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Feeding ecology of three tonguefishes, genus Cynoglossus (Cynoglossidae) in the Seto Inland Sea, Japan

Gun Wook Baeck[a], Joo Myun Park[b]* and Hiroaki Hashimoto[c]

[a]*Department of Marine Biology & Aquaculture, Institute of Marine Industry, College of Marine Science, Gyeongsang National University, Inpyeong-dong, Tongyeong, 650160, Republic of Korea;* [b]*Division of Marine Technology, Chonnam National University, Marine Technology, Yeosu, 550749, Republic of Korea;* [c]*Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Hiroshima, 7398528 Japan*

Feeding ecology was compared among the three tonguefishes *Cynoglossus abbreviatus*, *C. joyneri* and *C. robustus*, collected from Seto Inland Sea, Japan, from June 2000 to May 2001. They are benthivores, consuming mainly gammarid amphipods, shrimps, crabs, gastropods, bivalves and ophiuroids. *C. abbreviatus* consumed greater proportions of ophiuroids whereas *C. joyneri* and *C. robustus* ate more amphipods and shrimps. While *C. abbreviatus* consumed mostly ophiuroids in all size classes, the diets of *C. joyneri* and *C. robustus* showed ontogenetic changes in feeding habits; smaller individuals of *C. joyneri* and *C. robustus* consumed gammarid amphipods, whereas larger *C. joyneri* ate shrimps and gastropods, and larger *C. robustus* fed mainly on gastropods, crabs, bivalves and polychaetes. Cluster analysis based on diet similarities emphasized that the three *Cynoglossus* species could be categorized on a size-related basis into three feeding groups: smaller *C. joyneri* and *C. rubustus* (<25 cm TL) could be classified as group A, and the larger of them (>25 cm TL) as group B, whereas C. *abbreviatus* was categorized as group C. This means that some degree of resource partitioning can occur among the three *Cynoglossus* species. The seasonal changes in the diets were also significant for the three *Cynoglossus* species.

Keywords: feeding ecology; tonguefishes; *Cynoglossus abbreviatus*; *Cynoglossus joyneri*; *Cynoglossus robustus*; diet similarity; Seto Inland Sea

Introduction

Tonguefishes (Cynoglossidae) are demersal flatfish species that are economically and ecologically important in coastal areas throughout the world. The tongue-fishes *Cynoglossus abbreviatus*, *C. joyneri*, and *C. robustus* are mainly distributed in the coastal waters of China, Korea, and Japan (Yamada et al. 1986) and form a relatively abundant fishery resource in the Seto Inland Sea (Inaba 1988). All of these species live at the bottom of the water column, and their physical features such as flattened body, robust body shape, pale underside, and binocular topside make them well adapted to the benthic environment.

The fish community in the Seto Inland Sea has undergone severe exploitation and intensive fishing for several decades, leading to dramatic community shifts. Nagai (2003) observed that, since the 1930s, the fish catch from the Seto Inland Sea reached its maximum of 462,000 M/T in 1982 and gradually decreased until 2000. The decreases reflected large reductions in the catches of species such as spotlined sardine, anchovy, flatfishes, Spanish mackerel, tiger puffer, shrimps, short-necked clam, and sea cucumber (Nagai and Ogawa

1997; Sasaki 2006). The benthic habitat and megafauna are also subjected to intense fishing efforts in this ecosystem (Hall 1994). However, the effects of declining habitat on flatfish and changes in the benthic invertebrate community in this ecosystem remain unclear.

Knowledge of the trophic ecology of dominant fish species is necessary for understanding their functional roles within ecosystems (Wotton 1990; Brodeur and Pearcy 1992). The trophic ecology of *Cynoglossus* species has been studied throughout the world. The diet of *C. arel* and *C. lida* (Rajaguru 1992), *C. semifasciatus* (Seshappa and Bhimachar 1995), and *C. semilaevis* (Dou 1993, 1995) have been investigated, whereas little information has been obtained on the feeding habits of *C. abbreviatus, C. joyneri* and *C. robustus*. Ochiai (1966) and Choi et al. (1995) provided only limited results about the feeding habits of these species. Knowledge of the diet composition of these three *Cynoglossus* species is essential for understanding their trophic relationships in benthic ecosystems in the coastal waters of Japan.

In this study, we aimed to provide information on the feeding ecology of three *Cynoglossus* species and to conduct a preliminary comparison of their diets. Our specific objectives were to (1) examine the diets of three

Cynoglossus species, (2) determine any size-related and seasonal changes in the feeding habits of the three species, and (3) compare the diets of the three species on a size-related basis.

Materials and methods

Fish samples consisting of 688 tonguefish, *Cynoglossus abbreviatus*, *C. joyneri* and *C. robustus* were collected monthly in the Seto Inland Sea, Japan, from June 2000 to May 2001 (Figure 1). Fish samples were collected by small bottom trawl fisheries in the western part of the Hiuchi Nada Sea in the Seto Inland Sea, and were sampled at the fish markets of Imabari, Ehime Prefecture, Japan.

All specimens were packed into ice water immediately after collection, and the total length (TL) and the wet body weight (BW) were measured to the nearest millimeter and the nearest gram, respectively. The mouth size of each fish was measured to the nearest millimeter. Stomachs were then removed from the fishes, and their contents were fixed in 10% buffered formalin. For each specimen, prey items from the stomachs were identified, and numbers of each prey item were counted under a dissecting microscope. The maximum length of each prey item was measured to the nearest millimeter. The dry weight of each food item after drying for 24 h in an electric oven at 80°C was measured to the nearest 0.0001 g using an electronic balance.

Diet was quantified by frequency of occurrence (%F), numerical percentage (%N), and dry weight percentage (%W), which were calculated by the following equations.

$$\%F = A_i/N \times 100$$
$$\%N = N_i/N_{total} \times 100$$
$$\%W = W_i/W_{total} \times 100$$

where A_i is the number of fish preying on species i, N is the total number of fish examined, excluding individuals with empty stomachs, N_i (W_i) is the number (dry weight) of prey item i, and N_{total} (W_{total}) is total number (dry weight) of prey individuals. Then, the index of relative importance (*IRI*) (Pinkas et al. 1971) was calculated for each prey item as follows:

$$IRI = (\%N + \%W) \times \%F,$$

The index of relative prey importance was expressed as a percentage (%*IRI*),

$$\%IRI = IRI_i/\sum_{i=1}^{n} IRI \times 100,$$

A diet diversity index (H) expressed as the standard of utilization of food resources by each predator species

Figure 1. Location of the sampling area in the Seto Inland Sea, Japan.

Table 1. Summary of three *Cynoglossus* species by monthly sampling off Seto Inland Sea in 2000–2001.

Species	Code	SL (cm)	Stomachs			N	H
			Total	empty	empty (%)		
Cynoglossus abbreviatus	CA	16.9–45.0	240	61	25.4	15	2.12
C. joyneri	CJ	10.9–26.8	227	54	23.8	13	2.68
C. robustus	CR	10.7–43.5	221	31	14.0	24	3.06

(N : Total number of prey taxa, H : Diet diversity index.)

was calculated using the Shannon–Weaver formula (Petraitis 1979; Brodeur and Pearcy 1990).

$$H = \sum \left(P_{ij} \log 2^{p_{ij}} \right),$$

where P_{ij} is percentage weight of prey j in the diet of predator i.

Size-related and seasonal variations in diet were examined by dividing the tonguefish specimens into five size classes and four seasons: I < 20 cm, II 20–25 cm, III 25–30 cm, IV 30–35 cm and V > 35 cm; spring (March–May), summer (June–August), autumn (September–November) and winter (December–February). Statistical differences by size class and season in the dietary contribution of each major food item were tested using a chi-square test of the frequencies of a given prey (Sokal and Rohlf 1981). Statistical tests were conducted using SPSS software for PC; statistical differences were based on a 0.05 significance level. A diet overlap between size groups of three *Cynoglossus* species was adapted based on their diet compositions on %W by Pianka's index (Pianka 1973). The diet overlap index ranges from 0 (no overlap) to 1 (complete overlap), and the values over 0.6 are considered ''biologically significant'' for teleost (Pianka 1976). Hierarchical cluster analyses based on Pianka's similarity index were used for the classification and ordination of size classes into groups. Size classes were linked by diet similarities using 'group average' cluster mode. These were applied by the PRIMER software package (Clarke and Gorley 2001).

Results

General stomach contents

At least 25 taxa of prey were identified from the 688 stomachs of the three *Cynoglossus* species. The percentage of empty stomachs of each species ranged from 14.0 to 25.4, with the lowest percentage found in *C. robustus* and the highest in *C. abbreviatus* (Table 1). The diet diversity index based on food species ranged from 2.12 (*C. abbreviatus*) to 3.06 (*C. robustus*).

A total of 15 prey taxa were found in the 179 stomachs of *C. abbreviatus* (Table 2). Ophiuroids were the most common prey item, composing 30.83% of the diet by occurrence, 26.62% by number, 46.59% by dry weight, and 44.79% by *IRI*. Shrimps were the second largest dietary component, constituting 36.67% of the diet by occurrence, 18.18% by number, 15.30% by dry weight, and 24.36% by *IRI*. Polychaetes, crabs, bivalves, gastropods and amphipods followed, accounting for 11.67%, 10.05%, 9.05%, 3.80%, and 1.27% of the diet by dry weight, respectively. The remaining preys (cumaceans, isopods, stomatopods, and polychaetes, anthozoas, echinoides, fishes and algaes) constituted less than 1.0% of the diet by dry weight.

In the 173 stomachs of *C. joyneri*, 13 prey taxa were found (Table 2). *C. joyneri* mainly ingested amphipods and shrimps, composing 46.70% and 29.07% of the diet by occurrence, 38.89% and 13.47% by number, 16.38% and 35.12% by dry weight and 44.82% and 24.53% by *IRI*, respectively. The second most important foods were bivalves and gastropods, making up 14.98% and 10.43% of the diet by dry weight, respectively. Crabs, ophiuroids, stomatopods, cumaces, polychaetes, ostrocods, nemertines, algas and unidentified eggs constituted a small portion of the diet.

In the diet of the 190 stomachs of *C. robustus*, 25 texa of prey items were found (Table 2). The main prey items of *C. robustus* were shrimp, composing 45.25% of the diet by occurrence, 24.22% by number, 17.66% by dry weight and 37.53% by *IRI*. Amphipods (%F = 38.91; %N = 23.97; %W = 3.21; %IRI = 20.95) and gastropods (%F = 21.72; %N = 12.74; %W = 28.34; %IRI = 17.67) were the next most important dietary component. Crabs, polychaetes, bivalves and ophiuroids made up 11.22%, 10.58%, 10.03% and 8.80% of the diet by dry weight, respectively, and a small portion of the prey items (less than 2.0% in %W) was made up of ostrocods, cumaceans, isopods, stomatopods, cephalopods, poriferans, hydrozoans, anthozoans, plathelminthes, nemertians, sipunculoids, oligochaetes, echinoides, foraminiferans, fishes and algaes.

Changes in diet with fish size

Size-related variations in dietary composition of three *Cynoglossus* species were significant (*C. abbreviates*, x^2 = 152.3, df = 36, P < 0.05; *C. joyneri*, x^2 = 193.7,

Table 2. Percentage frequency of occurrence, number, dry weight and index of relative importance (*IRI*) of prey species in the diets of three *Cynoglossus* species.

Prey organisms	*Cynoglossus abbreviatus*				*Cynoglossus joyneri*				*Cynoglossus robustus*			
	%F	%N	%W	%IRI	%F	%N	%W	%IRI	%F	%N	%W	%IRI
ARTHROPODA												
Ostracoda					11.01	2.14	0.64	0.53	0.26	0.45	0.12	+
Cythere lutea					9.25	1.83	0.51					
Mutilus convoxa					0.44	0.06	0.01		0.90	0.15	0.04	
Notodromas sp.					0.88	0.13	0.10					
Trachyleberis scabrocuneata					0.44	0.06	0.01					
Unidentifed Ostracoda					0.44	0.06	0.01		1.36	0.30	0.08	
Cumacea	2.50	0.78	0.13	0.05	15.42	10.96	2.99	3.74	4.53	2.98	0.27	0.29
Iphinoe sagamiensis									0.90	0.22	0.03	
Dimorphostylis asiatica									1.36	0.22	0.05	
Unidentifed Cumacea									3.17	2.54	0.19	
Isopoda	0.83	0.09	0.55	0.01					3.62	0.74	1.86	0.19
Argathona japonica									0.90	0.15	0.77	
Cirolana harfordi japonica	0.83	0.09	0.55						0.45	0.07	0.50	
C. japonensis									0.45	0.07	0.43	
Unidentifed Isopoda									1.82	0.45	0.16	
Amphipoda	22.08	7.40	1.27	3.80	46.70	38.89	16.38	44.82	38.91	23.97	3.21	20.95
Caprelliea												
Caprella danilevskii					0.44	0.13	0.14					
Protella gracilis	0.42	0.08	0.01						0.45	0.07	+	
Gammaridea												
Allorchestes sp.									0.45	0.07	0.01	
Ampelisca brevicornis					0.44	0.06	0.09					
A. cyclops	1.25	0.69	0.12		7.49	1.86	0.82		2.71	0.75	0.15	
A. diadema	2.08	0.54	0.06		7.05	1.77	2.22		1.36	0.52	0.05	
Atylus japonicus	0.42	0.04	+						2.26	0.90	0.06	
Byblis japonicus	1.25	0.46	0.14						0.45	0.29	0.04	
Cerapus tubularis	0.42	0.05	0.01		0.44	0.06	0.03					
Ericthonius pugnax	0.83	0.12	0.01									
E. sp.	0.42	0.11	0.20						3.17	1.12	0.15	
Eriopisella sechellensis									0.90	0.22	0.01	
Leucothoe sp.					5.73	1.76	0.38		1.36	0.22	0.04	
Liljeborgia japonica	1.25	0.28	0.10						0.45	0.15	0.01	
Maera sp.	0.83	0.39	0.03									
Melita dentata					0.44	0.06	0.02					
M. Koreana	0.42	0.04	+		0.44	0.06	0.05					
Monoculodes carinatus	0.42	0.05	0.01		0.44	0.06	0.02					
M. sp.	1.67	0.23	0.04						1.36	1.05	0.49	
Orchomenella pinguis									0.90	0.30	0.05	
Pleustes panopla					0.88	0.31	0.18		3.62	1.49	0.16	
P. sp.	0.42	0.04	+									
Pontocrates altamarinus	0.83	0.19	0.02		22.91	19.23	6.13					
P. sp.									2.71	2.09	0.38	
Pontogeneia sp.	4.17	0.58	0.06						0.45	0.22	+	
Pseudocrangonyx sp.	0.42	0.04	+		0.88	0.13	0.05		4.07	1.12	0.32	
Unidentified Gammaridea	12.92	3.47	0.46		26.43	13.40	6.25		29.41	13.39	1.29	
Decapoda												
Macrura	36.67	18.18	15.30	24.36	29.07	13.47	35.12	24.53	45.25	24.22	17.66	37.53
Crangon affinis	1.25	0.19	0.06		2.20	0.77	3.05					

Table 2 (*Continued*)

Prey organisms	*Cynoglossus abbreviatus*				*Cynoglossus joyneri*				*Cynoglossus robustus*			
	%F	%N	%W	%IRI	%F	%N	%W	%IRI	%F	%N	%W	%IRI
Gnathophyllum americanum	0.42	0.07	0.36									
Latreutes planirostris	8.33	8.83	3.02		3.52	0.58	0.65		0.90	0.15	0.02	
Leptochela gracilis	1.25	0.39	0.59									
L. pugnax	1.25	0.36	0.61		1.76	0.31	1.24		4.52	1.72	0.82	
Metapeaeopsis sp.					0.88	0.19	0.37		0.90	0.53	0.23	
Ogyrides striaticauda	7.92	2.89	1.76		7.49	4.07	8.08		11.31	4.26	2.98	
Penaeus monodon									1.36	0.37	0.59	
Plesionika martia									0.45	0.07	0.06	
Processa sp.									1.36	0.45	0.99	
Unidentifed Macrura	23.33	5.45	8.90		18.06	7.55	21.73		34.84	16.67	11.97	
Brachyura	24.58	8.81	10.05	9.20	16.74	3.68	7.84	3.35	17.65	6.90	11.22	6.33
Arcania heptacantha					1.76	0.31	1.07		1.36	0.72	0.51	
Asthenognathus inaequipes					0.88	0.13	0.27					
Atergatis sp.	1.67	0.43	0.72									
Calappa gallus									0.90	0.15	0.05	
Cancer gibbosulus	2.50	1.00	0.88						0.45	0.15	0.50	
Charybdis bimuaculata	1.25	0.19	0.84									
C. sp.					0.88	0.06	0.03					
Eucrate crenata	0.83	0.12	0.19									
Goneplax renoculis	3.75	0.72	1.16									
Hemigrapsus sanguineus	0.42	0.19	0.57									
H. sp.									2.26	0.82	1.76	
Heteropilumnus sp.	0.83	0.12	0.07									
Liagore rubromaculata	2.08	0.44	0.65						0.45	0.22	0.08	
Matuta planipes					0.44	0.06	0.04					
M. sp.									0.45	0.07	0.06	
Pachygrapsus crassipes					0.88	0.19	0.70					
Parathranites orientalis					0.44	0.06	0.40					
Portunus hastatoides	1.25	0.15	0.16									
P. nipponensis					0.88	0.19	0.12					
P. spp.	0.42	0.08	0.01		0.44	0.06	0.15		0.90	0.22	0.16	
Philyra sp.					0.44	0.06	0.06					
Trapezia cymodoce areolata	0.42	0.08	0.03									
Tritodynamia rathbuni	1.25	1.54	1.29									
Typhlocarcinus villosus					0.44	0.06	0.11		1.36	0.22	0.14	
Uca lactea	0.83	0.08	0.22									
Meglopa					1.32	0.19	0.42					
Unidentifed Brachyura	15.42	3.67	3.26		12.78	2.31	4.47		14.03	4.33	7.96	
Stomatopoda	0.42	0.08	1.35	0.01	2.64	0.38	3.17	0.16	1.81	0.36	3.53	0.14
Anchisquilla fasciata	0.42	0.08	1.35						0.45	0.07	2.95	
Oratosquilla oratoria					1.76	0.25	2.39		0.45	0.07	0.10	
Lophosquilla costata									0.45	0.07	0.20	
Unidentifed Stomatopoda					0.88	0.13	0.78		0.90	0.15	0.28	
MOLLUSCA												
Gastropoda	15.00	4.47	3.80	2.46	22.03	7.26	10.43	6.77	21.72	12.74	28.34	17.67
Philine sp.	7.50	3.11	3.56		3.08	1.57	8.05		20.36	11.91	27.98	
Acteocina exilis	0.42	0.04	+									
Adamnestia japonica					1.32	0.19	0.19					
Nudibranchia	0.42	0.08	0.13									

Table 2 (*Continued*)

Prey organisms	Cynoglossus abbreviatus				Cynoglossus joyneri				Cynoglossus robustus			
	%F	%N	%W	%IRI	%F	%N	%W	%IRI	%F	%N	%W	%IRI
Unidentifed Gastropoda	7.92	1.24	0.11		19.82	5.50	2.19		3.62	0.83	0.36	
Bivalvia	14.58	30.85	9.05	11.55	25.99	18.36	14.98	15.05	23.53	12.25	10.03	10.38
Saccella confusa					6.61	5.46	4.82					
S. sp.	1.67	0.39	0.07									
Solen sp.	0.42	0.08	1.86									
S. strictus									0.45	0.09	0.10	
Chlamys sp.	0.42	0.05	0.04						0.90	0.20	0.15	
Luteamussium sp.	0.42	0.04	0.02									
Unidentifed Bivalvia	13.33	30.29	7.06		24.67	12.90	10.16		23.08	11.96	9.78	
Cephalopoda									0.45	0.15	1.02	0.01
PORIFERA												
Demospongiae									0.45	0.07	0.24	+
COELENTERATA												
Hydrozoa									0.90	0.15	0.32	0.01
Anthozoa	0.83	0.12	0.06	+					3.17	0.52	0.34	0.05
PLATHELMINTHES												
Turbellaria									1.81	0.59	0.17	0.03
Cestoidea									1.81	1.16	0.34	0.05
NEMERTINEA												
Enopla	2.50	0.31	0.02	0.02	2.20	0.82	0.26	0.04	5.43	1.57	0.53	0.23
SIPUNCULOIDEA												
Sipunculoidea									3.17	0.82	0.61	0.09
ANNELIDA												
Polychaeta	13.75	2.09	11.67	3.75	6.17	1.38	1.99	0.36	14.24	4.21	10.58	4.17
Oligochaeta									1.36	1.49	0.33	0.05
ECHINODERMATA												
Ophiuroidea	30.83	26.62	46.59	44.79	4.41	2.54	6.10	0.66	7.69	2.79	8.80	1.77
Echinoidea	0.42	0.04	0.13	+								
CHORDATA												
Pisecs	0.42	0.04	0.01	+					0.45	0.75	0.21	0.01
Algae	1.25	0.12	0.02	+	0.44	0.06	0.06	+	2.26	0.37	0.23	0.03
Unidentifed egg					0.44	0.06	0.04	+	1.36	0.75	0.03	0.02

+: less than 0.01.

df $= 18$, $P < 0.05$; *C. robustus*, $x^2 = 271.5$, df $= 36$, $P < 0.05$; Figure 2). Ophiuroids were the most important food at all size classes of *C. abbreviatus* and showed the highest frequency of dry weight at size class III (54.00%) (Figure 2). After ophiuroids, smaller individuals (size class I and II) of *C. abbreviatus* consumed shrimps to a large degree (making up 22.89% and 41.94% in %W, respectively). However, consumption of this prey decreased in the diet of larger individuals (size class III, IV and V), constituting 14.20%, 12.42% and 11.50% in %W, respectively. Bivalves (size class IV) and polychaetes (size class V) were the next most frequent prey items consumed.

In the diet of smaller individuals of *C. joyneri* (size class I), amphipods showed high frequency at 59.48% in %W (Figure 2). The portion of amphipods decreased with growing *C. joyneri* size, whereas shrimps and gastropods increased. The consumption of shrimps and gastropods in the diet of the largest individuals (size class III) was 35.70% and 30.77% in %W, respectively.

The main prey items of small predators of *C. robustus* were shrimps and amphipods, constituting 42.30% and 39.69% in %W for size class I, and 37.65% and 18.96% for size class II, respectively (Figure 2). The portion of these prey items decreased with increasing fish size; however, the consumption of gastropods
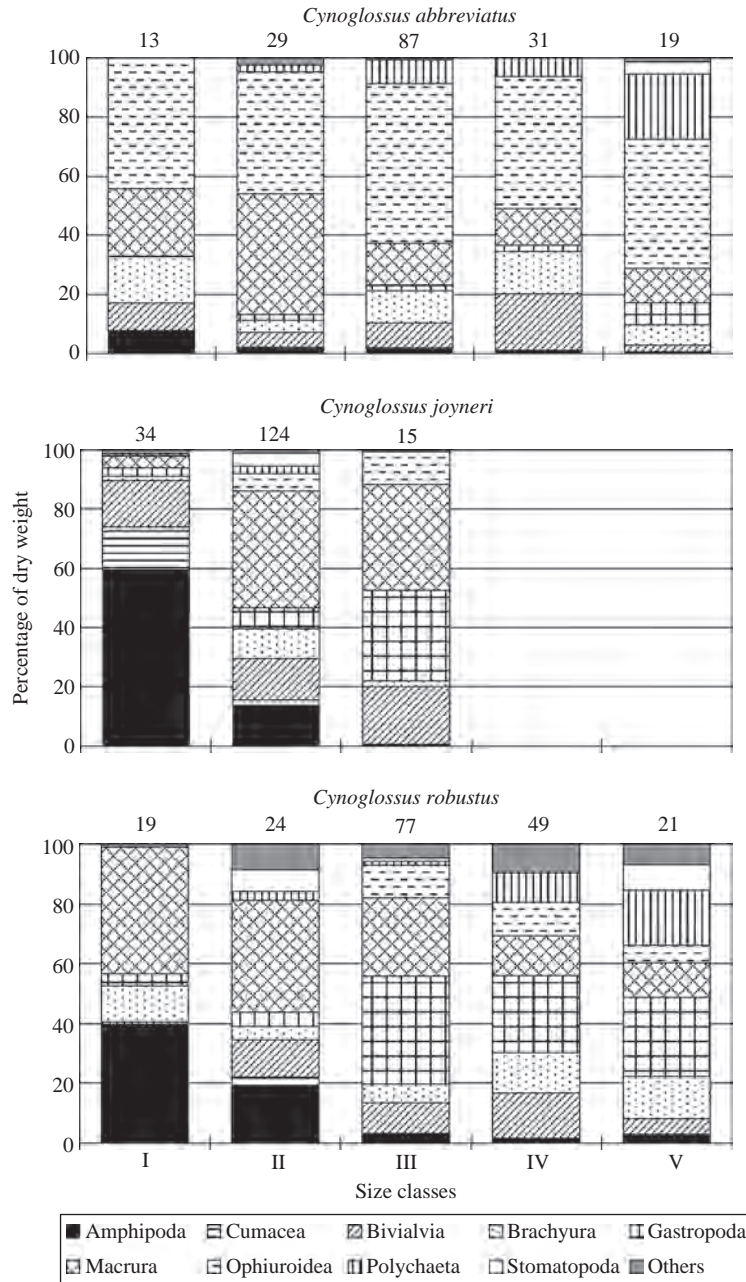
Figure 2. Ontogenetic changes in the composition of three *Cynoglossus* species diets (the number above each column is the number of individuals examined).

increased. The dominant preys of larger individuals (size class III, IV and V) were gastropods (36.09%, 25.85% and 26.35% in %W, respectively) and polychaetes (1.21%, 9.93% and 18.55% in %W, respectively) in %W.

The intraspecific values for Pianka's overlap index between successive size classes of both *C. joyneri* and *C. robustus* tended to increase with body size, reaching a maxima of 0.81 and 0.95 in the largest length classes, whereas those of *C. abbreviatus* showed high values among all size classes (Table 3). The interspecific

similarity between *C. joyneri* and *C. robustus* was higher than *C. abbreviatus*, and the highest value was only 0.97, being recorded between size class II of *C. joyneri* and *C. robustus*. The similarities among the dietary composi-tions of the three species in each size classes were illustrated by the cluster analysis (Figure 3). The three *Cynoglossus* species in each size classes could be categorized into three feeding groups (A–C) by their dietary compositions according to %W below 60% similarity. Smaller *C. joyneri* and *C. rubustus* (<25 cm TL) could be classified as group A, and the larger of

Table 3. Diet overlap coefficients between length classes among three tonguefish (genus *Cynoglossus*) off Seto, 2000–2001

Size classes	*Cynoglossus abbreviatus*					*C. joyneri*			*C. robustus*				
	I	II	III	IV	V	I	II	III	I	II	III	IV	V
C. abbreviatus													
I													
II	0.91												
III	0.94	0.85											
IV	0.94	0.80	0.92										
V	0.81	0.78	0.92	0.79									
C. joyneri													
I	0.37	0.29	0.17	0.36	0.16								
II	0.50	0.61	0.25	0.42	0.27	0.80							
III	0.36	0.53	0.22	0.38	0.28	0.51	0.81						
C. robustus													
I	0.46	0.52	0.20	0.27	0.21	0.76	0.88	0.55					
II	0.45	0.58	0.23	0.36	0.28	0.78	0.97	0.77	0.84				
III	0.31	0.43	0.19	0.31	0.29	0.49	0.74	0.96	0.50	0.71			
IV	0.31	0.33	0.22	0.38	0.37	0.54	0.67	0.83	0.38	0.68	0.91		
V	0.23	0.25	020	0.26	0.44	0.44	0.54	0.69	0.33	0.57	0.83	0.95	

them (>25 cm TL) as group B, whereas *C. abbreviatus* was categorized as group C.

Seasonal changes in diet composition

Seasonal changes in dietary composition of three *Cynoglossus* species were significant (*C. abbreviates*, $x^2 = 138.8$, df $= 36$, $P < 0.05$; *C. joyneri*, $x^2 = 227.3$, df $= 27$, $P < 0.05$; *C. robustus*, $x^2 = 248.3$, df $= 27$, $P < 0.05$; Figure 4). In the diets of *C. abbreviatus*, ophiuriods were preyed upon most frequently in all seasons, constituting more than 40% in %*W* (Figure 4). Besides ophiuriods, bivalves were consumed mainly in the summer (%*W* $= 28.30$), polychaetes in the autumn (%*W* $= 17.06$) and the winter (%*W* $= 23.03$) and shrimps in the spring (%*W* $= 12.87$). Medium volumes of shrimps were preyed upon throughout the year, making up more than 12% in %*W*. The remaining food items were minor preys of *C. abbreviatus* in all seasons.

In the diets of *C. joyneri*, shrimps were the most important prey during autumn, winter and spring, making up more than 44% in %*W*, while amphipods and gastropods were consumed mostly in summer, constituting 29.18% and 28.83% in %*W*, respectively (Figure 4). Amphipods, bivalves and crabs were present in the stomachs of *C. joyneri* throughout the year, with peak values recorded in spring (%*W* $= 29.18$), autumn (%*W* $= 22.86$) and winter (%*W* $= 14.40$), respectively. The rest of the preys were consumed in low volumes throughout the year.

For *C. robustus*, shrimps were the most important prey in autumn and winter, making up 27.85% and 41.01% in %*W*, respectively, whereas gastropods were

mainly preyed upon in spring and polychaetes in summer, representing 49.74% and 31.59% in %*W*, respectively (Figure 4). Crabs and bivalves showed peaks in autumn of 25.18% and 23.68% in %*W*, respectively. The remaining preys were not important preys during any season.

Discussion

Our results indicate that the three *Cynoglossus* species fed on a wide range of benthic invertebrates, such as
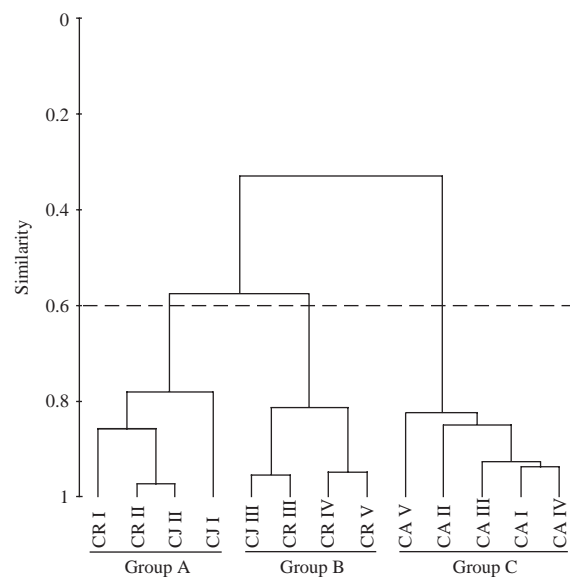

Figure 3. Cluster analysis based on %*W* for the each 5-cm size classes of three *Cynoglossus* species.
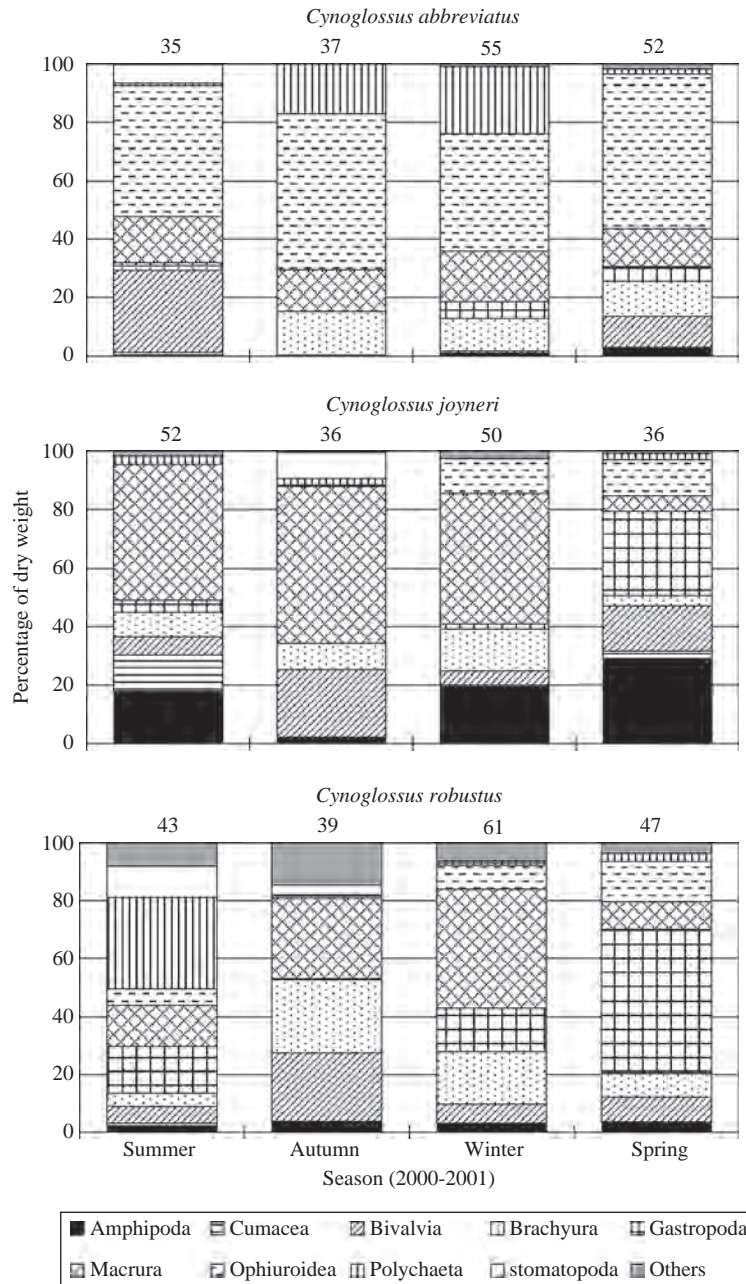
Figure 4. Seasonal change in the compositions of three *Cynoglossus* species diets (the number above each column is the number of individuals examined).

amphipods, shrimps, crabs, gastropods, bivalves and ophiuroids, but that the contribution of different food items to the total diet differed among species. Among the *Cynoglossus* species, *C. semifasciatus* (Seshappa and Bhimachar 1955), *C. arel*, *C. lida* (Rajaguru 1992) and *C. semilaevis* (Dou 1993) also consume benthic prey. The dominance of benthic prey reflects the demersal feeding behavior of *Cynoglossus* species. These benthic preys are important in the diets of many flatfish species (Seshappa and Bhimachar 1955; Ochiai 1966; Langton 1983; Dou 1995; Link et al. 2002). *Cynoglossus* species

have asymmetrical jaws, small stomachs and long intestines, and these morphological characters make it easier for them to forage and feed on benthic prey (Rajaguru 1992).

In the present study, large numbers of prey items were found in the diets of the three *Cynoglossus* species. While there was no dominant prey item, *C. abbreviatus* was shown to prey selectively on ophiuroids. The dietary diversities of the three *Cynoglossus* species were also relatively high (2.12–3.06). The wide range of prey items and high dietary diversities may be

indications of their generalized and opportunistic feeding habits. Many flatfishes, including *Cynoglossus* species, can be classified as generalist feeders, with their diets composed of a wide variety of preys (Dou 1995; Gibb 1997; Cabral et al. 2002; Vassilopoulou 2006). These generalized feeding habits appear to be common phenomena in flatfish. However, Serrano et al. (2003) suggested that benthic predators do not seem to take prey in proportion to their availability, but rather exhibit some degree of selection.

Our study highlights the importance of benthic crustacean preys such as amphipods, shrimps, crabs and stomatopods in the diets of three *Cynoglossus* species; these taxa were the first important prey items of *C. jonery* and *C. robust*, and secondary foods of *C. abbreviatus* in%W. De Groot (1971), Ramanathan et al. (1980) and Ochiai (1966) also observed the importance of these preys in the diets of other *Cynoglossus* species. In addition, crustaceans occasionally contributed importantly to the diets of younger stages of demersal piscivore species (Castillo-Rivera et al. 2000; Treloar et al. 2007; Šantić et al. 2009). Crustaceans are one of the most successful animals, and are abundant in the oceans. Therefore, demersal fishes could easily consume abundant benthic crustaceans.

Bottom-feeding carnivores sometimes use ophiuroids as a minor food source (Dou 1995; Gonzales et al. 1996; Kovačić 2001; Jaworski and Ragnarsson 2006). However, in one atypical result of the present study, *C. abbreviatus*, in all size classes and seasons, consumed mostly ophiuroids. This study is not the first to report the predation of ophiuroids as a major prey, although only a few species are known to specialize in ophiuroids (Jewett and Feder 1980; Gabriel and Pearcy 1981; Kaiser and Ramsay 1997; Ohmura et al. 2005). Ohmura et al. (2005) suggested that this specialized foraging strategy seems to reduce intra- and interspecific competition for food between co-occurring fish species. However, this hypothesis is not sufficient to explain this foraging strategy. Why certain fish species specialize in prey items which appear to be difficult to digest and have low energy content remains an interesting question.

Food composition and dietary overlap reveal significant changes in the diet of growing *C. joyneri* and *C. robustus*. Small-sized *C. joyneri* and *C. robustus* fed mainly on small prey such as amphipods, whereas larger individuals preferred larger prey (shrimps, gastropods and polychaetes). However, *C. abbreviatus* showed selective feeding on ophiuroids in all size classes. Ontogenetic diet shifts are a general trend among fish and have also been described for other *Cynoglossus* species (Ochiai 1966; Rajaguru 1992; Choi et al. 1995). Ontogenetic diet changes relate to digestive morphology, mouth structure and feeding behavior,

reflecting increased ability to consume larger prey (Stickney et al. 1974), and are often associated with the optimization of the energy gained from one or another type of diet (Stephens and Krebs 1986). In addition, Langton (1983) argued that ontogenetic changes in feeding habits could allow individuals in various growth stages to coexist by decreasing intraspecific competition.

Amphipods were important prey items in the diets of small-sized *Cynoglossus* species, especially *C. joyneri* and *C. robustus*. Many juvenile flatfishes, including *Cynoglossus* species, are known to heavily consume amphipods (Rajaguru 1992; Prisco et al. 2001). Among juvenile *Cynoglossus* species, *C. arel* (<12.8 cm TL) and *C. robustus* (<15.0 cm TL) consumed amphipods as their major prey (Rajaguru 1992; Baeck and Huh 2004). However, *C. lida* (<12.5 cm TL) fed mainly on copepods (Rajaguru 1992), and juvenile flatfishes from the Belgian coast consumed mainly polychaetes, shrimps and mysids (Beyst et al. 1999). It is not reasonable to conclude that flatfishes, including *Cynoglossus* species, mainly consume amphipods during their younger stages. Rather, it is likely that their food items depend on the abundant prey in their ambient environment.

The results of cluster analysis showed some differences in diet compositions among each size class of the three *Cynoglossus* species (Figure 3). Similar sizes of *C. joyneri* and *C. robustus* were classified into the same feeding group (groups A and B in Figure 3), whereas *C. abbreviatus* belonged to another group (group C in Figure 3). These differences should not imply that each of the species feeds on a completely different prey organism. The existence of similar diet composition also does not necessarily cause interspecific competition (Cabral et al. 2002), as each species uses a different microhabitat and generally consumes the most abundant prey. However, comparative feeding habits can provide information on potential conflicts over food resources (Kwak et al. 2005), because to some degree the habitat ranges and prey items overlapped.

Seasonal changes in the diet compositions of the three *Cynoglossus* species were significant, although little seasonal change was found in the diet of *C. abbreviates*. Such changes have also been found in the diets of other *Cynoglossus* species (Rajaguru 1992; Dou 1993). Seasonal diet changes are related to seasonal changes in food availability caused by environmental and seasonal physiological changes (Wotton 1990). In the present study, seasonal changes in the diets of the three *Cynoglossus* species were very complicated and we did not investigate the abundance, distribution or seasonal changes in the benthic invertebrates of the Seto Inland Sea. Although several prey items showed some seasonal trends (e.g. bivalves, polychaetes and

crabs in the diet of *C. abbreviatus*; amphipods, bivalves and gastropods in *C. joyneri*; and polychaetes, gastropods and bivalves in *C. robustus*), it was difficult to explain these trends due to insufficient information on seasonal variations in benthic organisms.

In conclusion, the present study provides information on the diets of three *Cynoglossus* species and examines differences in their diet compositions. Resource partitioning could determine species coexistence in the highly diverse marine environment. However, the mechanisms of this are still unclear and further studies are needed to evaluate the effects of spatial and temporal partitioning in this area. Also, studies of geographical differences in their foraging ecology need to understand their population structure because flatfish species have a highly polymorphic population structure, large population size and wide distribution (Nielsen et al. 2009; Kim et al. 2010).

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