

Partitioning of food resources among *Sillago japonica*, *Ditrema temmincki*, *Tridentiger trignocephalus*, *Hippocampus japonicus* and *Petroscirtes breviceps* in an eelgrass, *Zostera marina*, bed

Seok Nam Kwak^a, Sung-Hoi Huh^b & David W. Klumpp^c

^aKorea Inter-university Institutes of Ocean Science, Pukyong University, 599-1 Daeyeon-Dong, Namgu, Pusan 608-737, Korea (e-mail: seoknam@hotmail.com)

^bDepartment of Oceanography, Pukyong University, 599-1 Daeyeon-Dong, Namgu, Pusan 608-737, Korea

^cAustralian Institutes of Marine Science, PMB No 3, Townsville MC QLD 4810, Australia

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Synopsis

We carried out dietary analysis on five numerically abundant fishes, *Sillago japonica*, *Ditrema temmincki*, *Tridentiger trignocephalus*, *Hippocampus japonicus* and *Petroscirtes breviceps* in an eelgrass bed in Kwangyang Bay, Korea. Comparisons between species demonstrated that the dietary composition of each fish species was significantly different from that of every other species. Although gammarid amphipods and caprellid amphipods were consumed by all species, their individual contributions to each species' diet varied. Furthermore, polychaetes contributed to the diets of *S. japonica* and *T. trignocephalus* and crab larvae were consumed by *D. temmincki*. Algae and eelgrass were not consumed by four fish species and made only a minimal contribution to the diet of *P. breviceps*. The diet of each fish species except *H. japonicus* underwent size-related changes; smaller fishes consumed gammarid amphipods, mysids and copepods, while larger fishes ate polychaetes, gastropods, isopods and other fishes. Differences in the prey organisms consumed of each individual species could be often related to differences in mouth length and width. *S. japonica*, *D. temmincki*, *T. trignocephalus*, and *P. breviceps* underwent also a significant diel changes that could be related to differences in foraging behavior and/or prey availability. Thus, use of vision to detect prey would account for the greater daytime consumption of copepods by *S. japonica* and of crab larvae by *D. temmincki*, whereas the nocturnal emergence of gammarid amphipods, polychaetes and isopods from the substrate explained their greater consumption by *S. japonica*, *D. temmincki*, *T. trignocephalus* and *P. breviceps* at night. Dietary breadth was greater for species with larger mouth dimensions.

Introduction

Seagrass beds have been renowned worldwide as rich, productive nursery and feeding area for juvenile and adult fishes (Adams 1976, Stoner & Livingstone 1984, Klumpp et al. 1989, Edgar & Shaw 1995). In Kwangyang Bay, Korea, seagrass meadows of *Zostera marina* provide a habitat for

variety of invertebrates and small fishes, which in turn are the potential food of significant fisheries. About 70 total fish species are found in an eelgrass bed; our study focuses on five species which were abundant during our study period (*S. japonica* (Sillaginidae), *D. temmincki* (Embiotocidae), *T. trignocephalus* (Gobiidae), *H. japonicus* (Syngnathidae) and *P. breviceps* (Blenniidae)). *S. japonica*

and *D. temmincki* are economically important species and are harvested commercially (Kim & Kang 1993).

To date studies of fish assemblages in eelgrass beds in Korea have concentrated on community structure (Go & Cho 1997, Huh & Kwak 1997a, Lee et al. 2000) and were confined to the feeding habits of one particular species (Huh & Kwak 1997b, 1998a, b, c). Food resources partitioning among fishes in eelgrass beds has not been extensively studied. Worldwide, there have been a few study of feeding habits of *S. japonica* and *D. temmincki* but no reports on the diet of *T. trigonocephalus*, *H. japonicus* and *P. breviceps*, despite these species being dominant in eelgrass beds. For example, Horinouchi et al. (1998) recorded that cyclopoid copepods and gammarid amphipods were important prey for *D. temmincki* and Hayase & Tanaka (1980) found that *D. temmincki* fed on gammarid and caprellid amphipods in a *Zostera* bed in Japan. Kwak et al. (2001) found that *S. maculata*, a congener of *S. japonica*, consumed mainly gammarid amphipods, crabs and copepods in tropical seagrass beds. Amphipods made the greatest contributions to the stomach contents of all Sillaginid species in coastal waters, Australia (Hyndes et al. 1997).

The aim of this study was to investigate the feeding habits of five fish species in an eelgrass bed. Specifically, our objectives are: (1) to examine the diet of these species, (2) to determine the relationships between dietary composition and body length of five fish species, (3) to compare between the diets of these species during day and night, and (4) to explore the role that differences in mouth size play in determining food partitioning.

Methods

We carried out all the sampling out over an eelgrass bed off Dae Island, Kwangyang Bay, Korea (Figure 1). The eelgrass, *Zostera marina* is widespread in shallow areas, forming subtidal bands (300–500 m wide) along the shoreline of Dae Island. Water temperature at the study site ranged from 8.4 to 31.8°C, and salinity ranged from 28.1 to 33.2‰. The mean eelgrass biomass ranged from 36.1 to 225.6 g DWm² in 1994.

We collected a total of 502 *S. japonica*, 423 *D. temmincki*, 379 *T. trigonocephalus*, 367 *H. japonicus* and 267 *P. breviceps* with a 5-m otter trawl (1.9-cm mesh wing and body, 0.6-cm mesh liner). We carried out four 6-min tows during the daylight hours and between 1 and 3 h after sunset in an eelgrass bed throughout 1994. Collecting methods are described in detail in Huh & Kwak (1997a). We preserved all fish samples immediately in 10% formalin after capture and measured their standard length to the nearest millimeter in the laboratory. We also measured the mouth dimensions of as wide a range of standard lengths as possible for each species, using dividers and dial calipers. We measured the length of the upper jaw from the tip of the snout to the posterior end of the maxilla (designated mouth length, ML), and the distance between the posterior ends of the maxillae with jaw closed (mouth width, MW).

We removed stomach contents after 2 days and transferred them to 70% isopropanol for storage. We identified gut contents from each fish the lowest taxon possible and recorded the (1) occurrence, (2) number of individuals and (3) dry mass of each prey species. We determined dry mass of

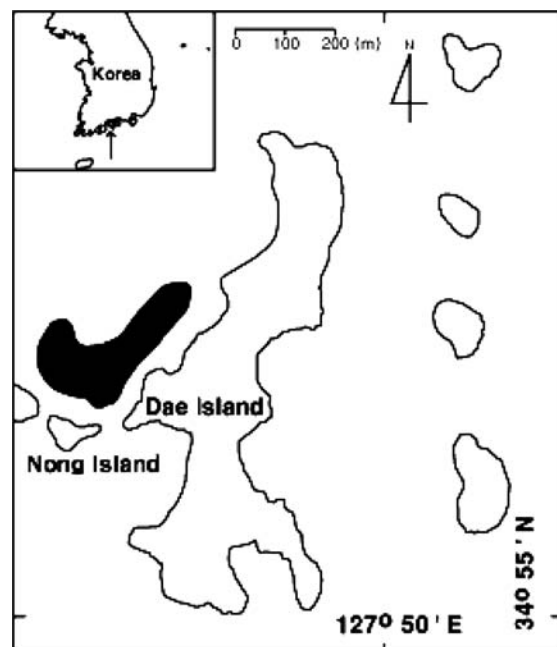


Figure 1. Location of the study area (the black area) in Kwangyang Bay, Korea.

the prey items from each fish sample to the nearest mg (Mettler electronic balance) after 24 h of oven drying at 80°C. We also recorded the sizes of ingested prey organisms to the nearest 0.1 mm with an ocular micrometer to obtain the mean size of prey selected by fish. The dimensions we chose for measurement were total length and maximum width and depth (excluding appendages) of each measurable item. We considered measurable items to be organisms which had been taken whole and remained unbroken (e.g. most amphipods) or parts of organisms (e.g. polychaetes) which clearly had been bitten off as on mouthful.

We calculated dietary breadth using Levin's standardized index (Krebs 1989):

$$B_i = 1/n - 1 \left(1 \sum_j P_{ij}^2 - 1 \right)$$

where B_i = Levin's standardized index for the predator i , P_{ij} = proportion of diet of predator i that is made up of prey j , and n = number of prey categories. This index ranges from 0 to 1, with low values indicating diets dominated by a few prey items (specialist predators) and higher values indicating generalist diets (Gibson & Ezzi 1987, Krebs 1989).

We used Schoener's index of dietary overlap (1970) to calculate overlap among species;

$$\alpha = 1 - 0.5 \left(\sum_{i=1}^n |P_{xi} - P_{yi}| \right)$$

where α is the overlap of species x on species y ; P_{xi} is the proportion (dry mass percentage) of a particular food i in the diet of species x ; P_{yi} is the proportion (dry mass percentage) of a particular food i in the diet of species y .

We used non-metric multi-dimensional scaling ordination (MDS) to plot each sample as a point on an ordination plot. We examined the extent to which the diets of the different species were either similar or different visually. For investigating whether the overall dietary composition of five species were significantly different, we calculated the dry mass of dietary categories (higher taxonomic group) of each species after pooling the data of prey species for both day and night. We calculated the mean dry mass of dietary category for

each species for determining whether the dietary composition of five species varied between day and night. We used Wilcoxon sign t -tests to determine those dietary categories which contributed most to day-night differences in diets. This was applied by SPSS PC software; statistical differences were based on the 0.05 significance level.

Results

General characterization of diets

We examined a total of 502 *S. japonica* stomachs, of which 22 (4.4%) were empty. The stomachs contained 29 identifiable prey components (Table 1). Crustaceans were by far the most important prey group, comprising 66.5% of the diet by mass, 94.1% of the diet by number. They occurred in 85.4% of all stomachs examined. Gammarid amphipods were the main component of the crustacean prey. Gammarid amphipods accounted for 49.7% of the diet by mass and *Ampelisca*, *Ericthonius* and *Ampithoe* were the principal gammarid amphipods items consumed. After gammarid amphipods, copepods accounted for almost half the diet by number and occurrence (42.1, 52.3%), although their proportion by mass was low. Polychaetes (26.8% of the diet by mass and 45.1 of the diet by occurrence) were the next largest dietary component. The polychaetes *Platynereis bicanaliculata*, and *Lumbrineirs* sp. were the principal prey items. Gastropods and fishes were of little importance, and constituted 4.1, 2.8% of the diet by mass, respectively.

We identified 12 prey taxa from 399 *D. temmincki* stomachs. Crustaceans were the major prey group for *D. temmincki*, comprising 96.3% of the diet by mass, 99.3% of the diet by number and occurring in 78.5% of all stomachs examined. Crab larvae were the most important crustaceans consumed, followed by gammarid amphipods, caprellid amphipods and isopods. Crab larvae and gammarid amphipods accounted for the largest percentage of the diet by mass (36.8, 29.2%) and caprellid amphipods were next important prey, making up 20.6% of the diet by mass. *Caprella kroeyeri* was principal prey species. Isopods were next most important prey group, accounting for

Table 1. Percentage occurrence, number and dry mass contributions of the prey organisms of five fish species.

Prey organisms/fish species	<i>Sillago japonicus</i>		<i>Ditrema temmincki</i>		<i>Tridentiger trigonocephalus</i>		<i>Hippocampus japonicus</i>		<i>Petroscirtes breviceps</i>						
	O(%)	N(%)	W(%)	O(%)	N(%)	W(%)	O(%)	N(%)	O(%)	N(%)	W(%)				
Crustacea	85.4	93.5	65.2	78.5	99.3	96.3	42.6	66.7	34.7	88.5	100.0	98.0	50.5	97.7	50.0
Amphipoda															
Gammaridea	53.6	47.5	49.7	35.6	39.8	29.2	38.9	59.8	30.9	71.8	86.1	88.4	56.9	97.7	50.0
<i>Erichthonius pugnax</i>	32.4	7.2	7.3							35.8	18.1	8.2			
<i>Erichthonius</i> sp.	25.4	9.8	10.0	27.6	12.8	9.3	24.7	32.5	16.8	5.5	1.3	1.5	47.8	38.6	19.7
<i>Ampelisca</i> sp.	17.5	9.3	10.1				18.7	8.6	4.4	30.6	16.7	16.9	33.8	10.3	5.2
<i>Ampithoe</i> sp.	20.5	9.5	9.7	20.2	7.8	5.5				13.5	6.6	6.9	38.5	12.9	6.6
<i>Corophium</i> sp.										29.7	14.4	14.6	43.6	35.9	18.5
<i>Leucothoe</i> sp.	15.5	6.1	6.5	13.8	5.5	4.0	23.3	18.7	9.7	11.1	4.4	4.9			
<i>Elasmopus</i> sp.	14.7	3.4	3.6							24.3	9.7	9.8			
<i>Melita</i> sp.	12.5	2.2	2.5							20.1	8.8	9.3			
<i>Podocerus</i> sp.				22.8	10.1	7.9				9.8	3.8	3.9			
<i>Cymadusa</i> sp.				9.6	3.6	2.5				7.7	2.3	2.4			
Caprellidea	6.9	0.7	0.5	41.1	18.4	20.6	28.7	5.6	3.4	13.6	7.9	5.9	7.8		
<i>Caprella kroeyeri</i>	6.9	0.4	0.3	32.9	15.1	16.9	14.5	2.3	1.4	15.6	6.1	4.6			
<i>Caprella tsugarensis</i>	3.0	0.3	0.2	10.9	3.3	3.7	13.5	2.2	1.3						
<i>Caprella scaura</i>							8.7	1.1	0.7	7.3	1.8	1.3			
<i>Caprella</i> sp.													7.8	2.3	1.2
Copepoda	52.3	42.1	8.6												
<i>Acartia omorii</i>	46.2	15.1	3.0												
<i>Calanus sinicus</i>	32.3	10.6	2.2												
<i>Centropages yamadai</i>	26.2	9.5	2.0												
<i>Oncaea</i> sp.	10.0	6.9	1.4												
Mysidacea	13.1	2.4	3.3												
Decapoda															
Caridea	3.1	0.6	2.9												
<i>Grangon affinis</i>	2.3	0.3	1.3												
<i>Alpheus brevicristatus</i>	0.8	0.2	1.1												
<i>Latreus acicularis</i>	0.8	0.1	0.5												
<i>Palaemon</i> sp.							5.8	0.8	2.0						
Brachyura				39.7	34.1	36.8									
Crab larvae				41.1	33.8	35.8									
<i>Hemigrapsus penicillatus</i>	3.1	0.6	1.3	1.9	0.3	1.0									
Isopoda															
<i>Cymodoce japonicus</i>	0.8	0.1	0.1	23.4	6.8	9.6									
Tanaidacea															
<i>Tanais cavolinii</i>	0.8	0.1	0.1	1.2	0.2	0.1	9.6	1.3	0.4						
Polychaeta	45.1	4.8	26.8				21.6	22.2	62.4						
<i>Platynereis bicanaliculata</i>	27.5	2.1	11.6				8.8	8.8	24.7						
<i>Platynereis bicanaliculata</i>										10.6	6.0	3.7			

<i>Lumbrineris</i> sp.	25.6	1.6	9.0			18.9	7.6	21.3	
<i>Cirratulus</i> sp.						20.8			
Unidentified	17.9	1.1	6.2			13.3	5.8	16.4	
Mollusca									
Gastropoda	6.9	0.6	4.1						
Bivalvia									
<i>Theora fragilis</i>				2.3	0.5	3.9			
Pisces									
<i>Favonigobius gymnauchen</i>	1.5	0.2	2.8						
<i>Acentrogobius pflaumi</i>	0.8	0.1	1.4						
Hydrozoa	0.8	0.1	1.4						
Algae	0.8	0.2	0.1			23.5	9.8	0.9	
<i>Polysiphonia</i> sp.									38.4
<i>Sargassum</i> sp.									22.1
Seagrass									30.1
<i>Zostera marina</i>						12.8	2.0	45.9	10.4

*O: occurrence, N: number, w: dry mass.

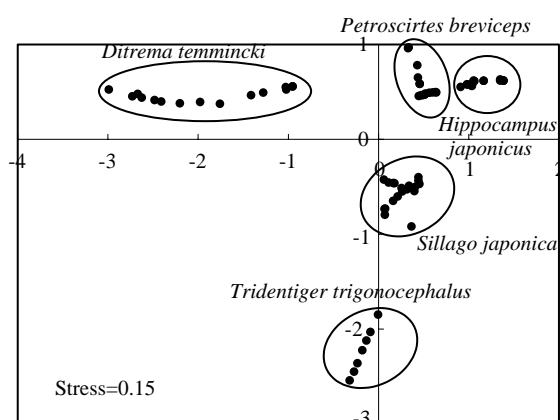


Figure 2. Non-metric MDS ordination of total dietary samples of five fish species in an eelgrass bed of Kwangyang Bay. Each point represent a dietary composition (percentage of dry mass) in each size classes of five species, respectively.

9.6% of the diet of mass. Bivalves and tanaids were of minor importance.

The 359 *T. trionocephalus* stomachs contained a total of 12 prey taxa. Polychaetes were the most important prey group, making up 62.4% of the diet by mass. *P. bicanaliculata* and *Lumbrineirs* sp. were the principal polychaetes consumed. After polychaetes, gammarid amphipods were secondary in importance and made up 30.9% of the diet by mass. Caprellid amphipods and caridean shrimps were of little importance and constituted 3.4, 2.0% of the diet by mass, respectively. Tanaids and hydrozoans composed a negligible portion of the diet.

We found 14 prey taxa in the 354 *H. japonicus* stomachs. Crustacean account for the entire diet by mass (98.0%). Gammarid amphipods were the most important crustaceans, constituting 88.4% of the diet by mass and 86.1% of the diet by number. *Erichthonius pugnax*, *Ampelisca* sp. and *Corophium* sp. were principle gammarid amphipods con-

sumed. After gammarid amphipods, caprellid amphipods was the next major prey group, making up 5.9% of the diet by mass. Tanaids and eelgrass, *Z. marina*, were of minor importance.

The 235 *P. breviceps* stomachs we analyzed contained 8 prey taxa. Crustacean accounted for almost half the diet by mass (50.0%) and almost the entire diet by number (97.7%). Gammarid amphipods were main component of the crustacean prey. *Ampelisca* sp. and *Corophium* sp. were principal gammarid amphipods consumed. Algae was the next largest percentage of the diet by mass (38.4%) and *Polysiphonia* sp., *Sargassum* sp. were the species consumed. Eelgrass, *Z. marina*, made up 10.4% of the diet by mass. Caprellid amphipods composed a negligible portion.

Comparisons among the dietary compositions of five species

The difference between the dietary compositions of the species is enhanced by the spatial MDS ordination (Figure 2). The five species appear separated from each other. The distance between the dietary samples of species reflects the extent of differences in dietary compositions; the greatest distance between *D. temmincki* and *T. trionocephalus* shows the larger differences of dietary composition, while the dietary composition of *P. breviceps* and *H. japonicus* was the least difference in dietary composition. The dietary overlap demonstrated that the dietary compositions of the five species differed (Table 2). The dietary overlap was greater than 0.50 in four of 10 possible pair comparisons and was less than 0.29 in the case of *D. temmincki* vs. *S. japonica*, *D. temmincki* vs. *T. trionocephalus*.

Table 2. Schoener's index of dietary overlap coefficients of *S. japonica*, *D. temmincki*, *T. trionocephalus*, *H. japonicus* and *P. breviceps*.

Species	<i>Sillago japonica</i>	<i>Ditrema temmincki</i>	<i>Tridentiger trionocephalus</i>	<i>Hippocampus japonicus</i>	<i>Petrosirtes breviceps</i>
<i>Sillago japonica</i>	1.00				
<i>Ditrema temmincki</i>	0.29	1.00			
<i>Tridentiger trionocephalus</i>	0.60	0.28	1.00		
<i>Hippocampus japonicus</i>	0.50	0.33	0.33	1.00	
<i>Petrosirtes breviceps</i>	0.50	0.31	0.31	0.53	1.00

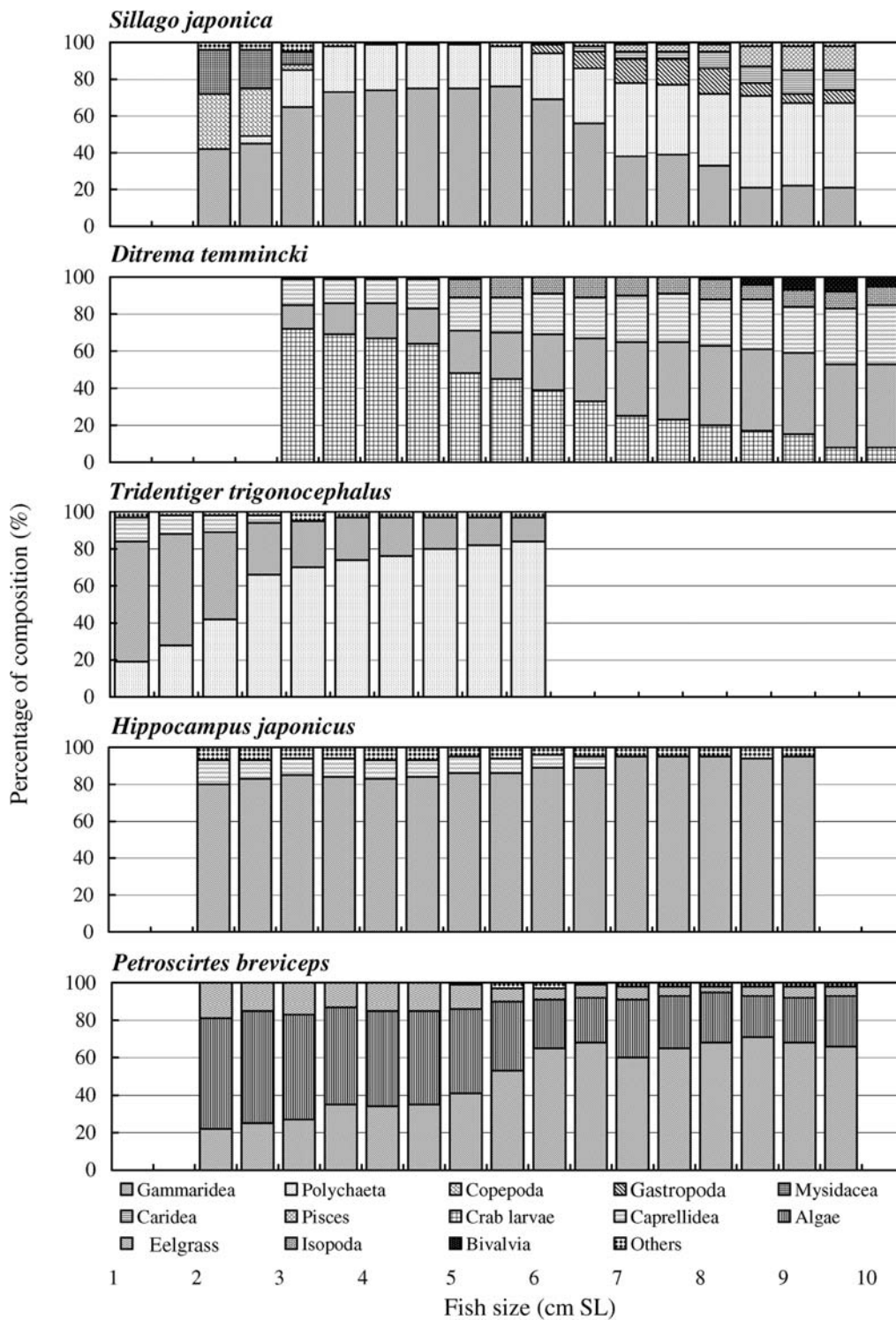


Figure 3. Relationships between dietary composition (percentage of dry mass) and body length of five fish species.

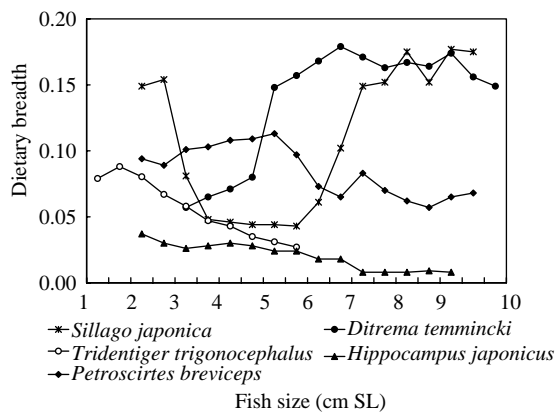


Figure 4. The size-related variations of dietary breadth of five fish species.

Variations of stomach contents in relation to each fish size

Although copepods, mysids and gammarid amphipods collectively contributed over 70% to the diet of the smaller (<3.4 cm SL) *S. japonica*, the first two categories were rarely ingested by the larger individuals (7.1–9.9 cm SL) (Figure 3). The portion of the diet attributable to copepods and mysids decreased sharply with increasing size. Larger individuals consumed a wide range of prey, including gammarid amphipods, polychaetes, carid decapods, fishes and gastropods. Crab larvae were the most important contributor to the diet of <5 cm SL individuals of *D. temmincki*, whereas proportions of crab larvae declined with increasing fish size and gammarid amphipods, caprellid amphipods and isopods were important prey for larger individuals. *T. trigonocephalus* showed a dramatic shift in which the smallest fish (<3 cm SL) fed exclusively gammarid amphipods and larger fish predominately ate polychaetes. Gammarid amphipods were the most important contributor to the diet of all size classes of *H. japonicus*. An increase in size by *P. breviceps* was characterized by a gradual decline in the mass of algae consumed and a pronounced increase in the mass of gammarid amphipods ingested. Eelgrass made a moderate contribution to the diet of smaller individuals of *P. breviceps*.

The dietary breadth of each species varied with fish size (Figure 4). The high dietary breadth of

smaller *S. japonica* declined to a minimum value at 5.5 cm SL, however, this value increased with larger fish size. The low dietary breadth of <5 cm SL individuals of *D. temmincki* increased very sharply with increasing fish size, while the dietary breadth of *P. breviceps* decreased with larger size (>5.5 cm SL). The dietary breadth of *T. trigonocephalus* and *H. japonicus* was lower than all other species; *H. japonicus* had the lowest value (<0.05) in all size classes.

Comparisons between the diets of fish during day and night

All species except *H. japonicus* exhibited strong diel feeding patterns. Ordination points of daytime *S. japonica* samples lay below and to the right of most nighttime points, except two outlying points on the bottom right (Figure 5). A Wilcoxon sign *t*-test revealed that the consumption of copepods, polychaetes and fishes eaten by *S. japonica* differed significantly between day and night samples ($p = 0.022$, $p < 0.05$). On the other hand, all points for the dietary data of *D. temmincki* during the day formed a tight group on the upper right side of the plot and below for night. In the case of *T. trigonocephalus* and *P. breviceps*, the points for the dietary compositions for fish during the night lay above and to the left side of those for the day. A Wilcoxon sign *t*-test confirmed that the dietary compositions of these fish species during day and night were significantly different ($p = 0.012$, $p < 0.05$). For example, gammarid amphipods consumed by *P. breviceps* were higher in night samples. In contrast to the situation just described for four fish species, the points for the day and nighttime samples of *H. japonicus* were highly interspersed.

Relationships between fish size and prey size

Linear regressions of mouth length on fish size and of mouth width on fish size were significant ($p < 0.05$) in five fish species (the equation between mouth length and mouth width (y) and fish size (x), *S. japonica*, $y = 0.033x + 0.040$, $y = 0.033x + 0.042$; *D. temmincki*, $y = 0.026x + 0.177$, $y = 0.029x + 0.209$; *T. trigonocephalus*, $y = 0.014x - 0.005$, $y = 0.026x + 0.085$; *H. japonicus*, $y = 0.007x + 0.082$, $y = 0.010x - 0.029$; *P. breviceps*, $y = 0.012x + 0.138$,

$y = 0.029x + 0.061$). Comparison of mouth length with mouth width for a given fish size demonstrated that mouth varied in shape from symmetrical (mouth length and width approximately equal), as in *S. japonica* and *D. temmincki* to asymmetrical such as *H. japonicus*. For a given fish size, mouth size varied widely from species with

large mouth width, e.g. *Tridentiger trignocephalus*, *Petroscirtes breviceps*, to ones with small mouth width, e.g. *Hippocampus japonicus*. Regressions of prey size and mouth width were significant ($p < 0.05$) for five fish species except *H. japonicus*. On the assumption that the dimensions most likely to limit the prey size that could be

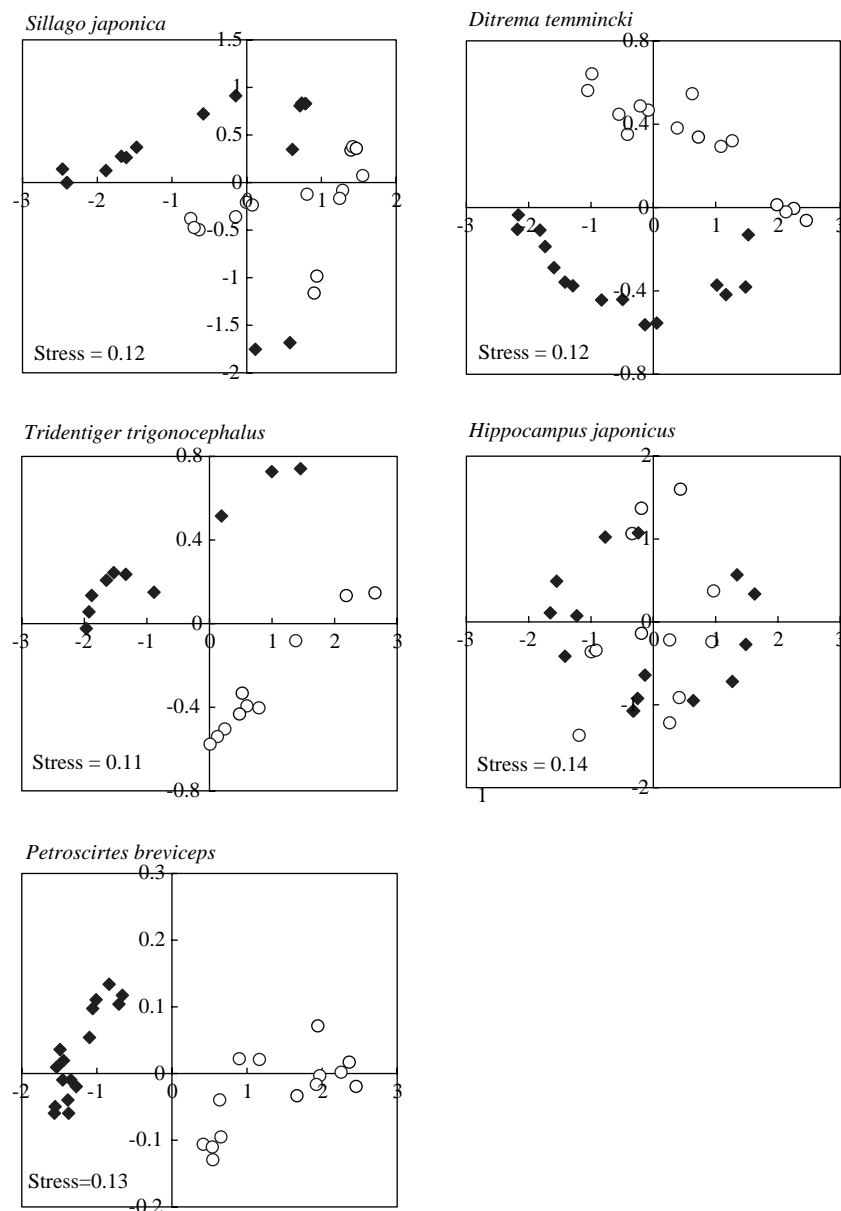


Figure 5. MDS ordination of the dietary composition (percentage of dry mass) in each size classes of five fish species during day (open symbols) and night (closed symbols).

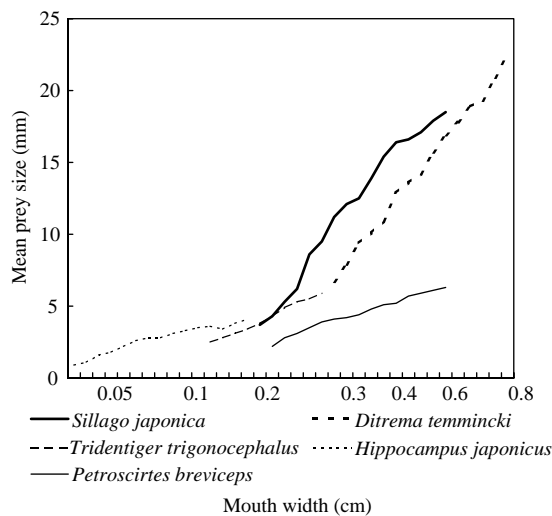


Figure 6. The relationships between mouth width and prey size.

consumed were prey width and mouth width, the relationships between these two variables demonstrated that most fish species took prey whose width, on average, is small relative to the width of their mouth (Figure 6). Consequently, the prey size as percentage of actual mouth width may well be lower. Figure 6 also showed that the wide range of prey size was taken by fish with equivalent mouth width and, conversely, that prey of a given size is taken by fish with a wide range of mouth size.

Discussion

The results of the present study show that the dietary compositions of the five fish species in an eelgrass bed were significantly different from each other. The dietary overlap value (0.50) between *S. japonica* and *H. japonicus*, and *P. breviceps* reflects an abundance of gammarid amphipods in the diets of these three species. This is presumably related to the great ease with which these prey would be able to be targeted because the abundance of gammarid amphipods was high in the study area (Kwak 1997). Most fishes mainly consumed gammarid amphipods in eelgrass beds (Huh & Kwak 1997b, 1998a, b, c), as it also is elsewhere (Livingstone 1982, Robertson 1984, Scott et al. 1986, Motta et al. 1995). Although gammarid amphipods were

mainly consumed by *S. japonica*, *H. japonicus* and *P. breviceps*, the dietary overlap was not high between the species. This result was largely related to the fact that while *S. japonica* consumed diverse prey species (including polychaetes, copepods, gastropods, carid decapods and fishes), *H. japonicus* fed primarily on gammarid amphipods, whereas *P. breviceps* ingested algae and eelgrass in similar magnitude. This inter-specific difference is probably due to differences in their mouth size. *S. japonica* was able to use their protrusive jaws and tube-like mouths to target larger size prey, while *H. japonicus* has a unique feeding behavior with smaller mouth width on the shoot of eelgrass and *P. breviceps* were picked small size gammarid amphipods off with smaller mouth and jaws (McKay 1985, Bergert & Wainwright 1997, Hydnes et al. 1997).

On the other hand, the low dietary overlap value between *D. temmincki* and other the fish species reflects the fact that *D. temmincki* fed on a variety of crustacean such as crab larvae, caprellid amphipods and isopods with larger mouth width, whereas these prey were rarely or never ingested by *S. japonica*, *T. trignocephalus*, *H. japonicus* and *P. breviceps*. Horinouchi et al. (1998) reported that *D. temmincki* fed on a large proportion of crustaceans with occurrence more frequently in the upper parts of water column of a *Zostera* bed at Aburatsubo, Japan. The dietary overlap between *T. trignocephalus* and *D. temmincki*, *H. japonicus*, *P. breviceps* was low, yet the *T. trignocephalus* vs *S. japonica* comparison was moderately high (0.60). *T. trignocephalus* consumed a large mass of polychaetes, whereas polychaetes were never consumed by other species. This implies that polychaete feeders such as *T. trignocephalus* are most of small-mouthed, small-bodied species mostly taking their prey from within the sediment.

The dietary samples for the successive size classes of each species indicated that the dietary composition of five fish species except *H. japonicus* undergoes a similar type of size-related changes. These changes involve a shift from the consumption by smaller fishes of small prey species such as copepods, caprellid amphipods and mysids to larger species such as polychaetes, gastropods and fishes by larger fishes. The domination by gammarid amphipods and copepods in the diet of the smaller of *S. japonica* in eelgrass beds paralleled

the reports of the diet of *S. maculata* in the tropical seagrass beds and *S. bassensis* in coastal waters in Australia (Hydnes et al. 1997, Kwak et al. 2001). Our finding that larger *D. temmincki* tended to target gammarid amphipods and caprellid amphipods paralleled feeding data collected on eelgrass bed of Odawa Bay, Japan (Hayase & Tanaka 1981).

The dietary composition of each fish species except *H. japonicus* also underwent a significant diel change. The diel differences in the dietary composition of *S. japonica* reflected a greater consumption of copepods during the day and of polychaetes, carid decapods and fishes at night. These differences suggest that *S. japonica* used vision to detect and pursue to prey in the water column during the day, while at night, when visual acuity would be reduced, it employs its protrusive jaws and large mouth, to suck up prey from the substrate surface (Gunn & Milward 1985, McKay 1985, Hydnes et al. 1997). In the case of *D. temmincki* and *T. trigonocephalus*, their stomach contents contained a far greater proportion of crab larvae and caprellid amphipods during the day than at night, whereas the reverse was true for gammarid amphipods, polychaetes and isopods. Likewise, *P. breviceps* consumed a larger volume of gammarid amphipods during the night than the day. The shift towards the above polychaetes and medium-sized crustaceans at night can be attributed to these prey becoming more available for predation, as a result of their nocturnal movement from the substrate into the water column (Robertson & Howard 1978, Robertson & Klumpp 1983). *H. japonicus* fed on similar prey during day and night parallels the situation with certain other syngnathid species, *Syngnathus schlegeli* (Huh & Kwak 1997b) in an eelgrass bed.

D. temmincki had the greatest dietary breadth of all fish species, which may be related to its relatively large mouth. The overall relative size of the mouth of *D. temmincki* was greater than that of any other species. *S. japonica* had the next largest mouth. The diversity of the prey ingested by *D. temmincki* and *S. japonica* ranged from small prey, copepods, to medium-sized prey such as gammarid amphipods and crab larvae, to larger prey such as polychaetes, carid decapods and fishes. The fact that they ingest such a wide variety of prey demonstrated that these two species were highly

opportunistic feeders. The possession by *H. japonicus* of the lowest overall dietary breadth was consistent with the fact that all size classes of this species targets a restricted suite of prey species such as gammarid amphipods.

In summary, the present study demonstrated that the food resources in an eelgrass bed were partitioned among the five fish species. This conclusion is based partly on the fact that, although gammarid amphipods were consumed by each of those of five fish species, their relative contributions to the diets of those species varied. Furthermore, other prey such as polychaetes, carid decapods, copepods, mysids and isopods, were ingested only by certain species. The dietary composition of each fish species was still shown to be significantly different from that of each of the species. It was also evident that the diet of each species changed with increasing fish size. The comparisons between the dietary compositions of five fish species highlight the role that factors, such as prey accessibility, were likely to play in influencing the prey types that will be targeted by these fish species. Differential utilization of a wide range of prey species by these five species and by different fish sizes would reduce the potential competition for prey in an eelgrass fish assemblage.

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