



Variations in food resource usage among eight fish species inhabiting inside and outside Jinju Bay, Korea

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Abstract Jinju Bay is a semi-closed bay located on the mid-southern coast of Korea. The dietary habits of eight dominant fish species—*Liparis tanakae* (Tanaka’s snailfish), *Zoarces gillii* (an eelpout), *Pennahia argentata* (silver croaker), *Conger myriaster* (whitespotted conger), *Callionymus valenciennesi* (Valenciennes’ dragonet), *Thryssa kammalensis* (Kammal thryssa), *Sillago japonica* (Japanese whiting), and *Pholis fangi* (a gunnel)—collected from inside and outside of Jinju Bay were analyzed using stomach content analyses. As a result of multivariate analysis for each season, there were significant differences in dietary composition between species and

sampling sites in all seasons, except between study sites during summer. The eight common species were divided into four groups based on the cluster analysis. The first group contained *C. valenciennesi* and *Z. gillii*, which showed preferences for amphipods, while the second group, comprising *T. kammalensis*, fed mainly on crabs and mantis shrimps. The two species (*P. fangi* and *S. japonica*) in the third group tended to specialize in feeding on polychaetes, whereas the three species (*L. tanakae*, *C. myriaster*, and *P. argentata*) in the fourth group preyed on carid shrimp and teleosts. Although the eight species occurred in the same habitat and ingested a similar range of food resources, the contributions of different prey items were different in each species’ diet—differences in food resource use between species were evident. In conclusion, the results of stomach content analyses of the eight species showed evidence of ecological separation between species occurring inside and outside Jinju Bay.

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Introduction

The size of coastal fishing grounds in Korean seas is gradually decreasing due to coastal development. Consequently, the biological resources in coastal waters are being depleted due to habitat loss,

overfishing, and environmental pollution (Yoo et al. 1999; Zhang et al. 2003; Yoon et al. 2014). Coastal areas often act as spawning and nursery grounds for numerous marine organisms, and are thus an important habitat during their early life history (Hajisamae and Chou 2003; Song et al. 2012). These areas also have high economic value owing to their high fishing productivity (Houde and Rutherford 1993). Among the 10 sea zones designated as fisheries resource-protected areas in Korea, eight are located on the southern coast; thus, the southern coastal regions are highly regarded for their importance in terms of fishery resources (Yoo et al. 1999; Lee et al. 2009). The study area, Jinju Bay, is located in the central part of the southern coast and is one of the previously mentioned fisheries resource-protected areas, connecting the Namgang River in the northern part to the open sea on the east side (Song et al. 2012). Approximately 25% of the bay area consists of a shallow intertidal zone (Choo and Yoon 2015).

Generally, bay environments are rich in planktonic organisms because of the introduction of a large amount of nutrients from the land through river discharge (Selleslagh et al. 2009; Newton et al. 2014); these areas provide abundant food resources during the early growth of young marine organisms (Swearer et al. 1999). As such, bay environmental conditions have partially attracted attention as spawning and nursery grounds to facilitate early growth and high survival rates during the early life history of marine organisms (Vasconcelos et al. 2010). Studies on fish communities in the southern coastal areas of Korea have been conducted in Gwangyang Bay and Yeosu Bay (Cha and Park 1997; Lee et al. 2011), and have reported that small-sized fish species such as *Nuchequula nuchalis* and *Thryssa adelae*, and/or younger specimens of *Konosirus punctatus* and *Pennahia argentata*, were dominant in these areas. In addition, a number of studies on the feeding relationships among co-occurring species in shallow coastal habitats have been conducted to explain their ecological function and biological relationships (e.g., Motta et al. 1995; Kwak et al. 2015). Recently, Park et al. (2018) reported on the feeding relationship among six major fish species in Gwangyang Bay in southern Korea and concluded that each species showed different feeding characteristics according to their preferences for different food resources. These results indicate that various fishes occurring in the same

area show different life-history strategies to minimize interspecific competition by sharing or separating available food resources (Platell and Potter 2001).

The eight dominant species in this study (Myoung et al. 2020)—*Liparis tanakae* (Tanaka's snailfish), *Zoarces gillii* (an eelpout), *Pennahia argentata* (silver croaker), *Conger myriaster* (whitespotted conger), *Callionymus valenciennei* (Valenciennes' dragonet), *Thryssa kammalensis* (Kammal thryssa), *Sillago japonica* (Japanese whiting), and *Pholis fangi* (a gunnel)—are mainly distributed in the shallow coastal area of southern Korea, including Jinju Bay, occasionally forming dominant fish groups (Kwak and Huh 2003; Lee et al. 2011; Kwak et al. 2012; Jeong et al. 2013; Park et al. 2020a, b). Jinju Bay may be used as a spawning and nursery ground for several fish species because their eggs and larvae have been collected from Jinju Bay (Myoung et al. 2021). Among the above species, *L. tanakae*, *Z. gillii*, *P. argentata*, and *C. myriaster* are important commercial fish species in Korea (Kim et al. 2005). For example, *L. tanakae* is a representative winter commercial species in Korea; not only the fish body but also the eggs attached to fishing gear (e.g., traps and gill nets) are used as food (Kosaka 1971; Kim et al. 1986; Myoung et al. 2016). In addition, *C. myriaster* is an economically important fish species that is exported to Japan (Ryu et al. 2009).

The purposes of this study were (1) to identify the feeding characteristics of eight abundant fish species inhabiting Jinju Bay via stomach content analyses and (2) to examine any differences in the utilization of food resources among the species. The results of this study can identify the feeding relationship between major fish species occurring in the bay and will serve as basic ecological data for the resource management of dominant species inhabiting the areas inside and outside of Jinju Bay. In addition, it is important to understand the characteristics of the bay ecosystem by identifying the structure of the food network between these co-occurring species.

Materials and methods

Survey area and sampling method

In this study, fish sampling was conducted at stations inside and outside Jinju Bay, located in the middle-southern waters off Korea (Fig. 1). The distance

between the two stations was approximately 15 km. The sampling stations were set based on the difference in the intensity of salinity stratification according to the strength of freshwater flows from Namgang Dam, located in the northern part of Jinju Bay (Kim et al. 2010; Kang et al. 2011). Fish samples were collected monthly from March 2015 to November 2015 using a shrimp beam trawl net with 6-m width, 1-m height, and 20-mm mesh. The shrimp beam trawl was towed at approximately 1.6 knots for 1 h, with an estimated 17,780 m² coverage per sampling event.

The collected fishes were identified according to the guideline of taxonomic classification for Korean fishes (Kim et al. 2005; Nakabo 2013), and the scientific name and taxonomic classification followed

Kim et al. (2019) and Nelson et al. (2016). This study analyzed the stomach contents of the eight abundant fish species among a total of 81 species collected by shrimp beam trawl (Myoung et al. 2020). For each specimen, the TL and weight were measured to the nearest 0.1 cm and 0.1 g, respectively. The stomach of each specimen was removed, and the contents were preserved in 99% ethanol.

Stomach contents analysis

The stomachs were cut open and incised using tweezers and scissors under a dissecting microscope. All prey items were identified to the lowest possible taxonomic level, and individuals that proved difficult to

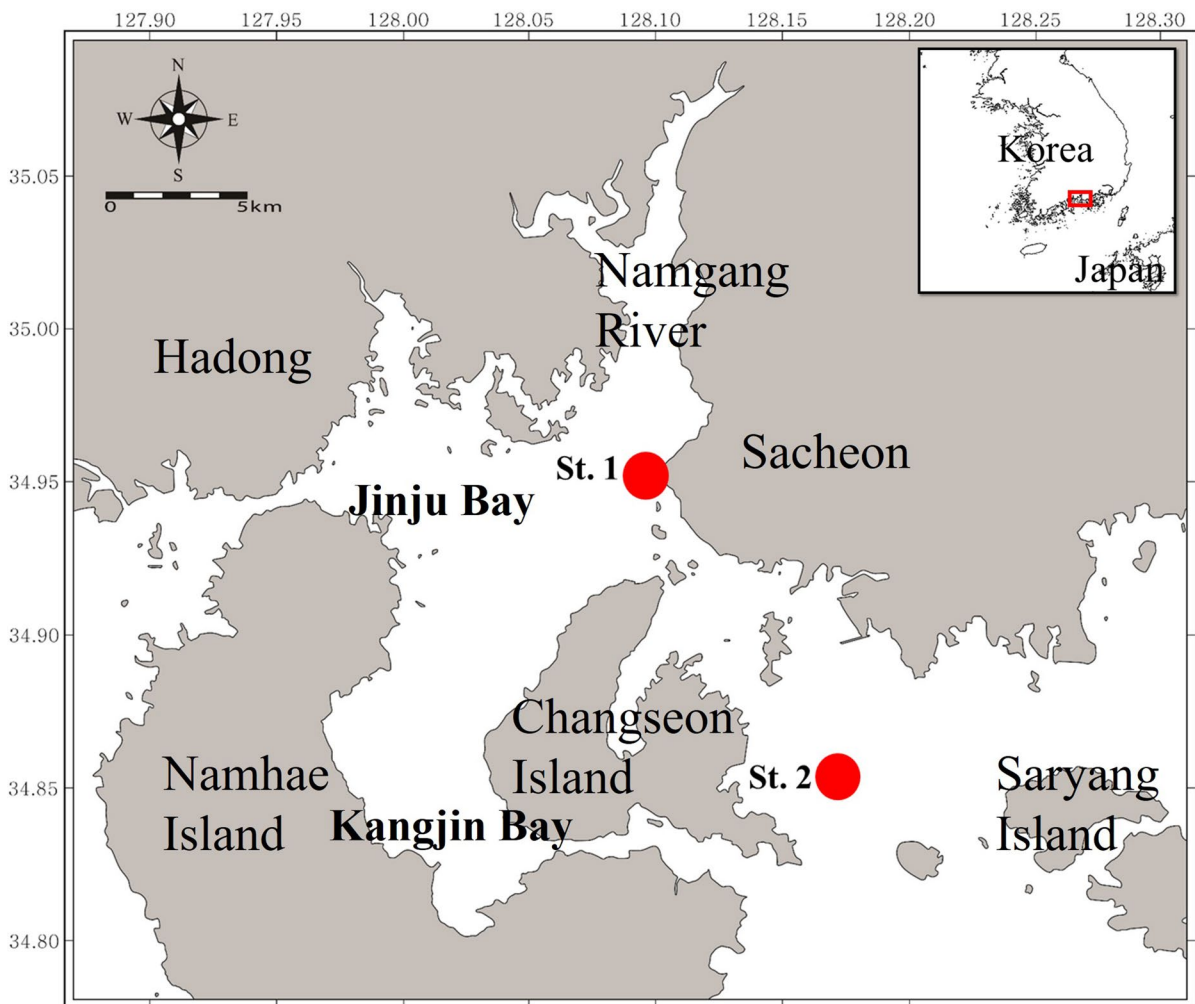


Fig. 1 Location of the sampling stations inside and outside of Jinju Bay, southern Korea

identify were classified to the family or order level. The number and weight of all food organisms in the stomach contents were measured. Because gravimetric dietary data are considered to best represent the relative importance of each prey taxon, especially when different-sized prey are ingested (Hyslop 1980), the dietary data were expressed as a percentage weight ($\%W = 100 \times W_i \times W_T^{-1}$) of all prey organisms for each specimen's stomach, where W_i is the weight of prey individual i and W_T is the total weight of prey items. The $\%W$ of each prey item in each stomach is expressed as the average value for all individuals.

Data analysis

Cumulative prey curves were calculated for each species to assess whether a sufficient number of stomachs were analyzed to describe the diet (Ferry and Cailliet 1996). The dietary data were randomized 100 times, and the cumulative number of new prey taxa was recounted for each randomization. Because visual examination of prey curves for an asymptote is unreliable, the slope of the linear regression (b) through the last five subsamples validated the sample size, where $b \leq 0.05$ signified acceptable leveling off of the prey curve for diet analyses (Bizzarro et al. 2009). The analysis was performed with R version 4.2.1 (R Core Team 2022) using the 'vegan' packages (Oksanen et al. 2022).

Multivariate analyses based on weight dietary data were used to analyze inter- and intraspecific feeding relationships. In this study, the dietary data of eight species were analyzed from two perspectives. First, since the eight dominant species did not occur together in each season, analyses of the intra- and interspecific feeding characteristics against seasonal available food resources were conducted separately for each season. Consequently, the feeding relationship (variations between species) in two habitats (inside and outside Jinju Bay) was analyzed according to each season (spring, summer, and autumn). Second, although the occurrence trends of the dominant species did not overlap seasonally, the sampling method and time (seasonal sampling) had limitations in including the true occurrence of dominant fish species in the study area. In addition, the overall feeding characteristics of fish species can be reflected by their average food consumption (aggregating feeding over potential habitats and seasons) inherent in each species (Gerking 1994). Therefore, the population level

feeding relationships were analyzed by considering only the "species."

To analyze the feeding relationship, three to five individuals collected at the same station and season were randomly sorted by species into subgroups, and the average weight percentage of the prey taxa was calculated for each subgroup to make a sample for multivariate analysis (Park et al. 2017b). Such subgrouping can reduce the number of prey taxa that show a weight contribution of "0" in the stomach contents, thus increasing the effectiveness of multivariate analysis (Platell and Potter 2001; White et al. 2004; Marshall et al. 2008). The dietary data were square root-transformed to avoid any tendency of the main dietary components being excessively dominant, and a similarity matrix was constructed using the Bray–Curtis similarity (Platell and Potter 2001). The Bray–Curtis similarity matrix was visualized using non-metric multidimensional scaling (nMDS) and cluster analysis. Significant differences in dietary composition between species and/or habitats were tested using permutational multivariate analysis of variance (PERMANOVA). PERMANOVA is a non-parametric distance-based analysis of variance that uses the permutation method to test a hypothesis. If there was a significant difference in the PERMANOVA analysis, posteriori pairwise PERMANOVA comparisons were performed to determine which interaction terms differed significantly among variables within each factor level. Canonical analysis of principal coordinates (CAP) was used to determine which prey taxon showed correlation coefficients contributing to the difference in the feeding relationships among species. The prey taxa with correlation coefficients higher than 0.4 were plotted on CAP component axes 1 and 2. For this analysis, the PRIMER v7 multivariate statistics package with the PERMANOVA + add-on module was used (Anderson et al. 2008; Clarke and Gorley 2015).

Diet overlap among eight 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 weight contribution) in the diet of species x and y . C_{xy} ranged from 0 (diets containing no items in common) to 1 (complete overlap). An index value > 0.6 indicated high diet similarity and was considered biologically significant (Langton 1982).

Results

Composition of stomach contents

In this study, the diets of 976 individuals of the eight species were examined. The proportion of empty stomachs ranged from 1.3% (*L. tanakae*) to 42.5% (*C. valenciennei*). Nineteen identifiable prey taxa were identified in the remaining 820 stomachs (after the removal of

empty ones) (Table 1). Cumulative prey curves for all species aggregating all seasons and sites reached stable asymptotes, indicating sufficient sample sizes for an accurate description of the diets of the species included in the study (Fig. S1). While the proportion of individuals sampled for stomach contents was not reached for some seasonal and spatial subgroups of *P. argentata*, *C. valenciennei*, *C. myriaster*, and *S. japonica*, all cumulative prey curves calculated for both sites according to

Table 1 Total number of specimens, range of total length, percentage of empty stomachs, and relative weight contributions of prey taxa in the diets of eight fish species in Jinju Bay, Korea. Species code: LT, *Liparis tanakae*; ZG, *Zoarces gillii*; PA,

Pennahia argentata; CM, *Conger myriaster*; CV, *Callionymus valenciennei*; TK, *Thryssa kammalensis*; SJ, *Sillago japonica*; PF, *Pholis fangi*. Numbers in bold indicate mass contributions of the three most typifying prey items for each species diet

Species code	LT	ZG	PA	CM	CV	TK	SJ	PF
Number of specimens	80	189	149	62	73	113	161	149
Range of total length	5.2–48.2	9.8–40.8	4.1–23.2	11.5–41.3	4.8–16.1	4.4–13.3	8.4–21.1	11.3–18.5
Empty (%)	1.3	7.4	17.4	12.9	42.5	24.8	17.4	13.4
Taxa								
ANELLIDA								
Polychaeta	0.3	9.0	6.8	8.8	10.8	2.5	54.0	47.9
MOLLUSCA								
Bivalvia	0.2	10.9	0.1	4.9	37.1	4.8	8.6	1.9
Cephalopoda	0.6	–	0.6	8.9	0.1	–	0.8	–
Gastropoda	–	0.9	–	–	7.5	–	–	–
Unidentified	–	–	–	1.3	–	–	5.4	–
CRUSTACEA								
Amphipoda								
Gammaridea	4.3	63.1	4.4	3.1	24.8	9.3	6.1	25.2
Caprellidea	–	<0.1	0.8	–	–	<0.1	3.5	2.0
Copepoda	–	0.2	<0.1	–	4.2	2.5	–	–
Cumacea	–	8.0	–	–	–	–	–	–
Euphausiacea	–	0.2	3.5	–	1.9	1.4	–	–
Isopoda	–	–	0.4	–	–	–	–	–
Mysidacea	–	–	–	–	–	0.6	–	–
Stomatopoda	–	–	10.6	0.1	1.9	16.6	0.8	–
Decapoda								
Brachyura	1.2	1.0	6.9	12.2	1.3	52.9	6.0	1.5
Caridea	85.4	4.2	31.3	32.0	–	8.2	7.1	19.1
Paguroidea	–	0.2	–	1.3	1.0	–	–	1.6
Ostracoda	–	–	–	–	9.4	–	–	–
ECHINODERMATA								
Ophiuroidea	–	2.1	–	–	–	–	4.2	–
CHORDATA								
Teleostei	8.0	<0.1	34.4	27.3	–	1.2	3.5	0.8
Others								
Seaweeds	0.1	–	–	–	–	–	–	–

three seasons for the diets of *L. tanakae*, *Z. gillii*, *T. kammalensis*, and *P. fangi* attained asymptoticity (Fig. S2).

In the diets of *L. tanakae*, carid shrimps were the most dominant prey taxon, with a %W of 85.4%. In the diets of *Z. gillii*, gammarid amphipods were the most abundant (63.1% in %W), followed by bivalves (10.9%). Both teleosts and carid shrimps were important prey items in the diets of *P. argentata* and *C. myriaster*, constituting 34.4% and 31.3% of the %W (teleosts) and 27.3% and 32.0% of the %W (carid shrimps), respectively. *C. valenciennei* mainly consumed bivalves (37.1%) and gammarid amphipods (24.8%), whereas *T. kammalensis* mostly ingested crabs (52.9%), followed by stomatopods (16.6%). Polychaetes only contributed to the diets of *S. japonica* and *P. fangi*, with %W values of 54.0% and 47.9%, respectively. Among the minor prey taxa, ostracods occurred only in the diets of *C. valenciennei* (9.4%), cumaceans in *Z. gillii* (8.0%), isopods in *P. argentata* (0.4%), and mysids in *T. kammalensis* (0.6%), whereas seaweed was found only in the diets of *L. tanakae* in small amounts (<0.1%).

Variations in stomach contents according to season and station

The eight dominant fish species showed different trends in food consumption according to season and habitat (Fig. 2). During the spring, *L. tanakae* and *Z. gillii* indicated similar diets inside and outside the bay in that they exclusively fed on carid shrimps and amphipods, respectively. *C. myriaster* and *P. fangi* showed a gradually increased consumption of carid shrimps and polychaetes, but decreased consumption of teleosts and carid shrimps at the outside site, respectively. However, *S. japonica* showed a more diverse dietary composition inside than outside the bay. Among the fish species that occurred in summer, *C. myriaster*, *P. argentata*, *T. kammalensis*, and *Z. gillii* showed significant differences in their diets between the inside and outside sites. These differences were mainly due to the increasing or decreasing consumption of specific food items at the outside site. For example, carid shrimps were more abundant in the diets of *C. myriaster* and *P. argentata*, and the consumption of crabs increased in the diets of *T. kammalensis* at the outside site. *P. fangi* and *S. japonica* collectively consumed polychaetes at both

sites, although the consumption of other food items differed slightly between the two sites. *Z. gillii* consumed mostly gammarid amphipods at the inside site, but both gammarid amphipods and bivalves contributed to the diet. Fish species collected during autumn also showed differences in their dietary compositions, as indicated by the spring and summer trends. *P. argentata* and *C. myriaster* collected at the inside site fed evenly on various food items, whereas both species mainly ingested teleosts at the outside site. In the case of *C. valenciennei*, gammarid amphipods mainly contributed to the diets at the inside site, whereas bivalves showed the highest contribution to the diet at the outside site. *S. japonica* fed mainly on polychaetes at both the inside and outside sites, and *T. kammalensis* showed a surprisingly high consumption of stomatopods at the outside site.

The two-way PERMANOVA for each season showed significant differences in the diets between species and between stations in all seasons except for between sites during summer (Table 2). There also were significant interactions between species and sites in all seasons. The PERMANOVA pairwise comparison of species–site interactions showed that the diets between the inside and outside sites were significantly different for *S. japonica* and *Z. gillii* during spring; for *S. japonica*, *T. kammalensis*, and *Z. gillii* during summer; and for *P. argentata*, *C. valenciennei*, and *S. japonica* during autumn (Table 3). In addition, there were significant differences in most comparisons between species in each season within each site. Between-species comparisons of *L. tanakae* and *P. fangi*, *L. tanakae* and *Z. gillii*, and *P. fangi* and *Z. gillii* collected during spring showed significant differences at both the inside and outside sites. During summer, 19 pairwise species comparisons were significantly different at the outside site, while only five comparisons were significantly different at the inside site. The pairs *P. argentata* and *C. valenciennei* and *P. argentata* and *S. japonica* collected during autumn also showed significant differences at both sites (Table 4).

Population level feeding relationships among eight species

PERMANOVA with unrestricted permutations of raw data showed a significant difference in dietary

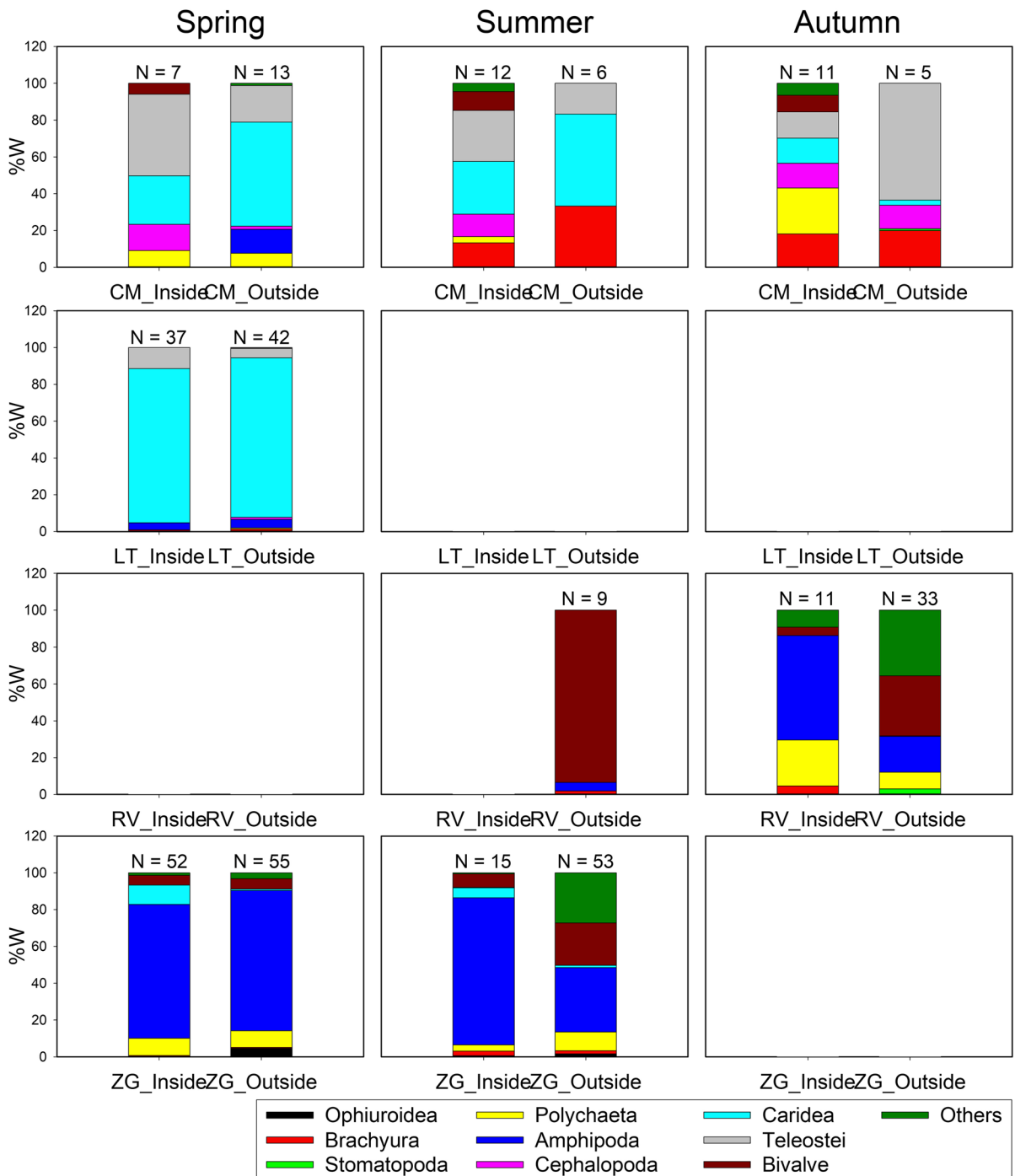


Fig. 2 Mean percentage weight contributions (%W) of the different dietary component of eight fish species in Jinju Bay, Korea. Species codes were shown in Table 1 legend

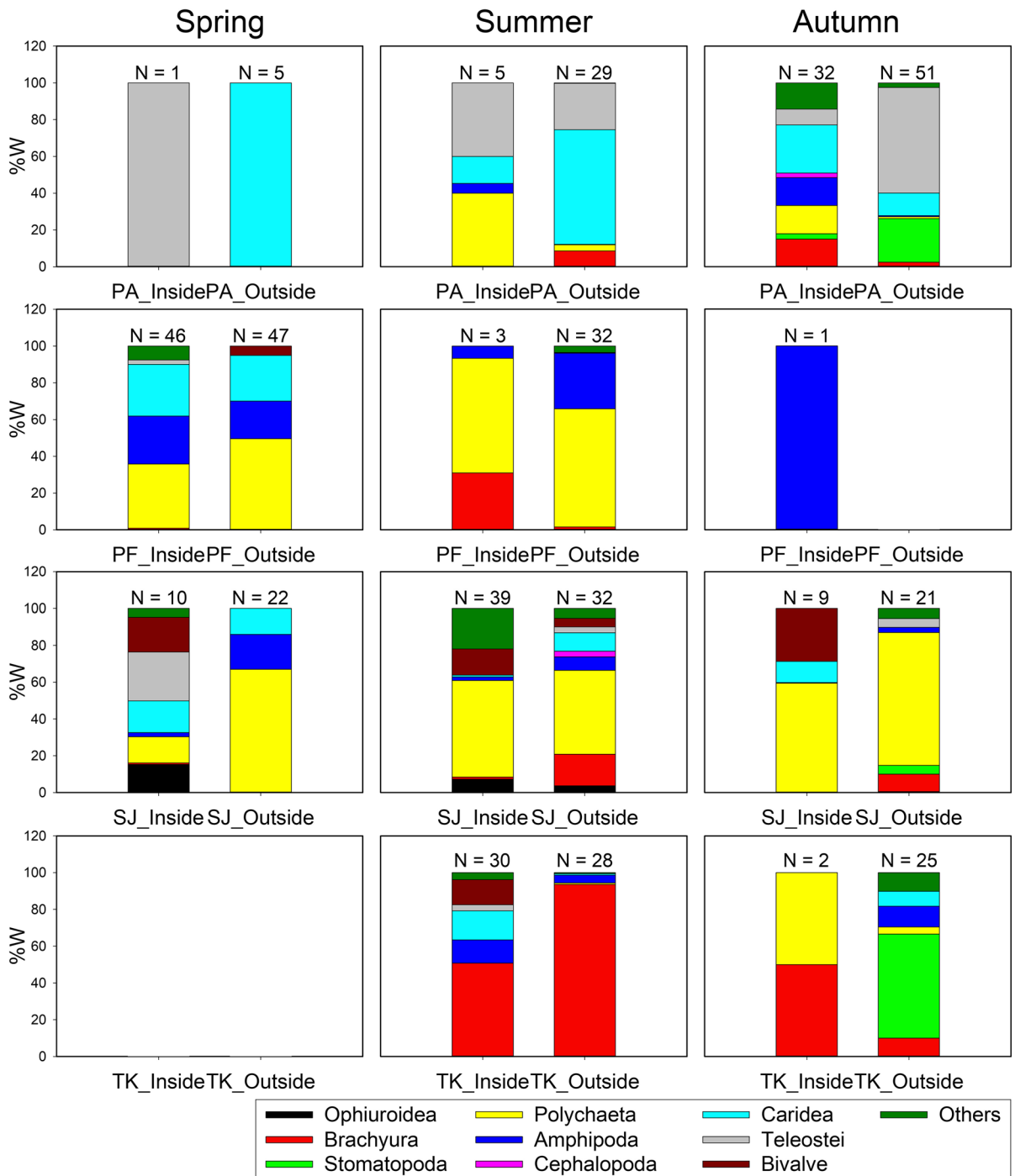


Fig. 2 (continued)

Table 2 Mean squares (MS), pseudo-*F* ratios, and significance levels (*p*) for a series of permutational multivariate analysis of variance (PERMANOVA) tests employing the Bray–Curtis similarity matrix derived from the mean percentage weight contributions of the various prey taxa to the stomach contents for differences in response to species, site, and interactions of the two factors. Values in bold indicate significance at $p \leq 0.05$

Source		df	MS	Pseudo- <i>F</i>	<i>P</i> (perm)
Spring	Species	5	16,592.0	33.476	0.001
	Site	1	4810.8	9.706	0.001
	Species × site	4	1875.8	3.784	0.001
	Residuals	61	495.7		
Summer	Species	6	12,943.0	22.381	0.001
	Site	1	1090.4	1.896	0.177
	Species × site	5	3004.2	5.195	0.001
	Residuals	50	578.3		
Autumn	Species	4	11,498.0	13.360	0.001
	Site	1	7841.5	9.112	0.001
	Species × site	4	3635.6	4.225	0.001
	Residuals	35	860.6		

Table 3 Results of pairwise permutational multivariate analysis of variance (PERMANOVA) tests between site comparisons within each species and season. *n.s.* no significance. Species codes are shown in the Table 1 legend

	Species	Spring	Summer	Autumn
Between site (Inside vs. Outside)	CM	n.s	n.s	n.s
	LT	n.s	–	–
	PA	–	n.s	***
	PF	–	n.s	–
	CV	–	–	**
	SJ	*	**	*
	TK	–	**	n.s
	ZG	**	**	–

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

composition among fish species (PERMANOVA, pseudo-*F* = 51.898, $p = 0.001$). The differences in the dietary compositions among the fish species were visually divided into four groups based on both cluster analysis and nMDS ordination plot at a similarity level of 55% (Fig. 3). The first group included *Z. gillii* and *C. valenciennei*, which mainly consumed gammarid amphipods and bivalves. Only one species (*T. kammalensis*) belonged to the second group. The third group (*P. fangi* and *S. japonica*) preferred

polychaetes as their primary food source. The fourth group included three species (*L. tanakae*, *C. myriaster*, and *P. argentata*), which ingested both carid shrimps and teleosts as their main prey items.

Canonical analyses of principal coordinates (CAP) further demonstrated that each feeding group could be classified according to the different contributions of each food item (Fig. 4). Gammarid amphipods distinguished *Z. gillii* and *C. valenciennei* from other groups, and polychaetes were key in separating *P. fangi* and *S. japonica* from other species. Three prey taxa (carid shrimps, teleosts, and stomatopods) were characteristic of the diets of *L. tanakae*, *P. argentata*, and *C. myriaster*, and crabs showed a strong contribution to the diets of *T. kammalensis*.

Dietary overlaps between species comparisons were mostly lower than the biological significance of 0.6; only the comparison between *C. myriaster* and *P. argentata*, and between *P. fangi* and *S. japonica*, revealed an overlap of > 0.6 (Table 5), whereas the overlap values were relatively low between species in feeding group A or B and group D (see Fig. 3), indicating that these groups of species had dissimilar diets.

Discussion

Individuals of the eight species collected from Jinju Bay were mostly juveniles comparable in size to the adults or small-sized specimens, but only some species included their adult conspecifics (Kim et al. 2005; Froese and Pauly 2022). For example, the length of maturity of *P. argentata* is 19.3-cm TL (Jeon et al. 2020) and the standard length of *L. tanakae* is 38.2 cm (Park 2010). In this study, only 16 mature individuals (> 21.7 cm TL) of the former species and one specimen (40.8 cm TL) of the latter species were collected; the proportions of immature individuals were 89.3% and 98.8%, respectively. In addition, the sizes of all *C. myriaster* specimens collected were less than the maturity size of 50.8 cm TL (Kim et al. 2011). *Callionymus valenciennei*, *T. kammalensis*, and *P. fangi* are relatively small-sized species, and their sizes at maturity do not reach 20-cm TL (Froese and Pauly 2022). Only *Z. gillii* and *S. japonica* included both their juvenile and adult specimens. Shallow coastal regions, including estuaries and

Table 4 Results of pairwise permutational multivariate analysis of variance (PERMANOVA) tests between predator comparisons within each site and season. *n.s.* no significance. Species codes are shown in the Table 1 legend

		Spring		Summer		Autumn	
		Inside	Outside	Inside	Outside	Inside	Outside
Between species	CM vs. LT	*	n.s	–	–	–	–
	CM vs. PA	–	n.s	n.s	n.s	*	n.s
	CM vs. PF	*	**	n.s	*	–	–
	CM vs. CV	–	–	–	n.s	n.s	–
	CM vs. SJ	n.s	*	**	*	n.s	–
	CM vs. TK	–	–	*	*	n.s	n.s
	CM vs. ZG	*	**	n.s	*	–	–
	LT vs. PA	–	n.s	–	–	–	–
	LT vs. PF	***	***	–	–	–	–
	LT vs. SJ	*	**	–	–	–	–
	LT vs. ZG	***	***	–	–	–	–
	PA vs. PF	–	n.s	–	***	–	–
	PA vs. CV	–	–	–	*	*	***
	PA vs. SJ	–	n.s	n.s	**	*	***
	PA vs. TK	–	–	n.s	**	n.s	***
	PA vs. ZG	–	n.s	n.s	**	–	–
	PF vs. CV	–	–	–	*	–	–
	PF vs. SJ	*	n.s	n.s	**	–	–
	PF vs. TK	–	–	n.s	***	–	–
	PF vs. ZG	***	***	n.s	***	–	–
CV vs. SJ	–	–	–	*	n.s	***	
CV vs. TK	–	–	–	*	n.s	***	
CV vs. ZG	–	–	–	*	–	–	
SJ vs. TK	–	–	***	**	n.s	**	
SJ vs. ZG	*	***	**	***	–	–	
TK vs. ZG	–	–	*	***	–	–	

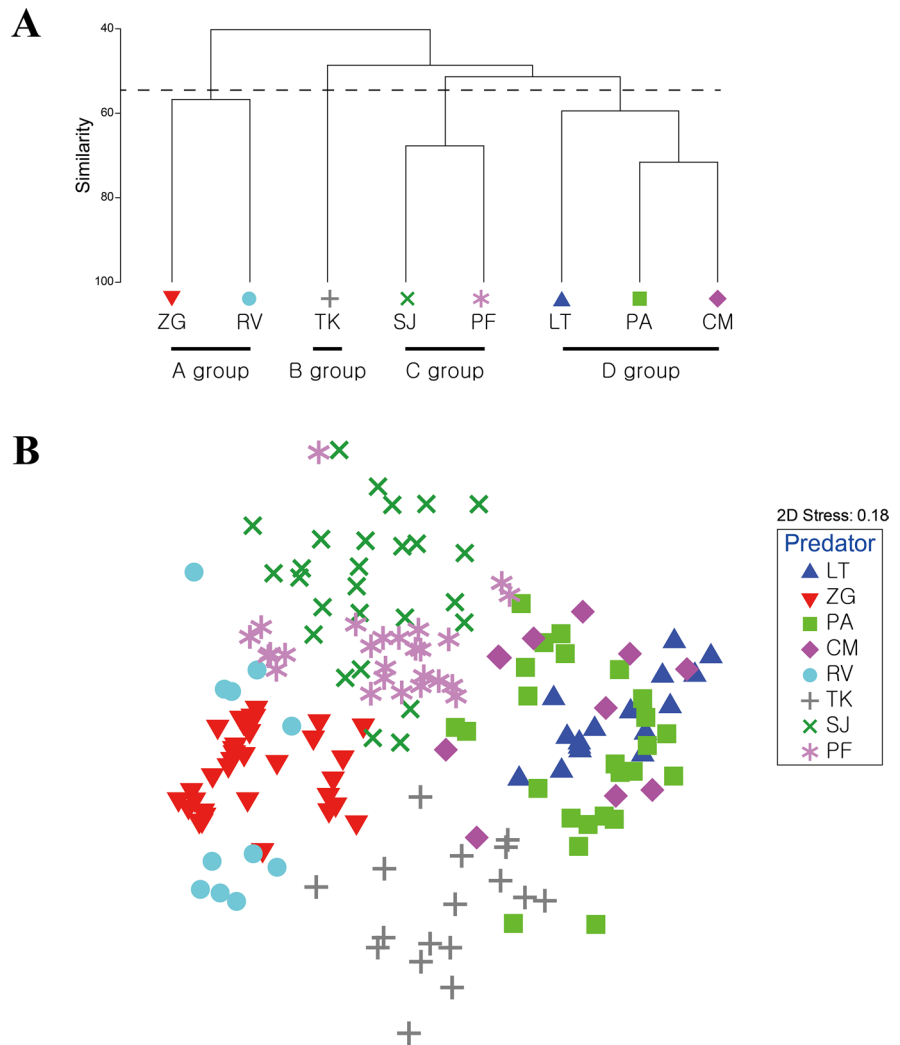
* $p < 0.05$; ** $p < 0.01$;
*** $p < 0.001$

seagrass habitats, are known as good places for nursery grounds for the early stages of marine organisms (Vasconcelos et al. 2010; Park and Kwak 2018); they provide a variety of food organisms compared to offshore coastal areas and are a safe habitat for the early growth and survival of various marine organisms (Lefcheck et al. 2019; Youn et al. 2019). Among the 81 fish species collected in the study area, 57 species from both the inside and outside sites were all immature specimens (Myoung et al. 2020). Song et al. (2019) also showed that more smaller and juvenile specimens were collected in the inner bay than in the offshore coastal waters of Namhae Island, Korea.

Most of the species analyzed in this study mainly consumed benthic prey organisms, but teleosts also showed moderate contributions to the diets of *P. argentata* and *C. myriaster* (Table 1).

Several previous studies have reported similar dietary compositions to the current study. In previous studies, *L. tanakae*, *Z. gillii*, and *C. valenciennei* inhabiting the southern sea of Korea were found to mainly consume benthic carid shrimps, gammarid amphipods, and polychaetes, respectively, which were also dominant in the diets of the same species in this study (Huh 1997; Huh and Kwak 1998; Huh and Baeck 2000, 2003). In addition, higher contributions of teleosts to the diets of *P. argentata* and *C. myriaster* have been reported previously (Huh and Kwak 1998; Koh et al. 2014). Although *T. kammalensis* is classified as a pelagic fish, it mainly preys on crabs. However, all crabs found in the diets of *T. kammalensis* were in the zoea stage. In previous studies, *T. kammalensis* was also found to feed on arrow worms and megalopa-stage crabs (Baeck et al. 2014). Therefore,

Fig. 3 Cluster analysis (A) and non-metric multidimensional scaling (nMDS) ordination (B) of dietary compositions constructed from Bray–Curtis similarity matrix for eight fish species inhabiting Jinju Bay, Korea. Species codes are shown in the Table 1 legend



T. kammalensis likely prefers large pelagic prey organisms with weak mobility.

In this study, *C. myriaster* and *P. argentata* consumed more teleosts than did other fish species. When comparing similar-sized specimens from previous studies, similar results to this study were also observed in the diets of *C. myriaster* inhabiting an eelgrass bed in Gwangyang Bay and *P. argentata* occurring around Sejon Island on the southern coast of Korea (Huh and Kwak 1998; Koh et al. 2014). However, *P. argentata* inhabiting the Nakdong River estuary showed results different from those in the present study (Huh et al. 2018). In the Nakdong River estuary, a similar total length of *P. argentata* (9.0–23.9 cm TL) consumed only a small amount of teleosts, but carid

shrimps constituted almost half of the diets (Huh et al. 2018). This is thought to be due to the high abundance of carid shrimps as food resources for predators in estuarine environments (Upchurch and Wenner 2008). Therefore, the regional differences in preferred food organisms are the result of the different types of available food resources harboring different habitats (Kim et al. 2013).

Carid shrimps accounted for most of the dietary content of *L. tanakae*, with crangonid shrimp being the most common carid species in the diets (Table S1). A high ratio of crangonid shrimps has also been found in the diets of *L. tanakae* occurring elsewhere, including the southern coast of Korea (Huh 1997), the southern part of the East Sea (Park et al. 2017b), the Seto Inland Sea of

Fig. 4 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. Species codes are shown in the Table 1 legend

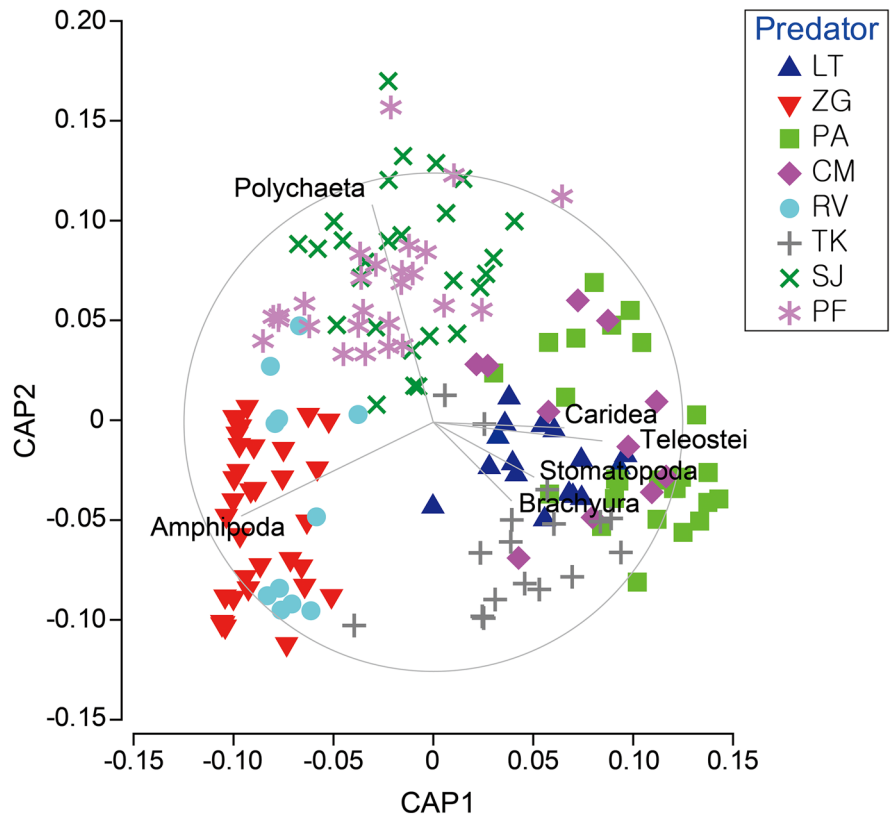


Table 5 Schoener’s indices of dietary overlap for the diets of the 28 pairwise comparisons among eight species inhabiting Jinju Bay, Korea. Values in bold indicate values > 0.6 (i.e., significant dietary overlap). Species codes are shown in the Table 1 legend

	LT	ZG	PA	CM	CV	TK	SJ	PF
LT	–							
ZG	0.10	–						
PA	0.46	0.17	–					
CM	0.45	0.22	0.76	–				
CV	0.06	0.47	0.17	0.19	–			
TK	0.15	0.22	0.35	0.32	0.24	–		
SJ	0.17	0.31	0.30	0.36	0.28	0.29	–	
PF	0.26	0.42	0.34	0.37	0.40	0.24	0.67	–

Japan (Kobayashi and Hiyama 1991), and the Yellow Sea off China (Jin et al. 2010). Crangonid shrimps mainly inhabit shallow coastal waters, including estuaries and inside the bay (Hanamura and Matsuoka 2003; Maher et al. 2013), and constitute a major group in the benthic community of Jinju Bay (Song et al. 2012). Abundant prey organisms in the marine ecosystem have a high probability of encountering predators and consequently provide an increase in catch success for predators (Persson and Diehl 1990). Similarly, the

highly diverse polychaetes in Jinju Bay (accounting for 80% of all benthic infauna; Kang et al. 2002) likely enhanced the foraging ratio of polychaetes for *P. fangi* and *S. japonica*.

Although stomatopods were not a common food item for the fish inhabiting Jinju Bay, it showed a tendency to increase in the diets of fishes collected outside of the bay during autumn. Stomatopods were ingested by *C. valenciennei*, *S. japonica*, *P. argentata*, and *T. kammalensis* during autumn and constituted 56.6% and 23.8% of the diets of

T. kammalensis and *P. argentata*, respectively. Most stomatopods ingested by the fishes are young juveniles of *Oratosquilla oratoria*. The spawning season of stomatopods occurs between May and September in the innermost coastal habitats of the Northwest Pacific regions, including Korean waters, and then they gradually move to deeper waters toward offshore as they grow (Hamano et al. 1987; Kodama et al. 2004). Because our autumn sampling was conducted between September and November, some fish species in this study likely had a high chance of capturing young stomatopods outside of Jinju Bay. In addition, because the stomatopods consumed were mostly pre-settled larvae and/or juveniles on the benthic layer (Hamano et al. 1987), they were more abundant in the diets of benthopelagic fishes (i.e., *P. argentata* and *T. kammalensis*), but were less important for other benthic fishes.

Although the eight species in this study ingested a similar range of food resources, the contribution of each prey item was different in each species' diet, and they were consequently divided into four feeding groups according to the type of food they consumed. Such differentiation of prey items among the eight species may reflect their different foraging behaviors and/or mouth morphologies (Hyndes et al. 1997; Park et al. 2017a). The two species (*Z. gillii* and *C. valenciennei*) in the first group are typical benthic fishes and show the development of a bottom-faced mouth morphology that facilitates feeding more on epifaunal prey items, such as gammarid amphipods, inhabiting the surface of the benthic layer (Fugi et al. 2001; Bonato et al. 2017). The body of *T. kammalensis* is suitable for feeding on small-sized pelagic prey items because the species is a small-sized pelagic fish and shows pelagic feeding behavior, unlike other fish species (Baeck et al. 2014). The two species (*S. japonica* and *P. fangi*) in the third group have relatively small heads and protruding mouth structures that are suitable for feeding on infaunal prey items such as polychaetes (Huh et al. 2018; Park et al. 2020a, b). In contrast, the fourth group of fishes, comprising *L. tanakae*, *P. argentata*, and *C. myriaster*, have relatively large mouth sizes and high mobility, which are advantageous for preying on large and mobile prey items, such as teleosts and carid shrimps (Huh 1997; Park et al. 2017b;

Huh et al. 2018). Diet overlaps also indicated relatively higher values between species within the same feeding group, but lower between different feeding groups, especially between groups A (epifaunal predators) and D (benthopelagic predators). Therefore, each of the major fish species in this study feeds on different prey items based on differences in their mouth morphology, behavior (pelagic vs. benthic), feeding strategy, and foraging ability; consequently, they can coexist by utilizing different types of food resources in the same area. Such differences in resource utilization are common among different species inhabiting the same habitat (Kwak et al. 2004; Nanjo et al. 2008), even within the same family (e.g., Park et al. 2017a), and/or the same genus (e.g., Hajisamae et al. 2006; Huh et al. 2016; Amariles et al. 2017), and can be important for maintaining ecosystem functions by minimizing competition for limited food resources and preventing the depletion of food resources (Krajewski et al. 2006; Adam et al. 2015; Park et al. 2018).

This study analyzed the dietary contents of eight abundant fish species inhabiting sites inside and outside of Jinju Bay. Except for *T. kammalensis*, all of the other studied species were benthic or semi-benthic predators, which commonly consumed carid shrimps, gammarid amphipods, polychaetes, and benthopelagic teleosts. However, the ratio of prey items was different in the diets of each species, and consequently, they could coexist in the same area by reducing competition for food resources. The feeding relationships among the eight dominant species in Jinju Bay were also evident according to the habitat and/or season. However, a lack of samples for identifying populations of prey organisms imposed limitations on our ability to describe direct prey–predator relationships in benthic ecosystems. The results from this study are important not only as a scientific basis for studying the trophic flow associated with the demersal food web in Jinju Bay, but also as basic data for further comparisons of the diets of the same species inhabiting different environments.

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Author contribution SHM, JKK, SNK, and JMP conceived the study. SHM and SNK contributed to sample preparation for stomach content analysis. JMP reviewed and revised the manuscript. JKK supervised the study.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author upon request.

Declarations

Ethic approval Not applicable for that section.

Consent to participate All authors have agreed to participate.

Consent for publication All authors have read and agreed to the published version of the manuscript.

Conflict of interest The authors declare no competing interests.

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