

Daily activity, feeding and rations in gobies and brown shrimp in the northern Wadden Sea

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ABSTRACT: A 24 h trawl fishery was conducted near the island of Sylt, northern Wadden Sea, Germany, to investigate and compare daily patterns of activity and feeding among the gobies *Pomatoschistus microps* Krøyer and *P. minutus* Pallas and the brown shrimp *Crangon crangon* L. Relative occurrence of the 3 species was generally consistent, with *C. crangon* dominating at about 93 %, except at midnight, when *P. minutus* and *P. microps* occurred at 68 % and 12 %, respectively. Peak abundances of *C. crangon* and *P. minutus* occurred at dawn and of *P. microps* at sunrise, coinciding with rising tide. Size distributions for the 3 species were constant on a diurnal basis. Intensity of feeding among the gobies was highest during daylight hours, at dusk and sunrise, whereas a feeding peak in shrimp occurred at dawn, with very little feeding at noon. Feeding peaks of the 3 species therefore roughly coincided with peak activity periods. Smaller specimens of the 3 species fed mostly on meiofauna, switching gradually to macrofauna with increase in size. Over a 24 h period, *C. crangon* cannibalism was low, but predation of *P. minutus* on *C. crangon* was prevalent, ranging from about 28 % of total gut contents by ash-free dry weight (<55 mm gobies) to 77 % (>55 mm gobies). On a population basis, however, this predation was only equivalent to 0.3 % of the total available biomass of shrimp, although with highest proportions among the new recruits. Gastric evacuation rates and resulting daily rations are comparable with the range of values in the literature.

KEY WORDS: Activity · Feeding · Daily rations · Gobies · Brown shrimp · Wadden Sea

INTRODUCTION

The gobies *Pomatoschistus microps* Krøyer and *P. minutus* Pallas and the brown shrimp *Crangon crangon* L. are common inhabitants of shallow-water habitats on European coasts (Tiews 1970, Fonds 1973, Miller 1973). They co-occur in high abundances and exploit similar resources over a relatively short season. These species have been reported to prey upon each other, depending on the timing of arrival of new recruits (Kühl 1972). Gobies, moreover, are reported to be one of the major predators of brown shrimp (Kühl 1964, Tiews 1978, Redant 1980) and responsible for the destruction of summer shrimp broods (Kuipers & Dapper 1984). Shrimp cannibalism is also quite commonly reported in the literature (Rolle 1982, Evans 1983), but its importance still remains unclear.

The dynamics of seasonal resource utilization by these species have been reported by other authors,

such as Evans & Tallmark (1979, 1984, 1985), Pihl & Rosenberg (1982), Thorman (1982) and Thorman & Wiederholm (1983, 1984, 1986) in Sweden. Daily patterns of resource utilization and how these are affected by abiotic factors were studied by Gibson & Hesthagen (1981) and Antholz et al. (1991), among others. In these latter studies, the species were considered separately.

To determine the nature of interactions among these 3 species and the extent to which they influence each other, we described and compared their daily patterns of activity and feeding in the northern Wadden Sea region. Patterns of relative co-occurrence, densities, stomach fullness and prey utilization were analyzed for a 24 h cycle. Overall niche overlaps between species and by length classes were compared, and the impact of predation in terms of available biomass was assessed. Daily rations were calculated and compared with values in the literature.

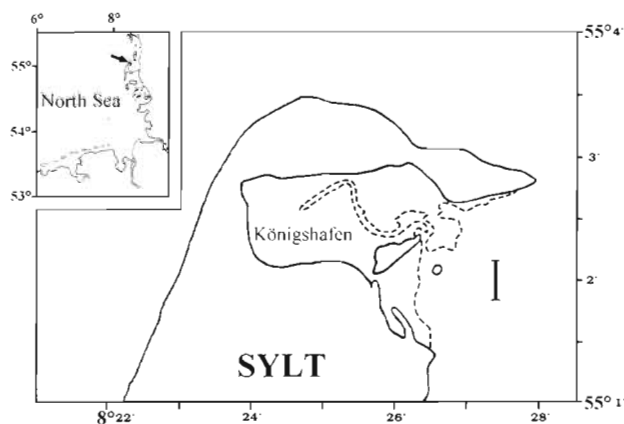


Fig. 1. Location of the sampling site in Königshafen, Sylt island (Germany), northern Wadden Sea. Thick bar indicates general location of tows

MATERIALS AND METHODS

The study was conducted off Königshafen, on the northeast coast of Sylt island, northern Wadden Sea (55° 01.95' N, 08° 27.38' E) (Fig. 1) in July 1992. The subtidal area is predominantly sandy and has a mean tidal range of 1.8 m. Samples were taken with a small vessel, using a 2 m beam trawl with a 5 mm mesh at the cod end. Hauls were done at depths ranging from 4 to 7 m during high tide and 2 to 5 m during low tide. Haul intervals were roughly 1.5 h, starting at 13:58 h and continuing until 14:47 h the next day, or a total of 17 hauls. Hauls generally lasted around 10 min. Average haul length and area were about 522 m and 1044 m², respectively. Hauling velocity was on average 2 to 3 knots.

Catches were taken on board and sorted, and total catch per species was recorded. Species densities by haul (ind. m⁻²) are plotted to depict activity patterns over a 24 h period. Random samples of gobies and shrimp were taken from each haul and preserved in 70% alcohol. In the laboratory, the specimens were measured to the nearest mm and then grouped into 5 mm length classes. Total lengths of shrimp were taken by measuring from the tip of the scaphocerite to the tip of the telson. Individual cohorts of each species were separated using the Bhattacharya method incorporated in the ELEFAN package (Gayanilo et al. 1989).

From each sample, at least 3 to 4 individuals per length class were taken for stomach content analysis. Since the gobies do not have a distinct stomach, the whole alimentary canal between the esophagus and rectum was taken, whereas only the foregut of shrimps was removed. Stomach content wet weights (g) were calculated from the difference of the weights of stomachs with contents and their corresponding stomach walls. Ash-free dry weights (AFDW) were assigned to

meiofauna and plankton found in the guts using values in the literature (Faubel 1982, Pihl 1985). Remaining parts of larger prey (macrofauna) were measured under the stereomicroscope and then expressed as total length and corresponding AFDW using regressions and length-weight relationships taken from the literature (e.g. Sander 1987). Total gut contents by length class and for each sample was expressed in percentage frequencies by prey item based on weight.

Fullness index (FI, in %) was computed for each individual following the equation of Hureau (1969):

$$FI = \frac{S}{W} \times 100 \quad (1)$$

where S is wet weight (g) of stomach contents and W is body wet weight (g) of fish or shrimp, without stomach contents. The means of the fullness indices were plotted against actual time of haul to depict the diel feeding pattern.

Food niche overlaps were calculated according to the equation:

$$C_{xy} = \sum \min(P_{xi}, P_{yi}) \quad (2)$$

given by Hurlbert (1978), where P_{xi} is relative frequency (by weight) of prey item i in the stomach of species x ; P_{yi} is the corresponding frequency in species y . The value of C_{xy} varies from 0 for no overlap to 1 for complete overlap. Classifications of prey items, on which food niche overlaps were based, were kept similar for all 3 predators. Food niche overlaps between species were compared by haul and also by length class to investigate the effect of predator size and weight.

To test the significance of changes in feeding intensity, 2 consecutive minima and 1 intermediate maximum of the fullness indices by species were compared using a Mann-Whitney test (Sokal & Rohlf 1981).

Evacuation rates were estimated by fitting negative linear curves to the descending segments of the fullness indices which were plotted against actual time of hauls. Hauls 10 to 15 (3:58 to 11:26 h) were used for *Crangon crangon*, whereas for both gobies, hauls 6 to 8 (21:30 to 01:21 h) were used (see Fig. 4). Daily food rations were estimated using Bajkov's (1935) linear model:

$$F = R \times 24 \text{ h} \quad (3)$$

where F is the daily food ration in g or % body weight and R the evacuation rate in g h⁻¹ or % body weight h⁻¹. To facilitate comparison of values in the literature, we also computed the daily rations using the exponential model, as follows:

$$F = ES \times 24 \text{ h} \quad (4)$$

where E is the exponential coefficient and S the average stomach content in g or % body weight.

RESULTS

Predator activity and relative occurrence

Overall percentage occurrence of *Crangon crangon* relative to the gobies was 93 %. Percentage occurrence of *Pomatoschistus minutus* was 6 %, while that of *P. microps* was 0.6 %. *C. crangon* showed consistent dominance in number over the gobies, except around midnight and noon (i.e. 00:21 and 13:01 h), when its occurrence decreased. At these times, percentage occurrences of *P. minutus* and *P. microps* were 68 and 3 %, respectively, for 00:21 h and 12 and 2 %, respectively, for 13:01 h.

Over the 24 h period, the size distributions of the 3 species did not change much from one haul to the next. Three shrimp cohorts could be separated, with mean lengths of 24.7, 36.6 and 54.5 mm, respectively (Fig. 2a). *Pomatoschistus minutus* had 3 cohorts with mean lengths of 31.3, 43.8 and 70.6 mm (Fig. 2b). Much fewer *P. microps* were caught during the 24 h period: there were 2 cohorts present, with mean lengths of 27.2 and 43.9 mm (Fig. 2c). Range of sizes caught was 11 to 69 mm for *Crangon crangon*, 21 to 84 mm for *P. minutus* and 17 to 45 mm for *P. microps*.

Despite the absence of replicate tows, the results show trends in the densities of the species over the 24 h period. The highest density peak for *Crangon crangon* and *Pomatoschistus minutus* occurred at dawn (03:58 h), coinciding with the period between low and high tide (Fig. 3a, b). During this time, the density of *C. crangon* was 17 ind. m⁻² and that of *P. minutus* was 0.4 ind. m⁻². The peak density of *P. microps* (= 0.06 ind. m⁻²) occurred some hours later (06:59 h), just after sunrise (Fig. 3c), and coincided with rising tide. Lowest shrimp densities occurred just after midnight (0.01 ind. m⁻²) and after noon (0.4 ind. m⁻²), both just before low tide. The pattern of occurrence of lowest densities of *P. minutus* was less pronounced, whereas that of *P. microps* was also similar to the pattern shown by *C. crangon*, with lowest densities around midnight and noon.

Diel feeding intensity

Differences between 2 consecutive minima and the intermediate maximum fullness indices were all significant (Table 1), indicating that significant increase ($p < 0.05$) and decrease ($p < 0.01$) in the level of feeding in the 3 species occurred.

A total of 553 *Crangon crangon* individuals representing all length classes available were examined for their gut contents. Fig. 4a shows the 24 h feeding pattern of *C. crangon* based on fullness indices. Increased feeding was observed in the afternoon, followed by a

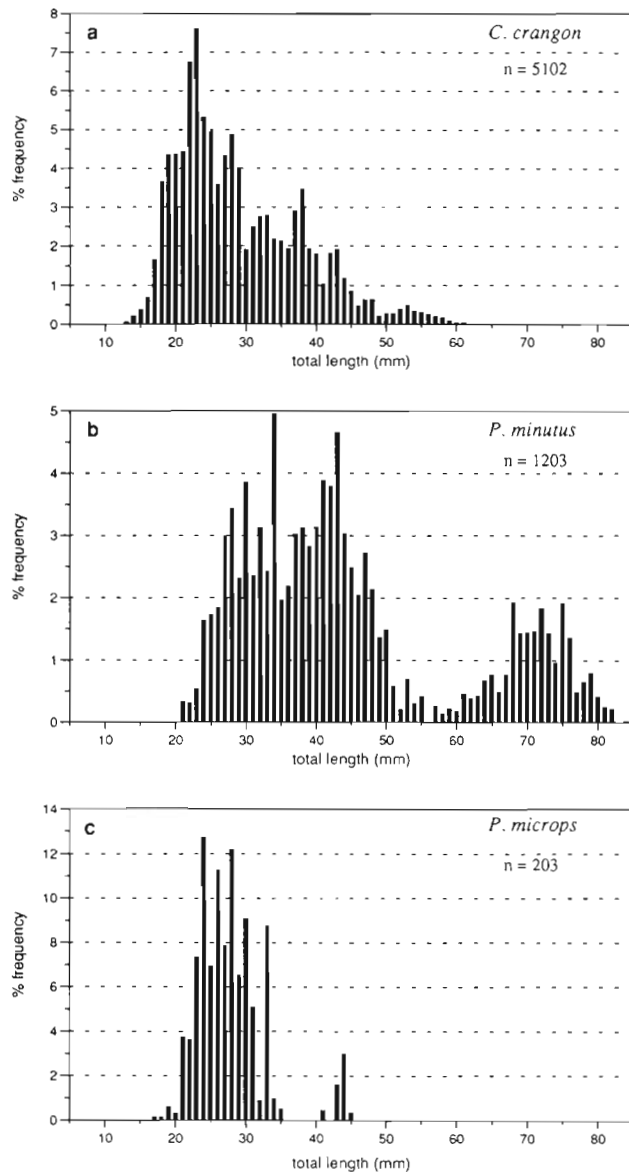


Fig. 2. Overall size distributions of (a) *Crangon crangon*, (b) *Pomatoschistus minutus* and (c) *P. microps*

Table 1. *Crangon crangon*, *Pomatoschistus minutus* and *P. microps*. Comparison of means of fullness indices (2 consecutive minima and the intermediate maximum)

Species and haul	n	Mann-Whitney test
<i>P. microps</i>		
Haul 4 vs haul 5	12	$U = 18^*$
Haul 5 vs haul 8	19	$U = 112^{**}$
<i>P. minutus</i>		
Haul 4 vs haul 6	51	$z = 5.48^{***}$
Haul 6 vs haul 8	42	$z = 2.82^{**}$
<i>C. crangon</i>		
Haul 8 vs haul 10	47	$z = 4.42^{***}$
Haul 10 vs haul 14	55	$z = 5.21^{***}$

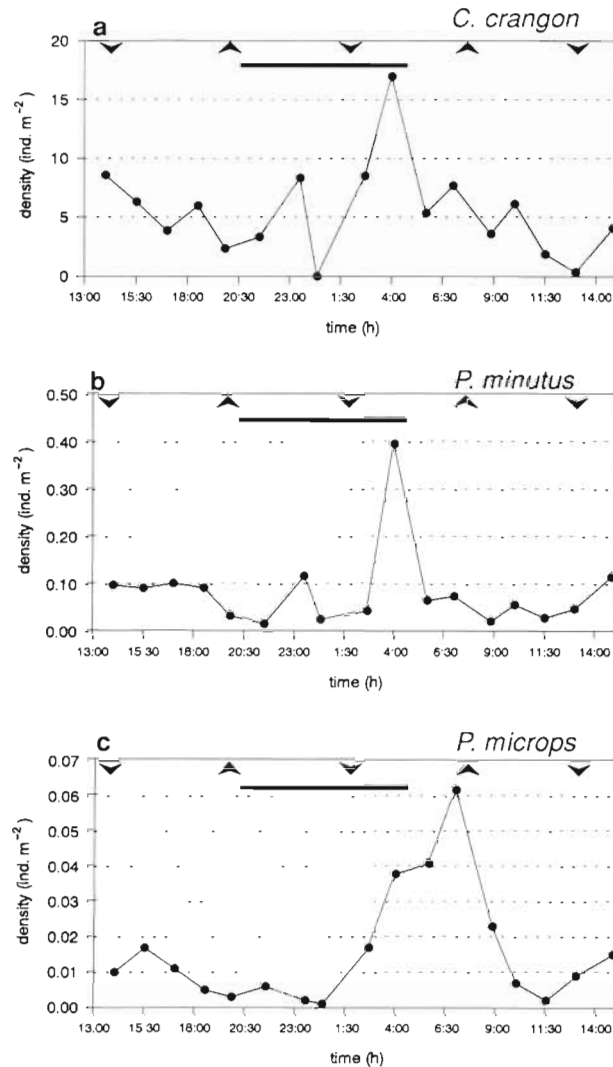


Fig. 3. Diel density patterns of (a) *Crangon crangon*, (b) *Pomatoschistus minutus* and (c) *P. microps*. Arrows: low (▼) and high (▲) tides; thick bar: nighttime

period of decreased feeding towards dusk. After midnight, feeding increased, attaining its peak at dawn, until just before sunrise, after which little feeding was observed until noon. The peaks of feeding observed coincided with the period between low and high tide, and paralleled closely the observed activity pattern.

Some 447 individuals of *Pomatoschistus minutus* were examined for gut contents. Stomach fullness increased with the rising tide and was highest during (08:54 h) or shortly after (21:30 h) slack high tide (Fig. 4b). The peak in fullness observed at 08:54 h was slightly delayed relative to the peak in density.

In comparison, less *Pomatoschistus microps* occurred in the samples, so that almost all individuals caught ($n = 184$) were examined for gut contents. Fig. 4c shows the diel feeding pattern of *P. microps*. Deviations from

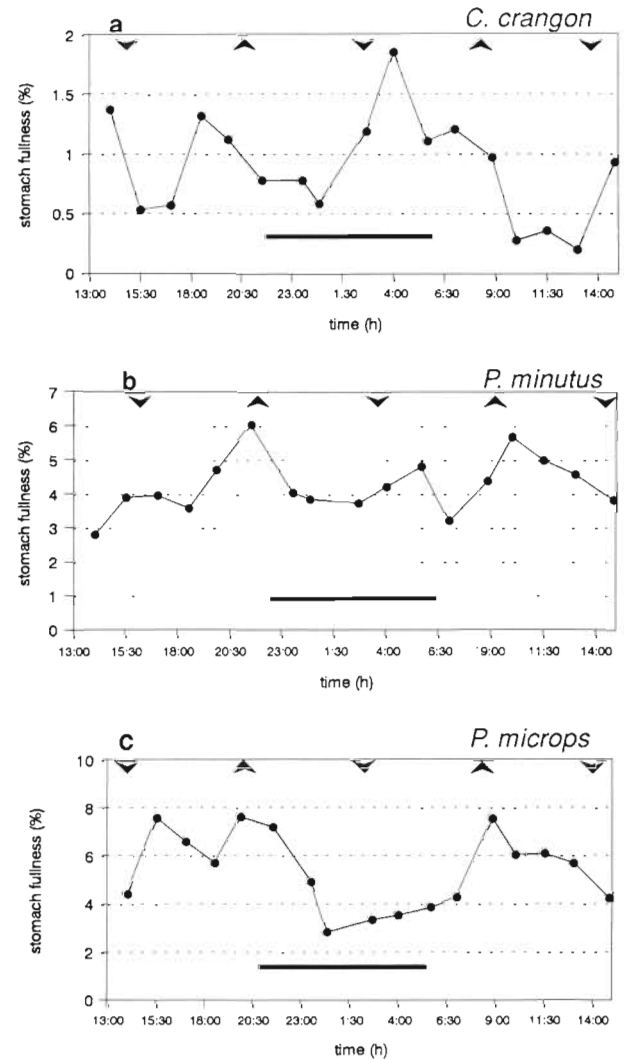


Fig. 4. Diel feeding patterns of (a) *Crangon crangon* ($n = 553$), (b) *Pomatoschistus minutus* ($n = 447$) and (c) *P. microps* ($n = 184$). Other symbols as in Fig. 3

an otherwise clear course of feeding were observed in some hauls where low catches occurred (e.g. 08:54 h). One may, however, roughly delineate 2 main feeding periods, one between afternoon (15:30 h) and dusk (19:53 h) and the other after sunrise. In general, feeding was highest at slack high tide and decreased with the outgoing tide.

Diet composition

Stomach contents of the 3 species expressed as % AFDW were summarized for the entire 24 h period by grouping together related prey items and presented according to the size of the predator. Fig. 5a shows the diet composition of *Crangon crangon* by length class.

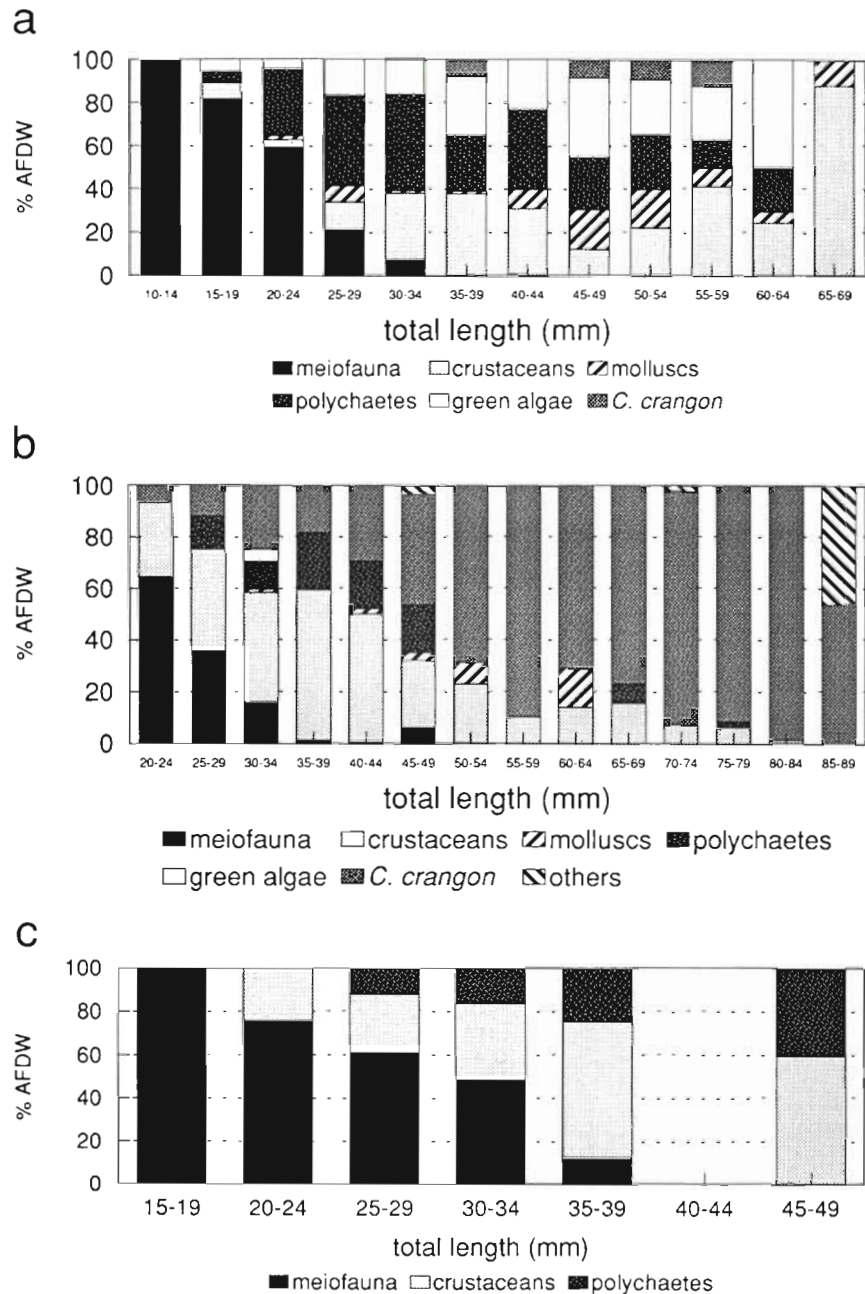


Fig. 5. Diet composition by length class of (a) *Crangon crangon* (n = 553); (b) *Pomatoschistus minutus* (n = 447) and (c) *P. microps* (n = 184) during the entire 24 h period

Shrimp fed mainly on crustaceans, mostly amphipods (25.9%), polychaetes (22.4%) and meiofauna (22.6%). The smallest sizes preyed mainly on meiofauna (mostly foraminiferans), with decreasing quantities as shrimp size increased. Thereafter, macrofaunal taxa, such as polychaetes, crustaceans and molluscs became more important in the shrimps' diet. Cannibalism comprised only 3.4% of the overall gut contents and was observed only among larger length classes.

The relative proportion of each prey type in the stomach contents of *Pomatoschistus minutus* according to size is shown in Fig. 5b. Meiofauna (mainly harpacti-

coids) was fed upon by the smallest individuals (up to 49 mm), together with macrofauna, e.g. crustaceans (mostly mysids), polychaetes and molluscs. However, the most important prey item overall was *Crangon crangon*, preyed upon by all lengths of the sand goby. The shrimp comprised 28% of the diet of smaller gobies (20 to 54 mm), while bigger gobies (>55 mm) fed only or predominantly (77%) on the shrimp. The overall quantity of shrimp found in guts of all sizes of the sand goby was equivalent to 51%.

Fig. 5c shows the stomach contents of *Pomatoschistus microps* by size class. Meiofauna (likewise mostly

harpacticoids), comprising almost half of the total gut contents, decreased in importance with increase in goby size. Crustaceans (amphipods and mysids), comprising about 35% of the total, and polychaetes (15.5%) were preyed upon increasingly with increase in predator size. Copepods and bivalves were also represented in the common goby's diet, however only in negligible quantities.

There was no discernible diel pattern in the diet composition of the 3 species. However, the sand goby fed consistently on the shrimp during the entire 24 h period, with quantities maintained at ca 50% of the total gut contents for each individual haul.

Food niche overlaps

Table 2 shows the food niche overlaps (C_{xy}), computed by haul and averaged for the 24 h period. In general, the overlaps were rather low (around 0.1 to 0.2), except in a few hauls. The overlaps by haul were quite variable, and did not show a clear pattern. The mean values did not also differ considerably from one another. Table 3 shows, on the other hand, the niche overlaps computed by length class. The overlaps between the shrimp and the gobies were likewise within the same magnitude as above. However, those between the gobies were higher, especially among the smallest length classes, decreasing gradually with size. Since *Pomatoschistus microps* occurred only in sizes

Table 2. *Crangon crangon*, *Pomatoschistus minutus* and *P. microps*. Niche overlaps (C_{xy}) between shrimp and gobies in a 24 h sampling period, northern Wadden Sea, July 1992

Haul no.	<i>C. crangon</i> / <i>P. microps</i>	<i>C. crangon</i> / <i>P. minutus</i>	<i>P. microps</i> / <i>P. minutus</i>
1	0.21	0.04	0.40
2	0.15	0.11	0.09
3	0.08	0.13	0.10
4	0.01	0.24	0.08
5	0.10	0.10	0.08
6	0.13	0.03	0.10
7	0.03	0.09	0.07
8	0.05	0.12	0.05
9	0.01	0.10	0.07
10	0.07	0.06	0.25
11	0.17	0.56	0.22
12	0.17	0.47	0.31
13	0.05	0.06	0.12
14	0.34	0.09	0.07
15	0.20	0.03	0.16
16	0.25	0.01	0.09
17	0.16	0.15	0.25
Mean	0.13	0.14	0.15
SD	0.09	0.15	0.10

Table 3. *Crangon crangon*, *Pomatoschistus minutus* and *P. microps*. Niche overlaps (C_{xy}) between shrimp and gobies by length class in a 24 h sampling period, northern Wadden Sea, July 1992

Length class (mm)	<i>C. crangon</i> / <i>P. microps</i>	<i>C. crangon</i> / <i>P. minutus</i>	<i>P. microps</i> / <i>P. minutus</i>
15–19	0.17	–	–
20–24	0.25	0.15	0.67
25–29	0.22	0.29	0.57
30–34	0.19	0.18	0.35
35–39	0.02	0.16	0.29
40–44	–	0.16	–
45–49	0.17	0.21	0.17
50–54		0.11	
55–59		0.23	
60–64		0.00	
65–69		0.01	

smaller than 49 mm, no niche overlaps for this species and the other 2 can be computed for larger sizes.

Daily rations

Table 4 shows the estimates of gastric evacuation rates and corresponding daily rations for *Pomatoschistus microps*, *P. minutus* and *Crangon crangon* based on the linear model. Computed daily rations based on the exponential model are presented later (see Table 6) for purposes of comparison with the literature. The daily ration estimates for *P. microps* and *P. minutus* were equivalent to 27.3% and 13% body weight, respectively. Estimates for *P. minutus* for all length classes were made, whereas data for *P. microps* and *C. crangon* were too patchy to allow separate calculations. In *P. minutus*, daily rations did not show any distinct pat-

Table 4. *Crangon crangon*, *Pomatoschistus minutus* and *P. microps*. Evacuation rates and daily rations at 18.5°C in the northern Wadden Sea, July 1992. bw: body weight

Species	Length (mm)	Evacuation rate (g h ⁻¹)	(%bw h ⁻¹)	SE	Daily ration (% bw)
<i>P. microps</i>	All sizes	0.001	1.14	0.02	27.3
<i>P. minutus</i>	20–29	0.001	0.67	0.20	16.1
	30–39	0.001	0.46	0.35	11.0
	40–49	0.003	0.60	0.09	14.3
	50–59	0.006	0.67	0.25	16.0
	60–69	0.016	0.79	0.24	18.9
	70–79	0.008	0.27	0.08	6.4
	80–89	0.015	0.38	0.16	9.0
	All sizes	0.006	0.54	0.07	13.0
<i>C. crangon</i>	All sizes	0.003	0.67	0.22	16.0

tern with increasing size. Average shrimp daily consumption was equivalent to 16 % body weight.

Predation impact

Fig. 6a shows the pattern of predation of *Pomatoschistus minutus* on *Crangon crangon* according to size, summarized for all guts examined. As *P. minutus* increased in size, the size of *C. crangon* (TL in mm) preyed upon also increased. The relationship of sand goby size to the size of shrimp preyed upon can be described by the following linear regression equation: shrimp length (mm) = $-8.658 + 0.425$ sand goby length (mm) ($R^2 = 0.539$, $n = 254$). The quantity of *C. crangon* as a proportion of total prey (in % AFDW) also increased with increase of goby size (Fig. 6b).

Size-specific predation impact on shrimp was examined by comparing estimates of the amount (weight) of shrimp preyed upon by size class with size-specific biomass estimates of shrimp available to gobies in the sampled area (Table 5). Biomass of available shrimp based on our own catch data was corrected for gear selection according to Berghahn (1984). The overall daily shrimp ration of *Pomatoschistus minutus* was computed by multiplying the daily ration estimate (13 %) with the actual proportion of shrimp > 10 mm TL (49.3 %) in sand goby gut contents. Together with the average sand goby biomass of $66.7 \text{ mg wet wt m}^{-2}$, the total daily shrimp ration of sand gobies was equivalent to $4.27 \text{ mg wet wt m}^{-2}$. Compared with the total available shrimp biomass of $1514.03 \text{ mg wet wt m}^{-2}$, the overall daily predation impact on the shrimp popula-

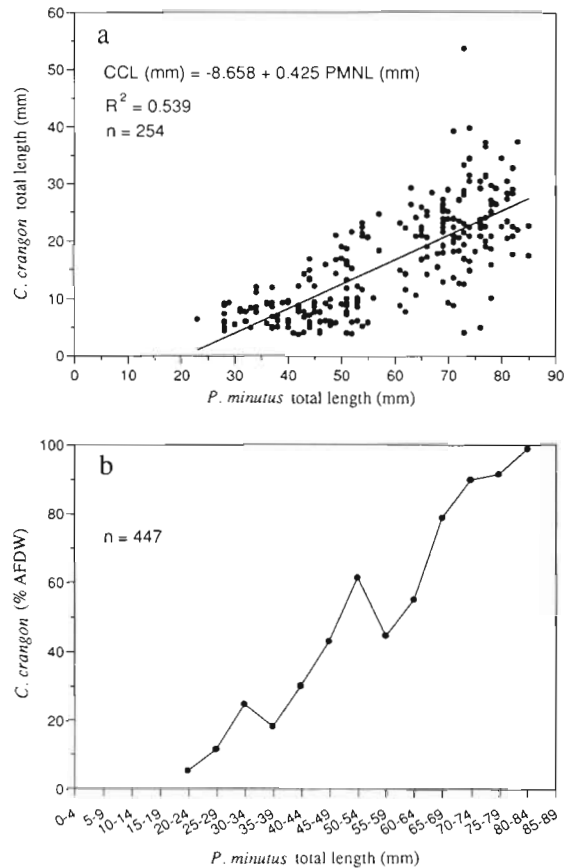


Fig. 6. *Pomatoschistus minutus* predation on brown shrimp *Crangon crangon* (CC). (a) Relationship of sand goby lengths (PMNL) (mm) to CC lengths (CCL) and (b) quantities of brown shrimp in percent AFDW of total sand goby gut contents

Table 5. Predation impact of *Pomatoschistus minutus* on *Crangon crangon* in a 24 h period, northern Wadden Sea, July 1992

Shrimp length class (mm)	<i>C. crangon</i> preyed upon by <i>P. minutus</i>		<i>C. crangon</i> occurrence in the area sampled (corrected)		
	Length-frequency dist. (%)	Daily shrimp ration of sand goby (mg wet wt m ⁻²)	Length-frequency dist. (%)	Available shrimp biomass (mg wet wt m ⁻²)	Daily sand goby predation impact on shrimp (%)
1-4	5.62	0.0004	0	0	—
5-9	32.13	0.05	0	0	—
10-14	11.62	0.09	4.55	3.27	2.75
15-19	12.05	0.29	16.98	37.30	0.78
20-24	20.08	1.12	27.83	140.80	0.80
25-29	12.45	1.35	18.30	180.28	0.75
30-34	4.02	0.76	10.25	175.91	0.43
35-39	2.01	0.61	10.46	288.52	0.21
40-44	0	0	6.54	273.69	0
45-49	0	0	2.42	146.19	0
50-54	0	0	1.54	130.22	0
55-59	0	0	0.92	105.35	0
60-64	0	0	0.15	22.74	0
65-69	0	0	0.05	9.76	0
Overall		4.27		1514.03	0.28

tion was estimated to be 0.28%. When computed according to length, predation rate decreased, more or less, with size and ranged from 2.75 to 0.21% for shrimp between 10–14 and 35–39 mm TL.

DISCUSSION

Patterns in activity, feeding and niche overlaps

All 3 species showed increasing densities towards dawn, with peaks shortly before or after dawn (Fig. 3a to c). The common goby *Pomatoschistus microps* was more active during the day, with peaks in activity occurring mainly at dawn to sunrise, and to a lesser extent in the afternoon. Meyer-Antholz (1987) showed that there are 2 peaks in the activity of *P. microps*, one at dawn and one at dusk. He concluded that this pattern is endogenous, with the main activity phase between 05:00 and 18:00 h. The same day-active pattern in the common goby was also found by Magnhagen & Wiederholm (1982). The pattern seen in *P. minutus* was more irregular, but the main peak was at dawn, between low and high tide. Gibson & Hesthagen (1981) found no endogenous rhythm in *P. minutus* caught from a nontidal area, while the same species from a tidal area showed an endogenous rhythm, most likely influenced by tides. Although Wiederholm (1987) reported a higher activity level during daytime for both goby species, inversions in the activity peak of *P. minutus* have been documented, i.e. diurnal during winter and, as in our results here, nocturnal during summer (Westin & Aneer 1987).

Both goby species showed similar feeding patterns with highest feeding during dawn and dusk (Fig. 4b, c). In both species, little feeding occurred during darkness. These results are consistent with those of previous studies conducted in other regions (Hesthagen 1971, Meyer 1982, Meyer-Antholz 1987, Antholz et al. 1991). Diurnal feeding and activity may be typical of gobies in general, as this has been observed in other species as well: *Gobius niger* (Hesthagen 1976, Nash 1982), *Gobiusculus flavescens* (Blegvad 1917), *Caffrogobius caffer* (Butler 1982), *Deltentosteus quadrimaculatus* (Villiers 1982) and *Pomatoschistus pictus* (Hesthagen 1980). Gibson (1969) observed the persistence of this pattern with and without the influence of tides. In nontidal areas, the trigger appears to be light (Hesthagen 1976, 1977, 1980, Manzer 1976, Meyer-Antholz 1987). For daylight feeders, it would be more advantageous to forage not during full daylight, but during the twilight hours (dusk and/or dawn), because they achieve cover from predation and, at the same time, take advantage of the vulnerability of the prey (Hesthagen 1973, 1976). Gobies and shrimp prey on ben-

thic and planktonic organisms which in turn may exhibit other patterns of diel behavior and are, in comparison, not mobile enough to escape successfully from their predators.

Daytime feeding suggests that both sand and common gobies are visual feeders, with their feeding associated with light-dark and tidal cycles. Both feeding peaks of *Pomatoschistus minutus* were observed during and shortly after slack high tide, decreasing with the outgoing tide (Fig. 4b). Healey (1971) observed peak feeding in *P. minutus* at the Ythan Estuary in Scotland, UK, to be at high tide.

While both gobies were generally active during the day, shrimp density and feeding were highest during darkness, with peaks at dawn and dusk. Highest density and feeding were observed at dawn, shortly after slack low tide. Dahm (1975) noted that the highest shrimp catches in the fishery are taken during slack in tides, when currents are at their lowest velocities. Such conditions, which facilitate the search for food, are exploited by the shrimp, which in turn are caught more easily. Pihl & Rosenberg (1984) observed similarly that the main feeding of *Crangon crangon* occurred during darkness, with peaks around dawn and dusk. In summer, however, a midday peak was also observed. Midday feeding, although not as pronounced, was also observed in the present study.

Estimates of niche overlap among the 3 species were low (Table 2). Similarly low overlap was observed by Pihl (1985) for July. While the data presented here represent only a single 24 h period, some size-related structure to these relationships among the 3 species can be recognized.

For the 3 species in general, prey size increased with predator size, their intake of meiofaunal taxa being gradually replaced by macrofaunal organisms. The feeding overlaps between *Pomatoschistus microps* and *P. minutus* of <40 mm TL were relatively high, the pattern being most pronounced among the smaller sizes within this range (Table 3). With increase in size, the values decreased, reflecting diversification in their diets (Fig. 5b, c). Hamerlynck et al. (1986) reported similarly strong overlaps between the likewise sympatric gobies *P. minutus* and *P. lozanoi* from the Belgian coast. They conclude, though, that such values do not necessarily indicate competition because, as in this case, the 2 gobies exhibited vertical spatial segregation, temporal segregation in spawning and absence of niche shifts when one was temporarily absent. Most of the common gobies recorded during the present study were within the size range 15 to 35 mm, which corresponds closely to the youngest cohort of *P. minutus* (Fig. 2b, c), with which higher overlap was shown. The absence of large *P. microps* probably reflects differences in preferred habitats of larger sand and common

gobies. High niche overlaps often, if not always, indicate high availability of food and that competition first occurs when food resources become limiting (Schoener 1974, Werner 1986). In such shallow soft-bottom habitats, partitioning of abundant resources prevents epibenthic predators like gobies from outcompeting one another (Evans 1983). The lack of data on food availability in the present study does not permit inferring the possibility of food limitation. The results, however, suggest that both sand and common gobies exhibit intraspecific niche segregation by means of diet diversification (Fig. 5b, c) as they grow.

Intraspecific differences in diet is also shown for brown shrimp (Fig. 5a), but niche overlap with the 2 gobies remained low for all sizes of shrimp (Table 3). Shrimp cannibalism was relatively rare, but in some cases when it was observed, the niche overlaps between *Crangon crangon* and *Pomatoschistus minutus* were also higher (e.g. 45–49 mm, 55–59 mm; Table 3).

Daily rations

Considering that the nonfeeding phases during the 24 h period were not that distinct in our data, we estimated the evacuation rates within a short segment of the emptying phase using a linear model.

The estimated daily ration for *Pomatoschistus microps* (27.3%) based on the linear model is comparable to the estimates of Thiel (1990) for the same species from the south Baltic Sea. Applying the Winberg method for data taken between April and October each year over a span of 2 yr, with temperatures ranging from 4.8 to 21.4°C, he estimated the average daily ration of *P. microps* to be 34.3% for age group 0 and 27.7% for age group 1. Andersen (1983) reported the daily ration of *P. microps* taken also from the Baltic to be 8.6% body weight (bw) at 17°C. Meyer-Antholz (1987), who sampled in the Schlei (Baltic Sea), reported a range of 4.18 to 6.5% for different temperatures (14 to 17.5°C), gut fullness and age of fish.

For comparison, we also applied the exponential evacuation model developed by Andersen (1984) for *Pomatoschistus microps*, which takes length of fish and temperature into consideration. Using the average temperature (18.5°C) during our sampling and the average fish size in our samples (27 mm), we derived much higher estimates of evacuation rate (0.43 h⁻¹) and daily ration (47.7% bw). Similarly applying Andersen's (1984) equation to the data of Cattijse (1986) on *P. lozanoi* with 12°C as average temperature, we derived evacuation rates almost 2 times higher (0.3 h⁻¹ for 25 mm TL and 0.23 h⁻¹ for 35 mm TL) compared to his own estimates (0.16 and 0.13 h⁻¹, respectively)

based on experimental work. Perhaps the reason for these higher estimates is the fact that Andersen (1984) only used *Nereis diversicolor* as feed during his lab experiments. Jones (1974) reported that in haddock and whiting, *Nereis* sp. and *Nephtys* sp. (polychaetes) are eliminated faster (0.31 g h⁻¹) than crustaceans (0.19 g h⁻¹), in this case, *Crangon* sp. Applying Andersen's (1984) model to our present data may have resulted in overestimates since, based on our field data, *P. microps* preferred crustaceans (gammarids, mysids, cumaceans) to polychaetes as food.

Our daily ration estimate for *Pomatoschistus minutus* of 13% bw at 18.5°C falls within reported values. Healey (1971) estimated an annual average daily ration for *P. minutus* of 3.13% bw, with values ranging from 0.65% in December to 14.13% bw in August. In Sweden (Kattegat), Evans (1984) reported the range of daily ration for *P. minutus* to be 5 to 12% bw at 5 and 15°C. In general, average stomach contents (*S*) of both gobies in our samples were much higher than those in the literature (Table 6).

Pihl & Rosenberg (1984) estimated the evacuation rate and daily food consumption of *Crangon crangon* through serial slaughter in the field. At 13.5 to 14°C, they derived an evacuation rate of 0.58% bw h⁻¹ and a daily consumption of 12.1% bw. They showed that evacuation was linear and under these conditions, food left the stomach within 2 h. Evans (1984) reported a daily ration of 3 to 7% bw for 5 and 15°C. Our higher estimate for *C. crangon* probably takes into account the higher temperature regime during our sampling.

To examine the variation in consumption with size, daily rations were also computed on a length class basis for *Pomatoschistus minutus*. Evacuation rates by length class varied rather considerably. This is probably due to the lack of appropriately sized individuals during some hauls and the irregular course of emptying in some length classes. However, if daily rations are averaged for size classes with similar gut contents, i.e. those smaller and larger than 55 mm TL, which respectively show a shift in selection from mixed meio-/macrofauna to pure macrofauna (Fig. 5c), a slight decrease (14.4 to 11.4%) in values is apparent.

Comparison with values reported in the literature should be done with care, since published data on gastric evacuation experiments for the 3 species cover only a limited range of food types, temperatures and predator size classes (Table 6).

Special complications are caused by different treatments of the experimental meal size. The experimental meal size usually has a significant influence on the evacuation rates. If linear evacuation is assumed, the linear rate tends to increase with meal size; if exponential evacuation is assumed, the instantaneous coefficient is negatively correlated with meal size

Table 6. *Crangon crangon*, *Pomatoschistus minutus* and *P. microps*. Comparison of evacuation and daily consumption estimates from the literature and this study for shrimp and gobies. *Reanalyzed/recalculated from graphs and data presented by the authors; S: stomach content; S₀: stomach content at t₀

Predator	Size (mm)	Food	Temperature (°C)	Linear rate (% h ⁻¹)	Exponential coefficient	Method	Date	Avg. S ₀ (%)	Avg. S (%)	Linear (%)	Daily consumption Exponential (%)	Source
<i>P. microps</i>	30	Natural	14–20				21–22 May 1981	0.50–2.7		4.18–6.5		Meyer–Antholz (1987)
	19		16–18.8				16–17 Jul 1981	1.53–2.9				
	25		14.5–16.5				15–16 Sep 1981	1.02–3.33				
			12–16.5				22–23 Sep 1984	1.57–3.81				
	20–24		13–21			24 h		0.8–2.9			8.6	Andersen (1983)
	25–29							0.8–2.1				
	30–34							1.2–2.5				
	35–39							0.7–3.4				
	>39											
	23.6	<i>Nereis diversicolor</i>	20		0.534	Lab. expt		10.0				Andersen (1984)
<i>P. minutus</i>	31.6		20		0.415			10.0				
	38.1		20		0.359			10.0				
	31.1		15		0.305			10.0				
	31.2		10		0.219			10.0				
	17–45	Natural	18.5	1.14	0.241	24 h	22–23 Jul 1992	5.4		27.3	31.23	This study
	20–40	Natural	5		0.123	Field expt	November					Evans (1984)
	41–60		5		0.127							
	20–40		15		0.150		August					
	41–60		15		0.158						6.12*	
	20–40		15			24 h	August	1.7			3.54*	
<i>C. crangon</i>	20–40		?			24 h	October	1.2				Healey (1971) with 10% stomach content as in Andersen (1984)
	30	Natural	18.5	0.64				10		15.36*		This study
	21–84	Natural	18.5	0.54	0.114	24 h	22–23 Jul 1992	4.58		13.0	12.55	
	16–47	Natural	13.5–14	0.58	0.47*	Field expt	Sep 1981	1.8*	1.27*	12.1	14.33*	Pihl & Rosenberg (1984)
	16–47	Natural	12–14	0.28*	0.42*	24 h	Sep 1978	1.2*	1.3*	6.72*	13.10*	Pihl & Rosenberg (1984)
	10–20	Natural	5		0.142	Field expt	November					Evans (1984)
	21–30		5		0.183							
	31–40		5		0.147							
	41–50		5		0.101							
	51–70		5		0.104							
	10–20	Natural	15		0.148	Field expt	August					
	21–30		15		0.159							
	31–40		15		0.145							
	41–50		15		0.153							
	51–70		15		0.060							
<i>C. crangon</i>	21–30	Natural	15			24 h	August	1.86			6.75*	
	21–30		?				October	1.31			5.75*	
	11–69	Natural	18.5	0.67	0.287	24 h	22–23 Jul 1992	0.93		16.0	6.41	This study

(Temming & Andersen 1992). If meal size is then used as a variable in linear or exponential models (e.g. Healey 1971, Meyer-Antholz 1987), the real meal size of the fish in the field has to be guessed in order to apply the model. It is, however, not even clear how to define a meal size in the field, e.g. if the fish feed more or less continuously. Models should preferably be reparameterized without the variable meal size (Temming & Andersen 1992). In some investigations, the meal size is kept in constant proportion of the body weight throughout the predator size range (Andersen 1984; Table 6). This is likely to be the reason why the estimated instantaneous coefficients of the exponential evacuation model decrease with increasing predator size. This is rather an effect of the increasing absolute meal size than of increasing predator size.

In Evans (1984; Table 6), the instantaneous coefficients of the exponential evacuation model decrease, in many cases, with temperature and in some cases, also with predator size. Presumably this again reflects the potential effect of variation in meal size.

During this study, feeding appeared to extend more or less throughout the whole 24 h cycle with less pronounced evacuation phases. The estimates reported here are therefore preliminary and should serve as baseline information for the area concerned. Because of rather limited information on evacuation rates, estimating reliable consumption rates for the investigated species will require further validation with more extensive sets of experimental data covering a wider range of conditions.

Predation impact

The estimate of overall predation impact on brown shrimp by the sand goby (0.28%) applies only to shrimps >10 mm in size. Based on the length distribution of shrimps in stomach contents, the sand goby preferred smaller shrimps, mainly those between 5–9 mm and 20–24 mm (Table 5). Although the estimated predation impact for smaller shrimps are higher compared to those of larger shrimps, the estimates for smaller sizes (<25 mm) may be unrealistic because these sizes could not be adequately sampled by the gear. This is not only due to gear selection (which we corrected for), but more importantly because smaller shrimps are more abundant in shallower areas, like the tidal flats, where they predominantly occur, until they adopt tidal migration at a size of about 25 mm (Janssen & Kuipers 1980). A daily predation impact of 0.3% of available biomass is probably not that significant in terms of the entire shrimp population, in view of their high turnover rates. Kuipers & Dapper (1981) reported an average shrimp P/B ratio of 8.0 yr^{-1} or about $2\% \text{ d}^{-1}$.

Shrimp recruitment occurs continuously over the year in brood waves, while the gobies recruit mainly in summer. In the present study, the sand goby preyed mainly upon 2 shrimp size groups, namely: (1) <10 mm which, based on a series of monthly length-frequency distributions independently made in the vicinity of the sampling area (including shallow flats), represents early summer recruits, which settled sometime between June and July; and (2) 20–24 mm which on the other hand corresponds to winter eggs. In the Dutch Wadden Sea, Kuipers & Dapper (1984) suggested that both *Pomatoschistus microps* and *P. minutus* could decimate the shrimp brood between June and December, that is, the bulk *only* of the summer recruits. In further contrast to their results, *P. microps* seems to be unimportant as a predator for *Crangon crangon*. The predation impact of *P. minutus* on the *Crangon* population is unlikely to control the recruitment of the summer brood, since part of the predation pertains to the winter brood and the remainder is low, when compared to production. The present results suggest though that the timing of the arrival of shrimp new recruits versus the sizes of gobies present which can actually prey on them is an important factor to consider in assessing predation impact.

In summary, the gobies *Pomatoschistus microps* and *P. minutus* and the brown shrimp *Crangon crangon* exhibit daily patterns in activity and feeding. However, these patterns, together with their functional significance, became more evident when size classes of the 3 species were examined and compared. Such patterns include the food niche overlap between small gobies, the spatial segregation between large sand and common gobies (apparent from size distributions) and food niche segregation between gobies as they grow (decreasing trend within size classes compared). The size distributions of shrimp in the stomachs of *P. minutus* led to the conclusion that more small shrimp are eaten than large shrimp and that these belong both to the winter and summer broods. For these shrimp and goby populations, it appears that predation plays a more meaningful role than competition in determining the nature and extent of their ecological interactions.

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