 |
| Others | | | | | | |
| Seaweed* | 11.5 | 0.7 | | | | 0.1 |
| Unidentifiable prey items | | | | 1.3 | | |

Inter-specific comparisons

The nMDS ordination revealed a clear difference in dietary composition among the six species (Fig. 2). *H. otakii* and *L. japonicus* were represented in the middle of the plot, with distributions in the upper and lower regions of the plot, respectively. The points representing the dietary samples of *S. inermis* and *S. schlegelii* were located on the right of the plot, while those of *H. agrammus* and *P. yokohamae* formed a distinct group on the left (Fig. 2).

PERMANOVA revealed that dietary compositions were significantly related to species (pseudo-F = 9.506, $P = 0.001$). Pairwise PERMANOVAs of diets revealed that nearly all

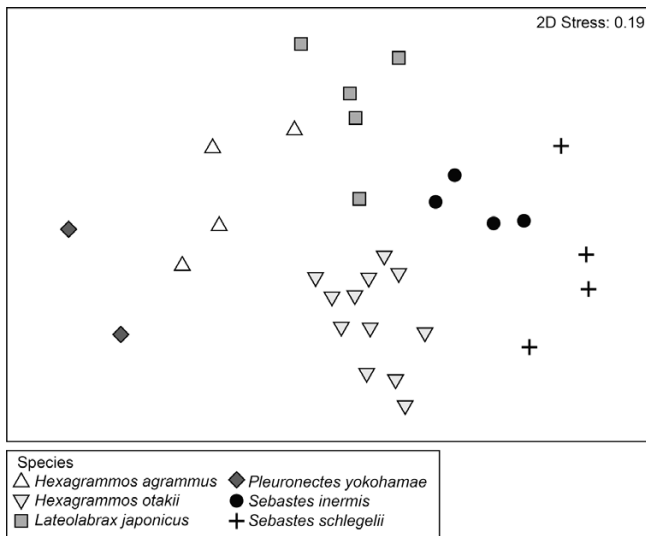


Fig. 2. nMDS ordination of dietary composition constructed from Bray–Curtis similarity matrices for six fish species in northeastern Gwangyang Bay, Korea

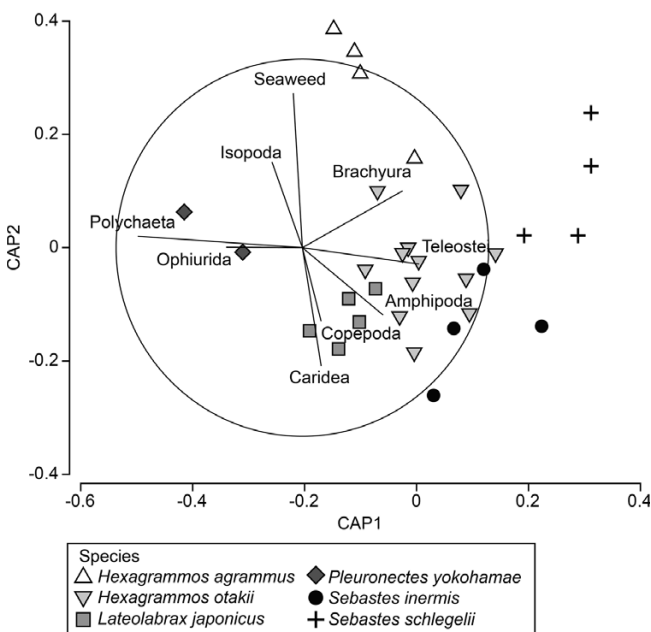


Fig. 3. Canonical analysis of principal coordinates (CAP) ordination plot to discriminate among the diets of species. Species correlations with each canonical axis are represented as vectors for species with correlations greater than 0.4. Vectors represent Pearson correlations, and the circle indicates a correlation of 1

pairwise comparisons of these differences were significant ($t > 2.61$, $P(\text{MS}) < 0.05$); however, the comparison between *S. inermis* and *S. schlegelii* was not significant ($t = 1.803$, $P(\text{MC}) > 0.05$).

CAP analyses also revealed significant differences among

the six species ($tr = 2.982$; $P = 0.001$; 999 permutations). Based on correlation vectors ($r > 0.4$) generated by CAP analyses (Fig. 3), polychaetes and ophiurids distinguished the *P. yokohamae* diet from those of other species, while seaweed and isopods distinguished the diet of *H. agrammus* from those of *L. japonicus*, *P. yokohamae* and *Sebastes* species. Teleosts characterized the diets of the two *Sebastes* species (Fig. 3).

SIMPER revealed that the dissimilarity between species ranged from 44.5% (between *H. otakii* and *S. inermis*) to 88.6% (between *P. yokohamae* and *S. schlegelii*), with eight prey taxa each contributing $> 10\%$ to the dietary dissimilarity among the six species (Table 2). The main typifying prey taxa of *L. japonicus* and *P. yokohamae* were polychaetes, whereas those of *H. agrammus* and *H. otakii* were seaweed and caridean shrimps, respectively. Although teleosts contributed mainly to the diets of *S. inermis* and *S. schlegelii*, amphipods were the most typifying prey taxa for *S. inermis*. Seaweed made the greatest contribution to the dissimilarities observed for most comparisons with *H. agrammus*, and teleosts contributed to the dissimilarities between *S. schlegelii* and other species. The most-observed prey items that contributed to the dissimilarity between *S. inermis* and other species were amphipods. The diet of *P. yokohamae* could be distinguished from those of other species by the consistently greater presence of polychaetes and ophiurids (Table 2).

Dietary overlaps for most comparisons were lower than biological significance (i.e. 0.6): only the comparison between *S. inermis* and *S. schlegelii* revealed an overlap of > 0.6 , although the values between *L. japonicus* and two *Sebastes* species were also close to 0.6 (Table 3). In contrast the overlap values were relatively low between the two *Sebastes* species and *P. yokohamae*, indicating that these species had dissimilar diets.

4. Discussion

The six species in the present study each fed mainly upon polychaetes, crustaceans, or teleosts, as well as other seagrass-associated marine organisms in Southern Korean waters (see also Table S1 and Kwak 1997). However, the dominant type of prey taxa differed among species, demonstrating the partitioning of food resources. Two species (*H. otakii* and *P. yokohamae*) were benthic invertebrate feeders that mainly consumed epibenthic crustaceans and polychaetes, respectively, whereas the diets of *L. japonicus* and *S. inermis* consisted

Table 2. Prey taxa identified by SIMPER for typifying (grey boxes) the dietary composition of each species, and distinguishing (unshaded boxes) among the dietary compositions of six fish species in northeastern Gwangyang Bay, Korea. “*” indicates that the percentage contribution of a prey taxon is greater for the species in the vertical column than in the horizontal row. Eight prey taxa that accounted for similarities or dissimilarities of > 10% were evaluated. Species codes are provided in Table 1

| | HA | HO | LJ | PY | SI | SS |
|----|---|--|---|--|--|-------------------------------------|
| HA | Seaweed Polychaeta Brachyura | | | | | |
| HO | Seaweed* Caridea Bivalvia Polychaeta* Amphipoda | Caridea Brachyura Amphipoda Bivalvia | | | | |
| LJ | Seaweed* Caridea Teleostei Brachyura* | Polychaeta Bivalvia* Amphipoda* Teleostei Brachyura* | Polychaeta Caridea | | | |
| PY | Seaweed* Brachyura* Ophiurida Bivalvia Polychaeta | Polychaeta Caridea* Brachyura* Ophiurida | Caridea* Ophiurida Bivalvia Amphipoda | Polychaeta Bivalvia | | |
| SI | Seaweed* Amphipoda Polychaeta* Teleostei Caridea | Bivalvia* Teleostei Amphipoda | Amphipoda Polychaeta* Teleostei | Polychaeta* Amphipoda Caridea Teleostei Ophiurida* | Amphipoda Teleostei Caridea Brachyura | |
| SS | Polychaeta* Teleostei Seaweed* Amphipoda | Teleostei Bivalvia* Caridea* Polychaeta* | Polychaeta* Teleostei Caridea* Amphipoda | Polychaeta* Teleostei Brachyura Ophiurida* | Amphipoda* Caridea* Teleostei Polychaeta* | Teleostei Brachyura Amphipoda |

Table 3. Schoener’s indices of dietary overlap for the diets of the nine pairwise comparisons of diet for species collected from the southern continental shelf of the East/Japan Sea, Korea. Bold letters indicate values > 0.6 (i.e., significant dietary overlap). Species codes are provided in Table 1

| | HA | HO | LJ | PY | SI | SS |
|----|------|------|------|------|-------------|----|
| HA | - | | | | | |
| HO | 0.48 | - | | | | |
| LJ | 0.45 | 0.30 | - | | | |
| PY | 0.36 | 0.25 | 0.28 | - | | |
| SI | 0.22 | 0.32 | 0.59 | 0.02 | - | |
| SS | 0.13 | 0.19 | 0.57 | 0.01 | 0.66 | - |

mainly of both benthic crustaceans and teleosts, with the later prey taxon being dominant in their diets. *S. schlegelii* fed heavily on teleosts (i.e., was piscivorous). Only *H. agrammus* was found to be omnivorous. Thus, although the six species

shared similar prey taxa, differential exploitations of prey were evident.

The diets of the six species reported here are comparable to those reported for other region in Korean waters. For example, amphipods, caridean shrimps, and teleosts dominated the diet of *H. otakii* in the western waters of Korea (Choi et al. 2017), but teleosts were not an important food resource in this study area. In the present study, teleosts were a substantial part of the *S. inermis* diet, which is inconsistent with the findings of previous studies (Huh and Kwak 1998). Such dietary inconsistencies between the present study and previous reports may be related to differences in locally available food resources, or to different lengths of fishes sampled. Generally, seagrass beds harbor higher densities of benthic invertebrates than other coastal habitats (Hemminga and Duarte 2000; Bloomfield and Gillanders 2005), and food

resources (i.e., benthic invertebrates) may not be limited for *H. otakii* in this type of habitat (Kwak et al. 2005). Thus, *H. otakii* can easily target seagrass-associated food resources rather than teleosts, which require more effort to capture and consume (Stoner and Livingston 1984). Furthermore, while *S. inermis* samples in previous studies included only juveniles (< 10 cm TL), samples in the present study included larger individuals. This may explain why teleosts featured more prominently in the diets of larger *S. inermis*, because Scorpaenidae species tend to increase their teleost consumption with size (Park et al. 2007; Baeck et al. 2013). Conversely, polychaetes (*P. yokohamae*) and teleosts (*L. japonicus* and *S. schlegelii*) were predominant in both the present study and previous dietary studies conducted in Korean waters (Kwak and Huh 2003; Huh et al. 2009; Park et al. 2007, 2016).

While all species (with the exception of *P. yokohamae*) consumed teleosts, the relative contribution of teleosts in the diet differed among species. Teleosts were a larger part of the diet for *L. japonicus*, *S. inermis*, and *S. schlegelii* than for other species. Teleosts are an important food resource for some fishes in coastal habitats (e.g., Bulman et al. 2001). Park et al. (2017b) reported that only one species (*Lophius litulon*) preyed heavily upon teleosts among nine co-occurring species in Southeastern Korea, and its diet was clearly distinguished from those of other species by the high contribution of teleosts. Platell and Potter (2001) also found that among 18 abundant benthic carnivorous fish species on the western coast of Australia, teleosts were a significant component of the diet of a single species of Platycephalidae. Although teleosts contributed most significantly to the *S. schlegelii* diet, they were not an important component of the diets of the two *Hexagrammos* species.

In addition to the present study, several other authors have compared diets between *H. agrammus* and *H. otakii* (Kwak et al. 2005), and between *H. otakii* and *S. schlegelii* (Seo and Hong 2007). Kwak et al. (2005) demonstrated that a higher degree of dietary overlap between *H. agrammus* and *H. otakii* was correlated with the abundance of a shared resource, but did not indicate the presence of interspecific competition for food resources. In contrast, Seo and Hong (2007) found that *H. otakii* and *S. schlegelii* had distinctly different dietary compositions and low indices of dietary overlap, indicating significant resource partitioning. Our results also revealed more dietary overlap between *H. agrammus* and *H. otakii*, and between *S. inermis* and *S. schlegelii*, compared with other between-species comparisons. From those studies, it is obvious

that high degrees of dietary overlap and lower levels of resource partitioning are prevalent between taxonomically similar species.

Because the six species in the present study coexist at shallow depths (< 10 m) over at least part of their ranges, the observed differences in diet may partly reflect their use of different microhabitats, which may house different suites of potential prey and/or require different types of foraging behavior (e.g., Lek et al. 2011). The two *Sebastes* species typically inhabit rocky reef matrices, whereas the greenling (Hexagrammidae) and flounder (Pleuronectidae) species are typically bottom-dwellers. Previous studies have also inferred microhabitat use. For example, Labropoulou and Machias (1998) observed that two sympatric gurnards, *Lepidotrigla cavillone* and *Trigla lastoviza*, exploited different habitats containing different prey.

The proportions of epibenthic crustaceans in the diets of *H. agrammus* and *H. otakii* suggested that these two species forage close to or just above the surface of the substratum, indicating a dependence on the suprabenthic and epibenthic communities. Meanwhile, the relatively high contribution of polychaetes to the *P. yokohamae* diet indicates that this species feeds within the substratum (see also Platell and Potter 1999). Piscivores typically feed in the water column, with benthopelagic prey resources (i.e., teleosts) being dominant in their diets (Bulman et al. 2001; Park et al. 2017a). In terms of niche width, the dietary niche breadth index was highest for *P. yokohamae*, followed by *H. agrammus*, *L. japonicus* and *H. otakii*, and the values were lowest for the two *Sebastes* species. These results indicate that benthic invertebrate feeders are more generalized predators than piscivores. Such differences in feeding behavior are important to facilitate resource partitioning among co-occurring fish species (Ross 1986; Platell and Potter 2001; Smith et al. 2011).

Partitioning of food resources is thought to occur when species whose distributions overlap exhibit differential predation to minimize competition for food (Krajewski et al. 2006). The six species in the present study displayed a low level of potential competition based on their diets. Multivariate analyses of dietary composition revealed that the diets of the six species differed significantly from one another, and this low level of dietary overlap indicated the existence of resource partitioning. Resource partitioning also has been observed among other fishes in Korean waters (e.g., Kwak et al. 2004; Park et al. 2017b), even between taxonomically similar species (e.g., Baeck et al. 2011).

The study characterized the diets and feeding relationships, and thus the resource partitioning, among six co-occurring species in northeastern Gwangyang Bay, Korea. Stomach contents revealed that all species were associated with the shallow coastal food web. Because all species consistently consumed benthic invertebrate and teleosts, they were placed within the range of secondary and/or tertiary consumers in the Southern Korean marine ecosystem, with piscivores representing a higher trophic level (Froese and Pauly 2017). Therefore, the ecological roles of these fishes as predators may be important in the marine ecosystem of these waters. Recently, loss of seagrasses in this region may be having a serious influence on the habitats and food resources that seagrass provide, and consequently food web structures may change, and primary and secondary production as well as the energy flow may decrease as a result of the reduction of seagrass beds (Heck et al. 1995). Due to the limited spatial and temporal range of samples collected, however, we were unable to shed light on possible changes in trophodynamic relationships among animals and to comprehensively characterize the diets of these species throughout their entire life histories. Nonetheless, our findings contribute to the understanding of prey–predator and predator–predator relationships in the coastal ecosystems of Korea.

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Appendix

Table S1. Prey taxa and identifiable prey items used in diet analyses of six fish species from northeastern Gwangyang Bay, Korea

| Taxa | Identifiable prey items (species or family level) |
|---------------|--|
| Amphipoda | Gammaridea: <i>Grandidierella</i> sp., <i>Pontogeneia</i> sp., Ampeliscidae, Leucothoidae, <i>Byblis japonicus</i> , <i>Monoculodes</i> sp.; Caprellidae: <i>Caprella acanthogaster</i> , <i>C. krojeri</i> , <i>C. scaura</i> , <i>C. tsugarensis</i> |
| Asciacea | Styelidae |
| Bivalve | Unknown |
| Caridea | Alpheidae, Crangonidae, <i>Heptacarpus rectirostris</i> , <i>Leptochela sydniensis</i> , <i>Latreutes planirostris</i> , <i>Pandalus gracillis</i> , <i>Plesionika grandis</i> , <i>Plesionika izumiae</i> , <i>Trachysalambria curvirostris</i> |
| Cephalopoda | <i>Sepioida</i> sp., <i>Loligo</i> sp. |
| Copepoda | Unknown |
| Crab | Juvenile crab (megalopal stage), <i>Cancer gibbosulus</i> , <i>Charybdis bimaculata</i> , Cheiragonidae, <i>Helice tridens</i> , <i>Hemigrapsus penicillatus</i> , <i>Parasesarma pictum</i> , <i>Pisoides bidentatus</i> , Portunidae, <i>Pugettia quadridens</i> , Pinnotheridae, <i>Anatolikos japonicus</i> , <i>Sphaerozius nitidus</i> |
| Cumacea | Unknown |
| Galattheoidea | <i>Pisidia serratifrons</i> |
| Gastropoda | Nassariidae, Nudibranchia |
| Isopoda | Unknown |
| Mysidacea | Unknown |
| Ophiurida | Unknown |
| Paguroidea | Diogenidae, Paguridae |
| Polychaeta | Ampharetidae, Capitellidae, <i>Glycinde</i> sp., <i>Lagis bocki</i> , <i>Lumbricalis japonica</i> , <i>L. longifolia</i> , <i>Lygdamis giardia</i> , <i>Nectoneanthes</i> sp., <i>Perinereis aibahitensis</i> , <i>Pherusa</i> sp., <i>Phylo felix asiaticus</i> , <i>Pista cristata</i> , Terebellidae |
| Penaeoidea | <i>Parapenaeopsis hardwickii</i> , <i>Parapenaeus lanceolatus</i> , <i>Metapenaeus joyneri</i> |
| Seaweed | Unknown |
| Teleosts | <i>Engraulis japonicus</i> , Gobiidae, Juvenile <i>Sebastes intermis</i> , <i>Nuquequula nuchalis</i> , <i>Thryssa kammalensis</i> |