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Feeding ecology of three amphipod species *Synchelidium lenorostralum*, *S. trioostegitum* and *Gitanopsis japonica* in the surf zone of a sandy shore

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ABSTRACT: The influence of seasonal and ontogenetic changes on the dietary composition of 3 amphipod species (*Synchelidium lenorostralum*, *S. trioostegitum* and *Gitanopsis japonica*) were studied in the surf zone of a sandy shore habitat in Dolsando, southern Korea. The 2 species of *Synchelidium* were found to be carnivorous feeders, consuming mainly benthic harpacticoid copepods, whereas *G. japonica* had a diet consisting of both copepods and detritus. The dietary composition of *S. lenorostralum* and *S. trioostegitum* overlapped for all ontogenetic stages. Little overlap was found in the dietary composition of *G. japonica* compared with the 2 *Synchelidium* species, a characteristic that might favor the co-existence of the 3 species. *S. lenorostralum* displayed significant differences in dietary composition between sexes, among developmental stages, and over the seasonal cycle. For *S. trioostegitum*, dietary composition varied over the seasonal cycle. Juveniles of *Synchelidium* fed mainly on copepod nauplii and nematodes as well as on benthic harpacticoid copepods. Our results suggest that the biological interactions between benthic amphipods and meiofauna, such as benthic harpacticoid copepods and nematodes, may be important in the trophic chain of sandy shore surf zone habitats.

KEY WORDS: *Synchelidium lenorostralum* · *S. trioostegitum* · *Gitanopsis japonica* · Amphipoda · Feeding · Sandy surf zone

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INTRODUCTION

Sandy shore surf zones comprise a significant area of coastal marine habitats (Ross et al. 1987, Brown & McLachlan 1990). Water circulation in the surf zone concentrates particulate foods such as detritus, planktonic microalgae and/or benthic microalgae. The biomass of zooplankton, which feed on particulate food, is known to be high in the surf zone and to decrease with distance from the shore. In addition, food chains in beach environments are known to be centered in the surf zone rather than in the intertidal zone (Ross et al. 1987).

The macrofauna of sandy beaches is often abundant and in some cases can reach exceptionally high densities (see review by McLachlan 1983). Macrofauna occupy a middle role in the food chain; they process food from the surf zone and in turn, are consumed by top predators such as birds and fish (McLachlan 1983). Several studies have reported that intertidal macrofauna constitute a major part of the diet of surf zone fishes (Ross et al. 1987, Ojeda & Dearborn 1991, Edgar & Shaw 1995, De Troch et al. 1998, Harvey 1998, Takahashi et al. 1999). However, there is little published information on the interactions between macrofauna and their prey in sandy beach habitats (McLachlan 1983, Brown & McLachlan 1990).

Amphipods are widespread throughout a diverse range of tropical, temperate and arctic intertidal

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sandy shore habitats, often dominating benthic macrofaunal communities in terms of both numbers and biomass (Fenchel et al. 1975, Wijnsma et al. 1999, Dittmann 2000). Moreover, amphipods are considered to be one of the most important secondary producers (Carrasco & Arcos 1984) and a major food source for a variety of marine predators (Kline & Wood 1996, Schlacher & Wooldridge 1996, Beare & Moore 1997, MacNeil et al. 1999, Takahashi et al. 1999). Amphipods play an important role in surf zone food webs, acting as a trophic link from primary producers to higher-order consumers. Clearly, quantitative assessments of trophic relationships between amphipods and their prey/predators are important for our understanding of energy flow in sandy shore surf zone environments (Gerdol & Hughes 1994).

Various aspects of amphipod feeding activity have been studied, including diet (Fenchel et al. 1975, Biernbaum 1979, Nielsen & Kofoed 1982, Icely & Nott 1985, Stuart et al. 1985), diel feeding patterns (Sainte-Marie 1986, Gerdol & Hughes 1994, Ingolfsson & Agnarsson 1999) and the influence of food quality on growth and reproduction (Gee 1988, Johnson & Wiederholm 1989, Delong et al. 1993, Pöckl 1995, Poltermann 2000). These studies have provided basic information on the feeding ecology of freshwater and marine amphipods inhabiting sublittoral and intertidal habitats. However, there is no information available on the feeding characteristics of amphipods in sandy shore surf zone habitats.

In the sandy shore surf zone of Dolsando, southern Korea, *Synchelidium lenorostralum*, *S. trioostegitum* and *Gitanopsis japonica* are the dominant amphipod species. These amphipods occupy the lower part of the water column from a depth of 1 m (measured at low water during the spring tide) and do not exhibit seasonal or diel migration (Yu 2001). *S. lenorostralum* is known to feed mainly upon benthic harpacticoid copepods, suggesting an important role in biological interactions of the sandy shore surf zone (Yu et al. 2002b). Despite their abundance and potentially important contribution to food webs of sandy shore surf zone habitats, there is no information on the feeding characteristics of different species or different ontogenetic stages within species.

The aim of this study is to determine the dietary composition as well as seasonal and ontogenetic variations in the diet of 3 amphipod species, *Synchelidium lenorostralum*, *S. trioostegitum* and *Gitanopsis japonica*, in the surf zone of a sandy shore habitat. The results reported here contribute to our understanding of amphipod feeding strategies, life history characteristics and the role of amphipods in sandy shore surf zone ecosystem processes.

MATERIALS AND METHODS

Benthic amphipods were collected monthly between July 1996 and June 1997 from a depth of 1 m at the low water mark of the spring tide in Dolsando (34° 37′ 39″ N, 127° 47′ 44″ E), southern Korea. The area is moderately sheltered and on average, particle sizes are composed of 66% fine and 26% medium sand. The beach slope at the sampling site is 1:48 and the width of the intertidal zone is 150 m. The spring tidal range at the study site is approximately 5 m. Detailed descriptions of the environmental characteristics at the sampling site are reported in Yu et al. (2002a,b).

Parallel to the shoreline, 5 samples were taken using a sledge net (mouth size: 12 × 30 cm; mesh size: 0.3 mm) over a distance of 20 m and at a speed of approximately 1 m s^{-1}. The sledge with a thick chain at the bottom leading edge was drawn across the substratum on 2 lateral skids. The sledge skimmed the surface at a depth of approximately 1 cm. Concentrated tow samples were immediately preserved in 5% buffered formalin in seawater.

Amphipods collected during each monthly sampling were divided into 4 categories: juveniles, males, non-ovigerous females and ovigerous females (see Donn & Croker 1986 for a detailed description). The gut of each amphipod was carefully removed and immersed in glycerol on a glass slide. The gut contents were examined under a differential interference microscope (Zeiss Axioskop) and a cold-field emission scanning electron microscope (Hitachi S-4700) for identification to the lowest possible taxonomic category. Prior to observation by SEM, the gut contents were dehydrated using a graded ethanol and *t*-butyl alcohol series and then freeze dried. Samples were mounted on stubs and sputter coated with platinum. The dietary composition was determined for each of the ontogenetic categories of all 3 amphipod species monthly.

Dietary composition was analyzed using the point method (Wear & Haddon 1987). This method is suitable for assessing the diets of crustaceans whose gut contents are macerated and difficult to quantify (Takahashi & Kawaguchi 1998, Oh et al. 2001). The gut fullness was estimated on a subjective 6-step scale from 0 to 1 as follows: a score of 0 was given for an empty gut; 0.02 for 5% full or only remnants; 0.25 for 25% full (<35 and >5%); 0.5 for 50% full (<65 and >35%); 0.75 for 75% full (<100 and >65%); and 1 for a 100% full gut. The relative contribution of each food item to the total gut content was subjectively assessed on a 5-step scale: 0 points for an item not found in the gut; 2.5 points if an item occupied less than 5% or only remnants; 25 points for 25% (<35 and >5%), 25 points; 50 points for 50% (<65 and >35%); 75 points for 75% (<100 and >65%); and 100 points for an item representing 95 to 100% of gut contents. The relative contribution of each food item was then weighted by multiplying it by the estimated value for gut fullness. The number of points obtained by each food item was expressed as a percentage of the total gut content. The frequency of occurrence (*F*) and relative abundance (*A*) for each food type was estimated using the following equations:

$$\% F = (n_i/N) \times 100$$
$$\% A = (\Sigma S_i/\Sigma S_t) \times 100$$

where n_i is the number of amphipods with food *i* in the gut, *N* is the total number of amphipods with gut contents, S_i the number of food *i* and S_t the total number of food items.

Based on the composition of the gut contents, an overlap index of diets was calculated (both intra- and interspecifically) using the following equation (Schoener 1970):

$$Ro = 100\ (1 - {}^1/_2\Sigma|px_i - py_i|)$$

where *Ro* is the overlap index expressed as a percentage, and px_i and py_i are the relative proportions of each food item *i* obtained for the *x*th and *y*th species.

Prior to statistical analyses, data were tested for homogeneity of variances and normality using Bartlett's test (Statistica version 5.1, Statsoft, 1984–1996). Normally distributed data were tested with parametric methods; otherwise, non-parametric methods were used. The Kruskal-Wallis and Friedman tests were used to examine differences in the abundance of food items between sampling months and between the 4 ontogenetic categories (MINITAB version 12.1, Minitab, 1998). The differences in gut content composition between categories was examined using the χ^2 test.

RESULTS

Synchelidium lenorostralum Hirayama 1986 (Oedicerotidae)

The most common food items in the gut of *Synchelidium lenorostralum* were found to be harpacticoid copepods (mainly *Robertgurneya* sp.), which occurred in over 80% of the guts examined and constituted more than 75% of total gut content (Fig. 1A). The other categories contributed only minor proportions to the diet (<10% of total abundance each).

Harpacticoid copepods were the dominant species found in the guts of all 4 ontogenetic categories (Table 1). Nematodes, crustacean fragments and copepod nauplii (mainly the nauplius I stage of harpacticoid copepods) represented from 5.4 to 6.4% of total gut contents in males. These food items occurred in very low abundance in the guts of non-ovigerous and ovigerous females. In juveniles, copepod nauplii and detritus represented more than 10%

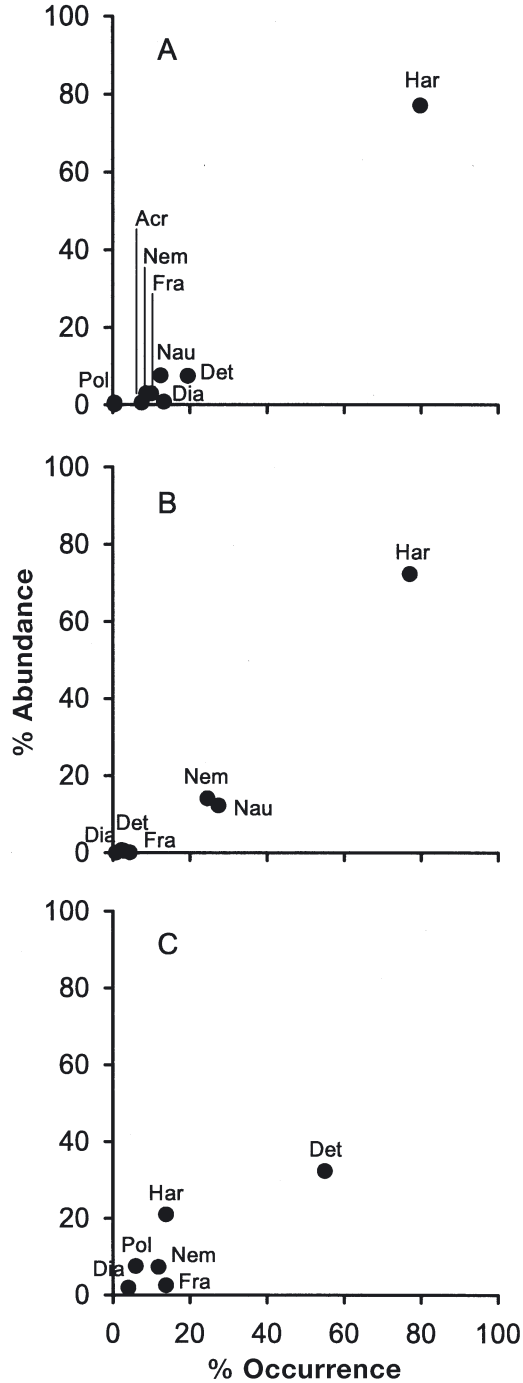

Fig. 1. Overall diet. Food items abundance plotted against frequency of occurrence of food item for (A) *Synchelidium lenorostralum*, (B) *S. trioostegitum* and (C) *Gitanopsis japonica*. Values are calculated for pooled samples irrespective of months and categories. Har: harpacticoid copepods; Nem: Nematodes; Acr: *Acartia* copepod species; Frg: crustacean fragments; Nau: copepod nauplii; Pol: Polychaetes; Dia: Diatoms; Det: detritus

Table 1. *Synchelidium lenorostralum*. Diet compositions in each ontogenetic category. % *A*: percentage of abundance; % *F*: frequency of occurrence; n: number of specimens examined

Food items	Juvenile (n = 81) % *A*	% *F*	Male (n = 62) % *A*	% *F*	Female (n = 51) % *A*	% *F*	Ovigerous female (n = 48) % *A*	% *F*
Harpacticoid copepods	64.3	63.0	76.4	80.6	89.6	94.1	89.0	91.7
Nematodes	2.7	7.4	6.4	12.9	1.0	9.8	0.6	4.2
Acartia sp.	0.0	0.0	0.0	0.0	0.0	0.0	3.3	2.1
Crustacean fragments	3.5	11.1	5.5	16.1	0.0	0.0	1.5	10.4
Copepod nauplii	15.6	19.8	5.4	14.5	2.5	7.8	0.5	2.1
Polychaetes juveniles	0.0	0.0	0.0	0.0	0.4	2.0	0.0	0.0
Gyrosigma sp.	0.5	6.2	1.0	16.1	0.9	13.7	1.1	20.8
Detritus	12.6	25.9	5.0	22.6	4.8	9.8	4.0	14.6
Sand	0.8	12.3	0.3	8.1	0.8	5.9	0.0	0.0

Table 2. *Synchelidium lenorostralum*. Contingency table analysis of 5 different categories of food items in each ontogenetic category. Values are the total number of food items with expected values in parentheses. χ^2 and *G*-statistics are significant (**p < 0.01)

Food items	Juvenile	Male	Female	Ovigerous female	N_i	χ^2	G_i
Harpacticoids	51 (60)	50 (56)	48 (38)	44 (39)	193	5.13	5.01
Nematodes	6 (7)	8 (6)	5 (4)	2 (4)	21	1.98	2.22
Crustaceans	25 (17)	19 (16)	4 (11)	7 (11)	55	10.13	11.27
Diatoms	5 (10)	10 (9)	7 (6)	10 (6)	32	4.54	4.80
Detritus	21 (15)	14 (14)	5 (9)	7 (10)	47	5.47	5.60
N_i	108	101	69	70	348		
χ^2	10.32	1.18	9.09	5.96		27.25**	
G_i	10.11	1.84	10.72	6.23			28.90**

of total gut contents. There were significant differences in gut content composition between the 4 ontogenetic categories (Table 2). A statistically significant difference (χ^2 = 9.63, df = 4, p < 0.05) in gut content composition was found between males and females. Among the range of food items, the main source of variation was crustaceans (χ^2 = 10.13), consisting mainly of crustacean fragments and copepod nauplii. Among the 4 ontogenetic categories, the main source of variation was juveniles (χ^2 = 10.32). The overlap index of gut content composition between juveniles and males was 82%. The indices obtained between juveniles and non-ovigerous females and between juveniles and ovigerous females were less than those for males (Table 3). However, the overlap indices between males and non-ovigerous females and between non-ovigerous and ovigerous females were 93 and 95%, respectively.

There was a significant difference between month and dietary composition of *Synchelidium lenorostralum* (Friedman test: *S* = 33.47, df = 6, p < 0.001). During the winter months, harpacticoid copepods accounted for more than 95% of the diet in % *A* and % *F*. However, in August and September, this fraction dropped to 40% and coincided with an increase in the amount of detritus, which accounted for more than 39% of abundance and 60% of occurrence (Table 4). The monthly variation in the proportion of harpacticoid copepods in the gut contents was statistically significant (Kruskal-Wallis test: *H* = 76.91, df = 11, p < 0.001). Copepod nauplii were detected in the gut contents only in November, April and May, contributing more than 40% to total gut contents with respect to both % *A* and % *F* in April.

There was a statistically significant variation in dietary composition throughout the year (for food

Table 3. Intraspecific overlap indices of diets in *Synchelidium lenorostralum*, *S. trioostegitum* and *Gitanopsis japonica* using the Schoener overlap index (*Ro*) and Spearman rank correlation (R_S) (in parentheses). *p < 0.05, **p < 0.01, ***p < 0.001; –: no data

Ontogenetic category	*S. lenorostralum*	*S. trioostegitum*	*G. japonica*
Juvenile vs Male	82 (0.832**)	76 (0.935***)	–
Juvenile vs Female	74 (0.752*)	86 (0.865**)	–
Juvenile vs Ovigerous female	72 (0.432)	90 (0.811*)	–
Male vs Female	93 (0.592)	93 (0.778*)	90 (0.766*)
Male vs Ovigerous female	84 (0.424)	79 (0.778*)	67 (0.323)
Female vs Ovigerous female	95 (0.336)	91 (0.964***)	74 (0.428)

Table 4. *Synchelidium lenorostralum*. Monthly variation of food items. % *A*: percentage of abundance; % *F*: frequency of occurrence; n: number of specimens examined

Month	n	Harpacticoid copepods		Nematodes		*Acartia* sp.		Crustacean fragments		Copepod nauplii		Polychaetes		*Gyrosigma* sp.		Detritus		Sand	
		% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*
1996																			
Jul	4	77.8	50.0	2.2	50.0	0.0	0.0	7.2	50.0	0.0	0.0	0.0	0.0	0.6	25.0	6.1	50.0	6.1	50.0
Aug	19	31.3	31.6	7.4	21.1	0.0	0.0	9.2	26.3	0.0	0.0	0.0	0.0	0.2	5.3	49.2	73.7	2.7	15.8
Sep	13	26.7	30.8	20.0	15.4	0.0	0.0	13.6	38.5	0.0	0.0	0.0	0.0	0.0	0.0	39.2	61.5	0.4	23.1
Oct	23	87.1	91.3	1.4	4.3	0.0	0.0	7.1	8.7	0.0	0.0	0.0	0.0	0.2	8.7	3.7	26.1	0.4	13.0
Nov	36	77.7	72.2	2.3	2.8	0.0	0.0	0.0	0.0	18.9	27.8	0.0	0.0	0.9	2.8	0.2	11.1	0.0	0.0
Dec	26	95.3	92.3	1.3	3.8	0.0	0.0	2.0	7.7	0.0	0.0	0.0	0.0	0.0	0.0	1.3	7.7	0.1	3.8
1997																			
Jan	12	96.7	100.0	1.7	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	50.0	0.0	0.0	0.1	8.3
Feb	15	99.8	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	6.7	0.0	0.0	0.0	0.0
Mar	27	85.8	96.3	1.8	11.1	0.0	0.0	4.0	14.8	0.0	0.0	1.1	3.7	4.7	59.3	2.3	7.4	0.3	7.4
Apr	29	48.9	75.9	0.2	6.9	0.0	0.0	2.2	10.3	42.7	58.6	0.0	0.0	0.0	0.0	4.1	17.2	1.8	6.9
May	27	90.8	96.3	1.5	7.4	4.1	3.7	0.1	3.7	3.1	11.1	0.0	0.0	0.1	7.4	0.3	3.7	0.0	0.0
Jun	11	82.0	81.8	4.8	18.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	18.2	10.7	27.3	0.1	9.1

items contributing >3% to total abundance) for different developmental stages of *Synchelidium lenorostralum* (Table 9). In juveniles, the dietary composition varied with month. In the summer (July to September), detritus accounted for over 50% of total gut content abundance, whereas harpacticoid copepods dominated gut contents in the winter (Fig. 2). The proportion of copepod nauplii in the gut contents showed 2 peaks, in November and April. In males, harpacticoid copepods were more common in the gut contents from November to March. During the summer, this proportion decreased and coincided with a proportional increase in the contribution from detritus and nematodes. In April, copepod nauplii accounted for over 50% of total gut contents. For non-ovigerous and ovigerous females, harpacticoid copepods were the most abundant component in the gut throughout the year. Some variation in the dietary composition of non-ovigerous and ovigerous females was also observed throughout the year (Table 9).

Synchelidium trioostegitum Jo 1990 (Oedicerotidae)

The most common food item found in the gut of *Synchelidium trioostegitum* was harpacticoid copepods (mainly *Robertgurneya* sp.), which occurred in over 75% of the guts examined and constituted more than 70% of total gut contents (Fig. 1B). Nematodes and copepod nauplii (mainly nauplius I stage of harpacticoid copepods) were the second major contributors to the diet. The other categories contributed only minor amounts to the diet (<10% of total abundance each).

Harpacticoid copepods were the dominant species in the guts of all 4 ontogenetic categories (Table 5). Copepod nauplii constituted 13.5% of the total abundance of food items in the guts of males, but occurred in a very low proportion in the guts of females. Nematodes represented more than 18% of total abundance in both non-ovigerous and ovigerous females. In juveniles, nematodes and copepod nauplii constituted over 18% of total gut contents. There was no significant difference in gut contents between the 4 ontogenetic categories ($\chi^2 = 11.47$, df = 6, $p > 0.05$). A high dietary overlap index was found between males and females. The lowest dietary overlap index was found between juveniles and males (Table 3). The Spearman rank coefficients were significant in all cases, indicating a high degree of similarity in diet between different ontogenetic stages.

There was a significant difference between months in the dietary composition of *Synchelidium trioostegitum* (Friedman test: $S = 39.56$, df = 5, $p < 0.001$). During winter, harpacticoid copepods accounted for over 70% of the diet for both % *A* and % *F*; however, in November and April, the proportion dropped to 50% (Kruskal-Wallis test: $H = 23.13$, df = 10, $p < 0.01$). This change coincided with an increase in the contribution of nematodes and copepod nauplii, which accounted for more than 30 and 40% of gut content abundance, respectively (Table 6). Nematodes accounted for over 20% of total gut contents from September to December, whereas copepod nauplii accounted for more than 35% of the diet in % *A* and % *F* in November and April.

Table 5. *Synchelidium trioostegitum*. Diet compositions in each ontogenetic category. % *A*: percentage of abundance, % *F*: frequency of occurrence; n: number of specimens examined

Food items	Juvenile (n = 38)		Male (n = 35)		Female (n = 39)		Ovigerous female (n = 27)	
	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*
Harpacticoid copepods	62.1	65.8	85.6	88.6	73.8	79.5	66.4	74.1
Nematodes	19.0	26.3	0.8	2.9	18.3	38.5	18.9	29.6
Crustacean fragments	0.0	0.0	0.0	0.0	0.5	2.6	2.2	11.1
Copepod nauplii	18.8	31.6	13.5	28.6	5.3	23.1	11.8	25.9
Hyalodiscus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	3.7
Detritus	0.0	2.6	0.0	0.0	2.0	2.6	0.4	3.7
Sand	0.1	2.6	0.1	5.7	0.1	2.6	0.2	7.4

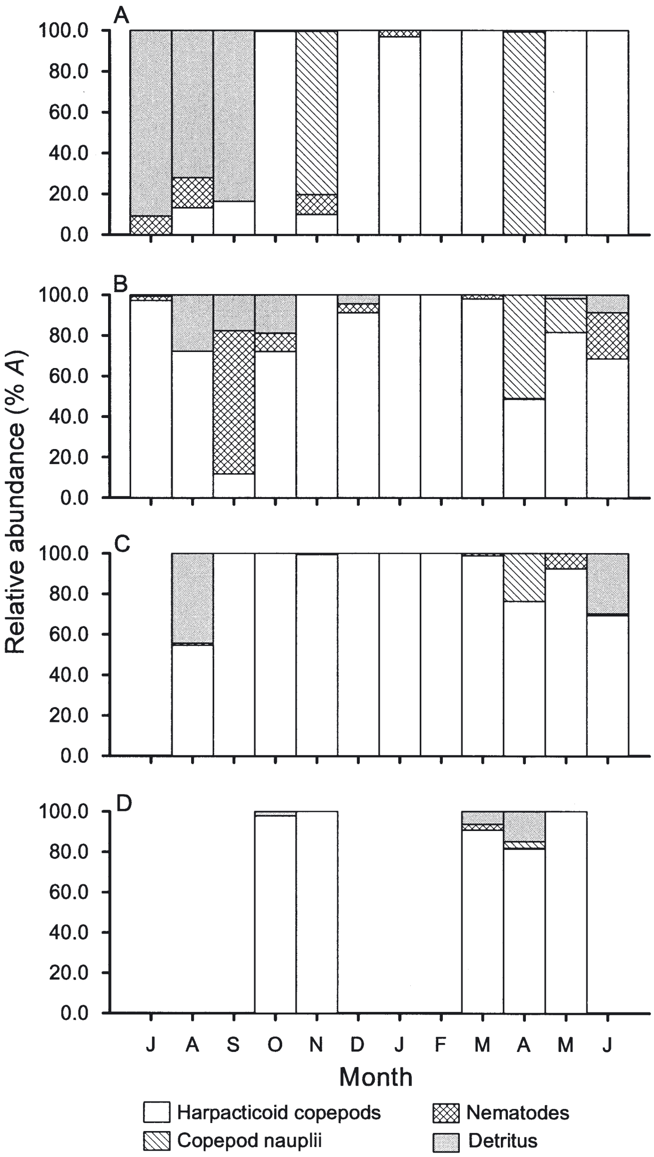

Fig. 2. Monthly relative abundance (% *A*) of harpacticoid copepods, nematodes, copepod nauplii and detritus consumed by *Synchelidium lenorostralum*. (A) Juveniles, (B) males, (C) females, (D) ovigerous females

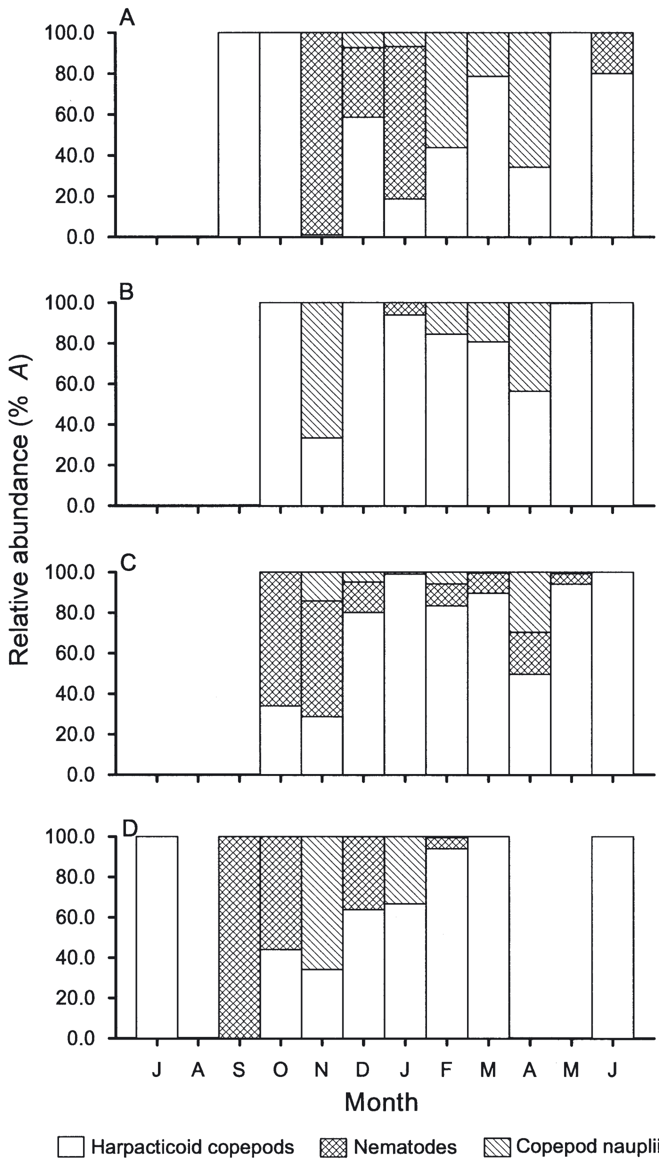

Fig. 3. Monthly relative abundance (% *A*) of harpacticoid copepods, nematodes and copepod nauplii consumed by *Synchelidium trioostegitum*. (A) Juveniles, (B) males, (C) females, (D) ovigerous females

Table 6. *Synchelidium trioostegitum*. Monthly variation of food items % *A*: percentage of abundance; % *F*: frequency of occurrence; n: number of specimens examined; –: no data

Month	n	Harpacticoid copepods		Nematodes		Crustacean fragments		Copepod nauplii		*Hyalodiscus* sp.		Detritus		Sand	
		% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*
1996															
Jul	1	100.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aug	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sep	3	50.0	33.3	50.0	66.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oct	15	61.5	66.7	38.5	46.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nov	12	25.1	58.3	37.8	41.7	0.0	0.0	36.8	58.3	0.3	8.3	0.0	0.0	0.0	0.0
Dec	18	72.6	72.2	21.2	38.9	1.1	5.6	4.7	16.7	0.0	0.0	0.5	5.6	0.0	0.0
1997															
Jan	14	79.9	78.6	17.5	28.6	0.0	0.0	2.5	35.7	0.0	0.0	0.0	0.0	0.0	0.0
Feb	19	79.4	89.5	4.0	15.8	1.4	5.3	15.0	36.8	0.0	0.0	0.0	0.0	0.1	5.3
Mar	20	80.8	80.0	1.9	10.0	1.1	10.0	11.5	20.0	0.0	0.0	4.3	5.0	0.5	20.0
Apr	14	45.2	64.3	5.6	14.3	0.0	0.0	49.0	71.4	0.0	0.0	0.0	0.0	0.2	7.1
May	15	97.7	100.0	1.8	6.7	0.0	0.0	0.4	13.3	0.0	0.0	0.0	0.0	0.0	0.0
Jun	8	93.7	87.5	6.1	12.5	0.0	0.0	0.0	0.0	0.0	0.0	0.2	12.5	0.0	0.0

There was significant variation in dietary composition throughout the year (for food items contributing >3% of total abundance overall) among the 4 ontogenetic categories of *S. trioostegitum* (Table 9). In juveniles, the dietary composition varied with month, particularly from November to April (Fig. 3). Nematodes accounted for over 50% of total gut contents in November and January. The copepod nauplii contribution peaked in February and April. For males, harpacticoid copepods dominated in the winter and spring (except for the month of April). In November and April, the proportion of harpacticoid copepods decreased to less than 40% of total gut contents and the contribution by copepod nauplii increased to more than 40%. In females, harpacticoid copepods were clearly the dominant food item throughout the year, except in October and November when more than 50% of total gut contents were composed of nematodes. In ovigerous females, the dietary composition varied from January to November, but the proportion of harpacticoid copepods remained high over this period.

Gitanopsis japonica Hirayama 1983 (Amphilochidae)

The most common food item in the gut of *Gitanopsis japonica* was detritus, which occurred in over 54% of the guts examined. Detritus constituted more than 32% of total gut contents (Fig. 1C). Harpacticoid copepods (mainly *Parastenhelia* sp.) were the second major food item. The other categories contributed only minor amounts to the diet (<10% of total abundance each).

The relative composition of gut contents differed between the 4 ontogenetic categories of *Gitanopsis japonica* (Table 7). Detritus and harpacticoid copepods were the dominant food items in the guts of mature males and females. Nematodes represented 17.3% of the gut contents of females but only 5.4% in males. In the guts of ovigerous females, harpacticoid copepods were the dominant item. Polychaetes were the second major component, followed by detritus. There was no significant difference in the composition of gut contents between the 4 ontogenetic categories (χ^2 = 5.42,

Table 7. *Gitanopsis japonica*. Diet compositions in each ontogenetic category. % *A*: percentage of abundance; % *F*: frequency of occurrence; n: number of specimens examined

Food items	Male (n = 21)		Female (n = 15)		Ovigerous female (n = 32)	
	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*
Harpacticoid copepods	16.2	9.5	23.0	13.3	24.0	18.8
Nematodes	5.4	14.3	17.3	20.0	0.0	0.0
Crustacean fragments	4.0	4.8	1.2	26.7	2.3	12.5
Polychaete juveniles	0.0	0.0	0.0	0.0	22.0	18.8
Diatoms	5.7	9.5	0.0	0.0	0.0	0.0
Detritus	43.8	61.9	32.5	53.3	20.9	43.8
Sand	3.3	47.6	5.8	40.0	1.3	31.3
Unidentified materials	21.6	19.0	20.2	13.3	29.5	25.0

Table 8. *Gitanopsis japonica*. Monthly variation of food items. % *A*: percentage of abundance; % *F*: frequency of occurrence; n: number of specimens examined; –: no data

Month	n	Harpacticoid copepods		Nematodes		Crustacean fragments		Polychaetes		Diatoms		Detritus		Sand		Unidentified material	
		% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*	% *A*	% *F*
1996																	
Jul	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aug	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sep	2	0.0	0.0	0.0	0.0	24.8	50.0	0.0	0.0	0.0	0.0	74.4	100.0	0.8	50.0	0.0	0.0
Oct	4	42.1	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.5	25.0	5.3	25.0	42.1	50.0
Nov	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	100.0
Dec	24	26.4	16.7	7.8	12.5	4.4	16.7	0.0	0.0	5.0	8.3	34.9	58.3	6.9	54.2	14.5	12.5
1997																	
Jan	2	50.0	50.0	50.0	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Feb	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mar	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	100.0
Apr	2	0.0	0.0	0.0	0.0	1.9	50.0	57.7	50.0	0.0	0.0	38.5	50.0	1.9	50.0	0.0	0.0
May	6	0.0	0.0	2.9	16.7	0.0	0.0	12.9	16.7	0.0	0.0	20.6	50.0	0.3	16.7	63.3	50.0
Jun	9	20.5	11.1	1.3	11.1	0.4	11.1	15.4	11.1	0.0	0.0	61.5	77.8	0.9	44.4	0.0	0.0

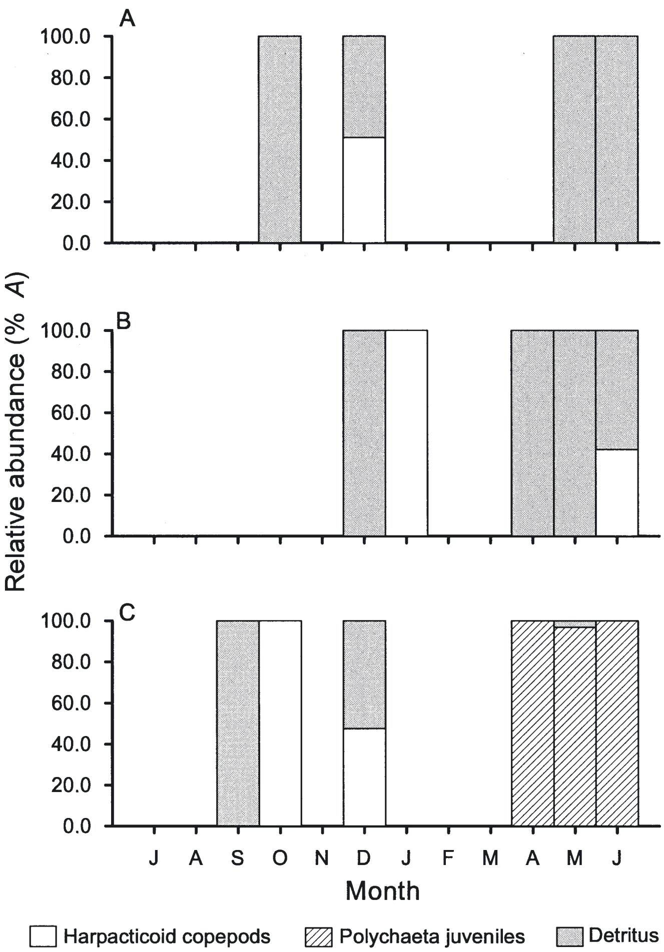

Fig. 4. Monthly relative abundance (% *A*) of harpacticoid copepods, polychaete juveniles and detritus consumed by *Gitanopsis japonica*. (A) Males, (B) females, (C) ovigerous females

df = 10, p > 0.9). The overlap index between males and females was 90% (Table 3).

There was no variation throughout the year in the dietary composition of *Gitanopsis japonica* (Friedman test: $S = 8.49$, df = 6, p > 0.1). Harpacticoid copepods accounted for over 40% of total gut contents in October and January. In September, detritus and crustacean fragments were the dominant food items. Polychaetes were found in the guts after April (Table 8).

Differences in dietary composition fluctuated monthly (for food items contributing >3% of total abundance overall) between the 4 ontogenetic categories of *Gitanopsis japonica* (Fig. 4). In males, the proportion of detritus continuously increased after December. In non-ovigerous females, harpacticoid copepods were clearly the main contributors to gut content in winter and spring, but accounted for less than 50% in other seasons. In ovigerous females, harpacticoid copepods occurred in October and December, whereas polychaetes accounted for over 50% of the total in April and June. However, these differences were not statistically significant for all ontogenetic stages (Table 9).

Interspecific overlap indices of food items

Overlap indices of gut contents were calculated for the 3 species (Table 10). An overlap index of 84% was found between *Synchelidium lenorostralum* and *S. trioostegitum*. There was little dietary overlap between *S. lenorostralum* and *Gitanopsis japonica* (49%) or between *S. trioostegitum* and *G. japonica* (43%).

Overlap indices of gut content composition were calculated between all ontogenetic categories of *Synche-*

Table 9. Result of Friedman analysis (*S*) of monthly variation of diet composition for each ontogenetic category of 3 amphipod species

Species	*S*	df	p
Synchelidium lenorostralum			
Juvenile	15.77	6	<0.05
Male	29.72	6	<0.001
Female	42.28	6	<0.001
Ovigerous female	19.99	6	<0.05
Synchelidium trioostegitum			
Juvenile	5.89	2	<0.05
Male	13.15	2	<0.001
Female	10.46	2	<0.005
Ovigerous female	5.52	2	>0.05
Gitanopsis japonica			
Male	8.43	5	>0.05
Female	5.42	4	>0.05
Ovigerous female	2.73	4	>0.05

Table 10. Interspecific overlap indices of diets among *Synchelidium lenorostralum*, *S. trioostegitum* and *Gitanopsis japonica*, using the Schoener overlap index (*Ro*) and Spearman rank correlation (R_S) (in parentheses). ***p < 0.001

Species	*Ro*
S. lenorostralum vs *S. trioostegitum*	84 (0.937***)
S. trioostegitum vs *G. japonica*	43 (–0.006)
S. lenorostralum vs *G. japonica*	49 (0.117)

lidium lenorostralum and *S. trioostegitum* (Table 11). The highest value (90%) was found between non-ovigerous females of *S. lenorostralum* and males of *S. trioostegitum*. The value of the index found between the juveniles, males and females of the 2 species was greater than 80%; however, for ovigerous females of the 2 species, a value of 71% was found. The Spearman rank coefficients were not statistically significant for ovigerous females of *S. lenorostralum*, indicating a low similarity in diet compared with other developmental stages of the 2 *Synchelidium* species.

Table 11. Interspecific overlap indices of diets among *Synchelidium lenorostralum* and *S. trioostegitum* discrimination ontogenetic categories, using the Schoener overlap index (*Ro*) and Spearman rank correlation (R_S) (in parentheses). *p < 0.05, **p < 0.01, ***p < 0.001

		S. trioostegitum			
		Juvenile	Male	Female	Ovigerous female
S. lenorostralum	Juvenile	81 (0.717*)	79 (0.660*)	75 (0.885***)	82 (0.882***)
	Male	74 (0.699*)	83 (0.642*)	88 (0.902***)	81 (0.966***)
	Female	66 (0.778**)	90 (0.642*)	80 (0.742*)	71 (0.668*)
	Ovigerous female	65 (0.118)	88 (–0.009)	79 (0.340)	71 (0.315)

DISCUSSION

Amphipods fall into 7 major categories based on their feeding methods: suspension-feeders, surface detritivores, buried detritivores, scavengers, carnivores, commensals and grazers on living food (Biernbaum 1979). These feeding methods may differ between species, between habitats or seasonally within the same species. In this study, *Synchelidium lenorostralum* and *S. trioostegitum* were found to be carnivorous, preying mainly on harpacticoid copepods, while *Gitanopsis japonica* was mainly a surficial detritus feeder with some carnivorous behavior.

In this study, harpacticoid copepods were the dominant food item of both *Synchelidium lenorostralum* and *S. trioostegitum*. However, their importance as a dietary component varied with month and with ontogenetic stage (Figs. 2 & 3). For example, Harpacticoid copepods accounted for over 95% *A* and 70% *F* of the dietary composition during the winter months, but a much lower proportion during other seasons. The seasonal variation in the composition of the diet may reflect, to some degree, the relative abundance and availability of the food item. According to Seon (2001), the abundance of Harpacticoid copepods at our study site was higher during winter than in other seasons. In contrast, for the gammarid *Gammarus troglophilus*, no seasonal changes in dietary composition were observed since the preferred food was present throughout the year (Jenio 1980). In another gammarid amphipod, *G. fasciatus*, the dietary composition is known to be related to the seasonal or temporal availability of food (Delong et al. 1993). Populations of *G. fasciatus* can persist in high numbers year-round because this species can take advantage of a range of food types (Summers et al. 1997). In the decapod crustacean *Calocaris macandreae*, variations in dietary composition were found to be related to changes in food abundance and availability within their benthic habitat (Pinn et al. 1998). The abundance of the 2 species of *Synchelidium* was higher during the winter and spring than in other seasons (Yu 2001, Yu et al. 2002a). Moreover, the mean dry weights of the 2 species were highest during the winter (Yu 2001). Thus, the density of food items, such as harpacticoid copepods, may be an important factor accounting for variation in the dietary composition of benthic amphipods in sandy shore surf zones.

For *Synchelidium lenorostralum*, there was a significant difference in dietary composition with different ontogenetic stages (Table 2). This species displays 2 main recruitment phases during the year; in fall (October to December) and in spring (March to May) (Yu et al. 2002a). Juveniles of *S. lenorostralum* are dependent upon harpacticoid copepod nauplii and detritus as food sources at the beginning of breeding periods (Fig. 2). As juveniles developed to adults, the proportion of copepod nauplii in gut contents decreased and was lowest in ovigerous females. The ovigerous females of *S. lenorostralum* fed on whole bodies of adult benthic harpacticoid copepods. The reason for this ontogenetic shift in food use is unclear, but we propose 2 possibilities. First, the variation of food items may be related to ontogenetic changes in morphology. It is possible that juveniles of *S. lenorostralum* feed only on detritus and copepod nauplii because their mouthparts (or gnathopods) are unable to process larger food items. Second, the shift in diet may be related to reproductive effort. Large *Synchelidium*, especially ovigerous females, exclude smaller food items such as copepod nauplii and detritus. In *Gammarus fasciatus*, the growth rate is known to increase with size as a result of a progressive change to a more nutritious diet (Delong et al. 1993). Summers et al. (1997) suggested that an increasing size of food item along with increasing body size may lead to higher growth rates and earlier maturity. Studies have shown that when high and low quality diets were simultaneously offered to *G. mucronatus* and *Elasmopus levis*, both species fed preferentially on the high quality diet, resulting in faster growth and higher fecundity (Cruz-Rivera & Hay 2000). Thus, the ontogenetic differences in the diet in *S. lenorostralum*, as observed in this study, may lead to faster growth rates and earlier reproduction.

The diets of *Synchelidium lenorostralum* and *S. trioostegitum* showed a high degree of overlap with each other, and a low degree of overlap with the diet of *Gitanopsis japonica* (Table 10). The large overlap in dietary composition may increase inter-specific competition for food, resulting in a low density of *S. trioostegitum* (Yu 2001). Also, food availability is an important factor influencing growth and productivity of a population (Poltermann 2000). The body size, brood size and egg size were greater in *S. lenorostralum* than in *S. trioostegitum* (Yu 2001), likely resulting from asymmetric competition for food. On the other hand, *G. japonica* was found to feed on a more varied diet, including items such as detritus, polychaete juveniles and harpacticoid copepods. *G. japonica* did not consume the same harpacticoid copepod species, which are the main food item of *Synchelidium* amphipods (Yu et al. 2002b). We suggest, therefore, that dietary differences lead to less competition for food between *G. japonica* and the 2 species of *Synchelidium* and that this favors coexistence.

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