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DIURNAL ACTIVITY AND FEEDING IN GOBIES AND BROWN SHRIMP IN THE NORTHERN WADDEN SEA

by

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ABSTRACT

A 24-h trawl fishery was conducted near the island of Sylt, northern Wadden Sea, 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 by 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-distribution patterns for the 3 species were uniform on a diurnal basis.

Feeding rates of *P. minutus* closely paralleled with the tidal pattern, while that of *P. microps*, with daylight hours. Feeding peak in *C. crangon* occurred at dawn, whereas very little feeding was observed at noon. Smaller sizes of the 3 species fed mostly on meiofauna, switching gradually to macrofauna with increase in size. Over a 24-h period, *Crangon* cannibalism was low, but predation of *P. minutus* on *Crangon* was considerably high, ranging from about 28 % of total gut contents by AFDW (< 55 mm gobies) to 75.5 % (> 55 mm gobies). On a population basis, this predation was equivalent to 0.35 % of the total available biomass of shrimp, with highest proportions among the new recruits. Gastric evacuation curves were fitted to the data and resulting daily rations were compared to values in the literature.

INTRODUCTION

The gobies *Pomatoschistus microps* Krøyer and *P. minutus* Pallas and the brown shrimp *Crangon crangon L.* are common inhabitants of shallow water habitats of European coasts (Fonds, 1973; Miller, 1973; Tiews, 1970). These species co-occur in high abundances and together, exploit similar resources over a relatively short season. To some extent, they also prey upon each other and can also comprise each other's food spectrum (Kühl, 1972; Kuipers & Dapper, 1984). The dynamics of seasonal resource utilization by these species have been tackled by some workers, most notably Evans & Tallmark (1979; 1984) and Pihl & Rosenberg (1982) in Sweden. Daily patterns of resource utilization and how these are affected by abiotic factors were studied by Gibson & Hesthagen (1981), Antholz, et al. (1991), etc. In the latter cases, the species were tackled separately.

In this paper, we describe and compare the diurnal patterns of activity and feeeding in these three species, taken from the northern Wadden Sea region. Patterns of relative co-occurrence, densities, stomach fullness and prey selection are analysed for a 24-h cycle. Estimates of daily ration, which are basic in the study of trophic relationships in ecosystems, were made.

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 (MTL) 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 4-7 m during high tide and 2-5 m during low tide. Haul intervals were roughly 1.5 hours, starting at 13.58 h to 14.47 h the next day, or a total of 17 hauls. Haul duration lasted generally around 10 minutes. Average haul length and area were about 522 m and 1,044 m^2, respectively.

Catches were taken on board, sorted and total catches per species were taken. Densities per species by haul (ind·m^{-2}) are plotted to depict activity patterns over a diurnal period. Samples of gobies and shrimp were taken per haul and preserved in 70 % alcohol. In the laboratory, the animals were measured to the nearest mm and then, grouped in 5 mm length classes. Whenever possible, at least 3-4 individuals per length class were taken for stomach content analysis. From each of these, stomach content wet weights (g) were taken. Prey organisms in the guts were identified, counted and measured under the stereomicroscope. Remaining parts of prey were also measured and expressed to total length from regressions taken from the literature. Length-weight relationships from the literature were also applied to express lengths of prey to AFDW. Fullness index (FI) was computed for each individual following the equation of Hureau (1969):

$$FI = \frac{S}{W} \cdot 100 \qquad (1)$$

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where S = wet weight of stomach contents in g and W = body wet weight (g) of fish or shrimp, without stomach contents. The means of the fullness indices were plotted against time or haul number to depict the diurnal feeding pattern. Trends in prey selection are analyzed by comparing food niche overlaps between the 3 species. To compute food niche overlap, the formula of Hurlbert (1978) was used as follows:

$$C_{xy} = \Sigma \min (P_{xi}, P_{yi}) \qquad (2)$$

where P_{xi} = relative frequency (in weight) of food category i in the stomach of species x; P_{yi} = corresponding frequency in species y. The value of C_{xy} varies from 0 for no overlap to 1 for complete overlap.

To evaluate the presence of a feeding rhythm, the means of two consecutive minima and one intermediate maximum of the fullness indices by species were compared, using t-test for the goby data, whereby variances were found to be equal. For the shrimp data, a modified t-test (Welch test) for unequal variances was used (Sokal & Rohlf, 1981).

Assuming linear evacuation, evacuation rates for the gobies were estimated by fitting curves to the descending limbs of the trajectories of the fullness indices. Daily food ration was computed following Bajkov (1935):

$$F = R \cdot 24 \qquad (3)$$

where F is the daily food ration in g and R the evacuation rate in g/h or % body weight/h. Daily food rations are expressed as % body weight.

RESULTS

1. Activity Patterns
1.1 Relative Occurrence

Fig. 2 shows the relative frequency of *P. microps, P. minutus* and *C. crangon* over a 24-h period. Overall, *C. crangon* dominates the gobies by about 93%. Percent occurrence of *P. minutus* was 6%, while that of *P. microps* was 0.6%. *Crangon* showed consistent dominance in number over the gobies, except during midnight and noon (i.e. 0.21 h and 13.01 h), when its occurrence decreased. During these times, percentage occurrences of *P. minutus* and *P.microps* were equal to 68% and 3%, respectively for 0.21 h and 12% and 2%, respectively, for 13.01 h.

1.2 Size distributions

Crangon crangon showed a uniform size distribution over a 24-h period. Three overlapping cohorts were present, with cohort 1 having an average length of 20 mm, cohort 2 with 35 mm and cohort 3 with 50-55 mm (Fig 3). Range of sizes caught was between 11-69 mm.

P. minutus had likewise, a uniform distribution over the 24-h period. Two well-separated cohorts exist: the first peak occurring an average of 35 mm and the second around 70 mm (Fig. 4). Sizes of *P. minutus* caught ranged between 21-84 mm.

Much fewer *P. microps* were caught during the 24-h period, but distribution was also uniform (Fig. 5). It appears that there are also 2 cohorts present, with average size of 27 mm and 44 mm. *P. microps* caught ranged from 17-45 mm.

1.3 Density Patterns

The highest density peak for *C. crangon* and *P. minutus* occurred at dawn (03.58 h), coinciding with period between low and high tide (Figs. 6-7). During this time, density of *Crangon* was 16.97 ind· m^{-2} and that of *P. minutus* was 0.4 ind·m^{-2}. The peak density of *P. microps* (= 0.07 ind·m^{-2}) occurred some hours later (06.59 h), just after sunrise (Fig. 8), and coinciding with rising tide. Lowest shrimp densities occurred just after midnight (0.01 ind·m^{-2}) and after noon with 0.35 ind·m^{-2}, both just before low tide (see also Fig. 2). 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 *Crangon*, with lowest densities around midnight and noon.

2. Feeding Patterns
2.1 Feeding Periodicity

In all cases except one, there were significant differences between two consecutive minima and the intermediate maximum fullness indices (Tab. 1), indicating that feeding rhythms are present in the three species (p < 0.05 and p < 0.001).

A total of 553 *Crangon* individuals representing all length classes available were examined for their gut contents. Fig. 9 shows the 24-h feeding cycle of *Crangon* based on fullness indices. Feeding activity was observed in the afternoon, followed by a period of decreased feeding towards dusk. After midnight, feeding increased attaining its peak at dawn, till just before sunrise, after which little feeding was observed until noontime. The peaks of feeding observed coincided with period between low and high tide, thereby paralleling closely the observed activity pattern. The number of empty stomachs fluctuated in accordance to feeding pattern: least empty stomachs were observed during peak feeding, increasing with decreased feeding.

Some 447 individuals of *P. minutus* were examined for gut contents. The plot of fullness indices shows that the peaks of feeding occurred at dusk till sunset (around 21.30 h), decreasing thereafter and increasing again at dawn with another peak at 08.54 h (Fig. 10). This feeding pattern is more in-phase with the tidal cycle, with low feeding occurring during ebb and peak feeding at rising or high tide.

In comparison, less *P. microps* occurred in the samples, so that almost all individuals caught (n = 184) were examined for gut contents. In some cases, length classes were not well-represented with the number of individuals caught. Fig. 11 shows the diurnal feeding cycle of *P. microps*. In general, the pattern was more difficult to interpret due to lack of samples in some hauls. If the curves are smoothened out, one may roughly delineate 2 main feeding periods, one between afternoon (15.30 h) and dusk (19.53 h) and the other more clearly pronounced peak after sunrise. It is however clear, that little feeding occurs during darkness,

pointing out that *P. microps* is a visual feeder, and that its feeding cycle is more closely associated to light-dark cycles, just like the peak in its activity (Fig. 8).

2.2 Feeding Selection
2.2.1 Ontogenetic Feeding Progressions

In this section, prey selection during peak feeding times is presented according to the size of the predator. Fig. 12 shows the prey selection *C. crangon* taken during haul 10 (03.58 h). The smallest shrimps (10-19 mm) preyed exclusively on meiofauna, particularly forams. The middle sizes (20-44 mm) preyed mostly on polychaetes, especially *Eteone longa* and green algae (*Ulva lactuca*), whereas the biggest sizes (45-69 mm) fed more on crustaceans, like amphipods, and to a lesser extent, on bivalves, gastropods and algae. Cannibalism was observed only in the 35-39 mm length class, and was, in other hauls, likewise rare.

The typical prey selection of *P. microps*, shown in Fig. 13, was observed based on two combined hauls, representing peak feeding times at 19.53 h and 21.30 h). The sizes between 20-29 mm ate a mixture of meiofauna (harpacticoids, ostracods, forams) and to some extent, macrofauna (mysids). The bigger sizes, however, fed only on macrofauna, namely: mysids (*Neomysis integer*), polychaetes (*Nereis diversicolor*, *Heteromastus filiformis*), including amphipods (*Gammarus locusta*) and bivalves (*Macoma balthica*).

Ontogenetic feeding progression in *P. minutus* was observed at peak feeding time of 19.53 h (Fig. 14). One can delineate roughly, based on prey selection, between gobies less than 55 mm and greater than 55 mm total length. Gobies smaller than 55 mm in size had a mixed diet of meiofauna (esp. harpacticoids) for the smallest lengths, replaced gradually by mysids (*Neomysis integer* and *Praunus flexuosus*) and other macrofaunal oraganisms (polychaetes, bivalves, amphipods). Bigger *P. minutus* (> 55 mm TL) however, fed predominantly or only on *C. crangon*. Fig. 15 shows the pattern of *P. minutus* predation on *C. crangon* according to size, summarized for all guts examined. With increase in size of *P. minutus* , the size of *Crangon* (TL in mm) preyed upon, (Fig. 15a) as well as the quantity of *Crangon* as proportion of total prey (in % AFDW) (Fig. 15b), also increased.

2.2.2. Daily Prey Selection

Fig. 16 shows the prey selection of *C. crangon* over a diurnal cycle, averaged for all length classes. The three most important prey items are: polychaetes, comprising 30.29 % AFDW of all prey organisms, meiofauna (22.56%) and crustaceans (19.3%), together representing 72.15% of total stomach contents (n = 553). In general, the pattern of prey selection over time was not consistent. The fourth most important food item in the stomachs of *Crangon* was green algae (esp. *Ulva*), whose pattern of occurrence in the stomachs was likewise, not clear.

The food selection of *P. microps* against time is shown in Fig. 17. For the entire 24-h cycle, meiofaunal taxa, comprising a total of 57.73 %, were consistently important food items. The quantities taken roughly parallel the diurnal feeding pattern. The other important food items on a diurnal basis were crustaceans (31.44 %) and polychaetes (10.35 %), which together with the meiofauna comprise 99.52 % of the total stomach contents.

P. minutus preyed mostly on the following over a daily cycle (Fig. 18): *C. crangon*, comprising almost half of the total food items (49.77 % AFDW), other crustaceans like mysids and amphipods (29.33 %) and polychaetes (9.52 %), or a total of 88.62 % of the total gut

contents. *C. crangon* was preyed upon consistently during the entire 24-h period, comprising also in each individual haul, roughly 50% in AFDW of the total food items. The proportion of *C. crangon* in total gut contents of *P. minutus* less than 55 mm in size was equivalent to 28 %, whereas that of *P. minutus* greater than 55 mm in size was 76. 5 %.

Fig. 19 shows the comparison of shrimp sizes preyed upon by *P. minutus* and the actual sizes which occurred where sampling was conducted. The latter underrepresents the smallest sizes (< 10 mm), not caught by the gear. *P. minutus* preyed most heavily on the smallest sizes of shrimp (< 14 mm TL), comprising 49.4 % of total amount of shrimp found in the guts of *P. minutus*. The rest (50.6 %) is represented by shrimp sizes between 15-39 mm, with peak around 20-24 mm.

2.2.3 Predation impact

Tab. 2 shows the length-frequency distributions and corresponding biomasses of shrimp preyed upon by *P. minutus* and shrimp actually sampled by the fishing gear during the 24-h period of sampling. The length-frequency distribution and biomass of available (or caught) shrimp were adjusted for gear selection by applying the correction factors in Berghahn (1984). Although the smallest sizes of shrimp preyed upon by the sand goby was between 4-9 mm, these length classes cannot be evaluated for predation impact because these sizes did not occur at all in the catches. As shown in this table, the resulting percentages of shrimp available biomass eaten by the sand goby ranged from 0.26-3.46 %. For the whole shrimp population, regardless of size, the average predation impact was equivalent to 0.35 %.

2.2.4. Food niche overlaps

Food niche overlap is the common utilization of the same food resources by 2 or more organisms regardless of resource abundance (Evans, 1983). Tab. 3 shows the computed overlaps (C_{xy}), computed by haul and averaged for the 24-h period. In general, the overlaps were rather low (around 0.1-0.2), except in a few hauls. The overlaps by haul were quite variable, and did not show a distinct pattern. The averaged values did not also differ considerably with one another. Tab. 3a 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 *P. microps* occurred only in sizes smaller than 49 mm, no niche overlaps for this species and the other two can be computed for bigger sizes.

2.3 Daily rations

The resulting estimates of gastric evacuation rates and corresponding daily rations (in % body weight) for *P. microps*, *P. minutus* and *C. crangon* are shown in Tab. 4. The daily consumption estimate for *P. microps* was rather high (27.26 %), whereas that for *P. minutus* was 13.04 % bw. Estimates for *P. minutus* for all length classes (i.e. 20-29 mm to 80-89 mm) were made, whereas this was only possible for shrimp length classes from 10-20 to 31-40 mm. Shrimp daily consumption ranged from 17.17 % to 26.46 %, decreasing with size.

DISCUSSION

1. Activity patterns

The common goby, *P. microps*, was more active during the day, with peaks in activity occurring mainly at dawn, and to a lesser extent, at dusk. Meyer-Antholz (1987) showed that there are two peaks in activity in *P. microps*, one at dawn and one at dusk. This pattern appears to be endogenous, with the main activity phase between 05.00 to 18.00 hours. The same day-active pattern was also found by Magnhagen & Widerholm (1982) in *P. microps*. Hesthagen (1980) observed such pattern in *P. pictus* and Hesthagen (1976) and Nash (1982) in *Gobius niger*. The pattern seen in *P. minutus* is 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 non-tidal area; however, the same species from a tidal area showed an endogenous rhythm, most likely influenced by tides.

Shrimp activity was highest during darkness, with peak occurring at dawn, coinciding with period between low and high tides. 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 better search for food are exploited by the shrimp, which in turn are caught more easily.

2. Feeding patterns

Highest feeding in *P. microps* occurred during daylight, likewise with peaks during dawn and dusk. Thus, the feeding pattern parallels the activity pattern. Such daylight feeding was observed in other gobies, namely: *Gobius niger* and *Gobiusculus flavescens* (Blegvad, 1917); *P. minutus* (Hesthagen, 1971); *Caffrogobius caffer* (Butler, 1982); *Deltentosteus quadrimaculatus* (Villiers, 1982), as well as in *P. microps* (Meyer, 1982; Meyer-Antholz, 1987; Antholz et al., 1991). Gibson (1969) observed the persistence of this pattern with and without the influence of tides. In non-tidal areas, the Zeitgeber appears to be light (Hesthagen, 1976; 1977; 1980; Manzer, 1976; Meyer-Antholz, 1987). For daylight feeders, it would be more advantageous to prey not during full daylight, rather during twilight and/or dawn, because at the same time, they also achieve cover from predation and take advantage of the vulnerability of prey (Hesthagen, 1973; 1976).

Pihl & Rosenberg (1984) observed similarly that the main feeding of *C. crangon* occurred during darkness, with peaks around dawn and dusk. In summer however, a midday peak was also observed. This midday peak was not shown in the present study.

Although the feeding peaks of *P. minutus* were also during dusk and dawn, similar to that of *P. microps*, the pattern seemed to follow more closely the tidal cycle. Healey (1971) observed peak feeding in *P. minutus* at the Ythan estuary in Scotland to be at high tide. Because the feeding peaks of *P. minutus* occurred sometime after the high tides, it is possible that the tides facilitate the exploitation of food rich areas, in this case, the shallow intertidal areas. *P. minutus* most likely, did feeding migrations to the shallow inundated tidal flats during high tide and fed on the newly-settled *C. crangon* there.

2.1. Predation impact

Due to gear selection, the smallest length classes (< 10 mm) of *Crangon* preyed upon by *P. minutus* were not sampled by the gear. At this point therefore, it is not quite posssible to compare precisely the proportion of these smallest sizes preyed upon, to the actual biomass

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based on catches. The smallest sizes of shrimp occur anyway in the shallowest intertidal areas, remain there when the water recedes (Berghahn, 1984) and will therefore, not be adequately sampled in the subtidal areas. Based on a series of monthly length-frequency distributions independently made in the vicinity of the sampling area (including shallow flats), the smallest shrimp size group preyed upon (4-9 mm) by *P. minutus* represent early summer recruits, which settled sometime between June-July. The bigger group of shrimp (20-24 mm) exploited by *P. minutus*, correspond, on the other hand, to winter eggs. In comparison, Kuipers & Dapper (1984) pointed out that the both species of gobies decimate the shrimp brood during June-December, or mainly the bulk of the summer recruits.

Although the resulting predation impact values were relatively low and that in general, *Crangon* overdominates the gobies in terms of relative occurrence, the sand goby, *P. minutus*, exerts a considerable impact on the shrimp population by preying on the newly-recruits. Earlier works (e. g. Kühl, 1964, Tiews, 1978) on shrimp predation in German coastal waters likewise show the gobies as one of the numerous fish species which prey on the shrimp populations.

In the present study though, no shrimps were found in the stomachs of *P. microps*, which in comparison, were smaller than *P. minutus* in sizes and thus, preferred other small prey.

2.2 Niche overlap

For the 3 species in general, prey size increased with predator size, their intake of meiofaunal taxa, being gradually replaced by macrofaunal organisms. The values of food niche overlaps presented here represent only a 24- h period. Shrimp cannibalism was relatively rare, but whenever it was observed, the niche overlaps between *C. crangon* and *P. minutus* were also high. Although the estimates by haul were low, they are comparable to those reported by Pihl (1985) for July. The estimates between *P. microps* and *P. minutus* were higher, the pattern being most pronounced among the smaller sizes. With growth, the values decreased, as their diets became more diversified. Hamerlynck et al. (1986) reported similarly strong overlaps between the likewise sympatric gobies *P. minutus* and *P. lozanoi* from the Belgian coasts. They conclude though, that such values do not necessarily indicate competition, because in this case, the 2 gobies exhibit vertical spatial segregation, temporal segregation in spawning and absence of niche shifts when one was temporarily absent.

Despite the lack of data on food availability in the present study, these results suggest that these epibenthic predators exhibit niche segregation (Evans, 1983), in that they are able to partition the abundant resources without outcompeting one another.

3. Daily rations

Several methods exist in determining daily rations of fish. One can either estimate from stomach content analysis the actual amounts of food consumed (e.g. Elliot, 1972; Jones, 1974; Jobling, 1982, etc.) or estimate daily ration from growth estimates in the field and from the energy required for metabolism (e.g. Jones, 1978).

In field studies, daily ration can be estimated by taking the stomach contents at regular intervals over a 24-h period, and then with a known gastric evacuation rate, compute the daily ration for the period in consideration. Then again, a wide variety of models exists for the

determination of both evacuation rate and daily ration. Each of these models have innate advantages and disadvantages. The most important thing however, is to choose a model or method whose basic assumptions are met by the data set at hand.

When the evacuation process proceeds quickly within a short time period, the evacuation rate is easily estimated by applying an appropriate model. Considering that the non-feeding phases during the 24-h period were not as distinct in our data, we estimated the evacuation rates within a short segment of the emptying phase using a linear model. In the following, we compare the results with other methods in the literature.

The estimated evacuation rate and daily ration for *P. microps* turned out to be too high compared to values in the literature (Tab. 4 & 5). Andersen (1983) estimated the daily ration of *P. microps* at 17 °C to be 8.6 % of body weight (bw), whereas Meyer-Antholz (1987) reported a range of 4.18-6.5 % for different temperatures (14-17.5 °C), gut fullness and age of fish. Andersen (1984) developed an exponential equation, taking length of fish and temperature into consideration, to estimate depletion rates in *P. microps*. We applied this equation to our data, using 18.5 °C for temperature and the average fish size of 27.42 mm. These figures fall within the ranges on which Andersen (1984) based his equation. This resulted to even higher estimates of evacuation rate (0.426/hr) and daily ration (47.66 % bw). Applying similarly Andersen's (1984) equation to his 24-h data on *P. lozanoi*, Cattrijsse (1986) derived evacuation rates almost 2 times higher (as recomputed based on values presented) compared to his own estimates. Perhaps the reason behind these, 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* and *Nepthys* (polychaetes) are eliminated faster (0.31 g/h) than crustaceans (0.19 g/h), in this case, *Crangon*. In the field, *P. microps* preferred crustaceans (gammarids, mysids, cumaceans) more than polychaetes as food. Therefore, applying Andersen's (1984) equation may have resulted to overestimates.

Estimates of evacuation rates and daily ration are comparatively fewer for *P. minutus* and *C. crangon*. Healey (1971) estimated an annual average of daily ration for *P. minutus* equivalent to 3.13 % bw. The values ranged from 0.651 % for December to 14.13 % bw for August. In Sweden, Evans (1984) reported the range of daily ration for *P. minutus* to be 5-12 % bw at 5 and 15 °C. Our estimate of 13.04 % bw for 18.5 °C fall within these reported values. We also tried analysing the *P. minutus* on a length class basis (Tab. 4). The estimates of daily ration however, did not, as expected, uniformly decrease with increase in size. This is probably due to the lack of appropriately-sized individuals during some hauls and the irregular course of emptying in some length classes.

Pihl & Rosenberg (1984) estimated the evacuation rate and daily food consumption of *C. crangon* through serial slaughter in the field. At 13.5-14 °C , they derived an evacuation rate of 0.58 % bw/h and a daily consumption of 12.1 % bw. They showed that evacuation was linear and under these conditions, food left the stomach within 2 hours. Evans (1984) reported a daily ration of 3-7 % body weight for 5 and 15 °C. Our higher estimates for *Crangon* probably take into account the higher temperature regime during our sampling. Applying Pihl & Rosenberg's (1984) exponential coefficient of 0.58 %/h to our own data for *Crangon,* we derive a daily consumption estimate of 12.92 % bw. This reflects, most probably, the lower limit of shrimp daily ration under this higher temperature condition.

The main problem in the estimation of reliable consumption rates is the limited information on gastric evacuation of the three investigated species. Data from a 24-h fishery

exhibited no clear evacuation phases. Feeding appeared to extend, more or less, throughout the whole 24-h cycle.

Published data on gastric evacuation experiments, on the other hand, cover only a limited number of food types, temperatures and predator size classes. Special complications are caused by different treatments of the 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 (Temming & Andersen, 1992). If meal size is then used as a variable in linear or exponential models (e.g. Meyer-Antholz, 1987 or Healey, 1971), 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, if e.g. 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; Tab. 5). 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; Tab. 5), 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.

The daily ration estimates reported here are preliminary for the area concerned. They should however, serve as baseline information for the area concerned, until further validated with more extensive sets of experimental data covering a wider range of conditions.

ACKNOWLEDGMENTS

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SPECIES	n	F-test	Welch test (mod. t-test)	t-test
C. crangon				
H8 vs. H10	37	5.875***	4.197***	
H10 vs. H14	55	7.779***	6.160***	
P. minutus				
H4 vs. H6	51	1.121 n.s.	-	2.619*
H6 vs. H8	42	1.404 n.s.	-	3.362***
P. microps				
H4 vs. H5	12	1.075 n.s.	-	1.983 n.s.
H5 vs. H9	19	2.492 n.s.	-	6.859***

Tab. 1: Comparison of means of fullness indices (two consecutive minima and the intermediate maximum) in C. crangon, P. minutus and P. microps.

Shrimp Length class (mm)	Crangon preyed upon by P. minutus		Crangon sampled by gear (corrected)		Percentage of avail. Biomass eaten (%)
	Length frequency dist. (%)	eaten Biomass (mg/m2)	Length frequency dist. (%)	available Biomass (mg/m2)	
1-4	5.62	-	0	0	-
5-9	32.13	0.010	0	0	-
10-14	11.62	0.021	4.55	0.599	3.46
15-19	12.05	0.066	16.98	6.839	0.96
20-24	20.08	0.252	27.83	25.819	0.98
25-29	12.45	0.304	18.30	33.062	0.92
30-34	4.02	0.171	10.25	32.261	0.53
35-39	2.01	0.137	10.46	52.908	0.26
40-44	0	0	6.54	50.190	0
45-49	0	0	2.42	26.813	0
50-54	0	0	1.54	23.884	0
55-59	0	0	0.92	19.315	0
60-64	0	0	0.15	4.169	0
65-69	0	0	0.05	1.794	0

Tab. 2: Predation impact of P. minutus on C. crangon on a 24-h period, northern Wadden Sea, July 1992.

HAUL NO.	C. crangon/ P.microps	C. crangon/ P. minutus	P.microps/ P. minutus
1	0.209	0.035	0.403
2	0.155	0.113	0.091
3	0.076	0.131	0.099
4	0.015	0.243	0.080
5	0.095	0.097	0.077
6	0.130	0.030	0.095
7	0.029	0.091	0.069
8	0.052	0.119	0.052
9	0.008	0.099	0.070
10	0.068	0.057	0.247
11	0.167	0.555	0.222
12	0.169	0.467	0.314
13	0.047	0.061	0.119
14	0.342	0.087	0.067
15	0.195	0.032	0.162
16	0.250	0.009	0.085
17	0.159	0.149	0.254
mean	0.127	0.140	0.147
sd	0.089	0.147	0.100

Tab. 3: Niche overlaps (Cxy) between shrimp and gobies
on a 24-h sampling period, northern Wadden Sea, July 1992.

LENGTH CLASS (mm)	C. crangon/ P.microps	C.crangon/ P.minutus	P.microps/ P. minutus
15-19	0.174	-	-
20-24	0.254	0.151	0.670
25-29	0.221	0.290	0.574
30-34	0.189	0.184	0.354
35-39	0.023	0.164	0.288
40-44	-	0.156	-
45-49	0.168	0.215	0.165
50-54		0.111	
55-59		0.229	
60-64		0.002	
65-69		0.014	

Tab. 3a: Niche overlaps (Cxy) between shrimp and gobies by
length class on a 24-h sampling period, northern Wadden
Sea, July 1992.

SPECIES	LENGTH (mm)	EVACUATION (g/h)	RATE (% bw/h)	DAILY RATION (% body weight)
P. microps	all sizes	0.0012	1.14	27.26
P. minutus	20-29	0.0006	0.67	16.10
	30-39	0.0011	0.46	10.99
	40-49	0.0030	0.60	14.32
	50-59	0.0063	0.67	16.01
	60-69	0.0159	0.79	18.93
	70-79	0.0084	0.27	6.44
	80-89	0.0155	0.38	8.99
	all sizes	0.0061	0.54	13.04
C. crangon	10-20	0.0006	1.51	26.46
	21-30	0.0011	1.06	18.57
	31-40	0.0022	0.98	17.17

Tab. 4: Evacuation rates (g/h and % body weight/h) and daily rations (% body weight) of P. microps, P. minutus and C. crangon at 18.5 lC in the northern Wadden Sea.

PREDATOR	SIZE (mm)	FOOD	TEMP. (°C)	LINEAR RATE (%/h)	EXP. COEFF.	METHOD	DATE	ave So %	ave. S (field) %	DAILY (lin.) %	CONSUMPTION (exp.) %	AUTHOR
P. microps	30	natural	14-20				05.21/22.81		0.50-2.7			Meyer-Antholz (1987)
	19		16-18.8				07.16/17.81		1.53-2.9			
	25		14.5-16.5				09.15/16.81		1.02-3.33			
			12-16.5				09.22/23.84		1.57-3.81			
	20-24		13-21			24-h			0.8-2.9			Andersen (1983)
	25-29								0.8-2.1			
	30-34								1.2-2.5			
	35-39								0.7-3.4			
	> 39											
	23.6	Nereis	20		0.534	lab. exp.		10.0				Andersen (1984)
	31.6		20		0.415			"				
	38.1		20		0.359			"				
	31.1		15		0.305			"				
	31.2		10		0.219			"				
	27.4	natural	18.5	1.14	0.241	24-h	07.22/23.92		5.4	27.26	31.23	this study
P.lozanoi	25	Artemia	12		0.16	lab. exp.		0.81 5.0				Cattrijsse (1987)
	35		12					2.25 5.0				
P. minutus	20-40	natural	5		0.123	field exp.	Nov.					Evans (1984)
	41-60		5		0.127							
	20-40		15		0.150		Aug.					
	41-60		15		0.158							
	20-40		15			24-h	Aug			1.7		6.12*	
	20-40		?			"	Oct			1.2		3.54*	
	30	"	18.5	0.64						10	15.36*		applying Healey (1971) with 10 % stomach content as in Andersen (1984)
	48.88	"	18.5	0.54	0.114	24-h	07.22/23.92			4.58	13.04	12.55	
C. crangon	16-38	"	13.5-14	0.58	0.47*	field exp.	09.81	1.8*	1.27*	12.1	14.33*	Pihl & Rosenberg (1984)
	"	"	12-14	0.28*	0.42*	24-h	09.78	1.2*	1.3*	6.72*	13.10*	Pihl & Rosenberg (1984) recalculated
	10-20	"	5		0.142	field exp.	Nov					Evans (1984)
	21-30		5		0.183							
	31-40		5		0.147							
	41-50		5		0.101							
	51-70		5		0.104							
	10-20	"	15		0.148	field exp.	Aug	?				
	21-30		15		0.159							
	31-40		15		0.145							
	41-50		15		0.153							
	51-70		15		0.060							
	20-40	"	15			24-h	Aug			1.86		6.75*	
	"		?				Oct			1.31		5.75*	

Tab. 5: Comparison of evacuation and daily consumption estimates from the literature and this study for shrimp and gobies. (Note: * reanalyzed/recalculated from graphs and data presented by the authors.
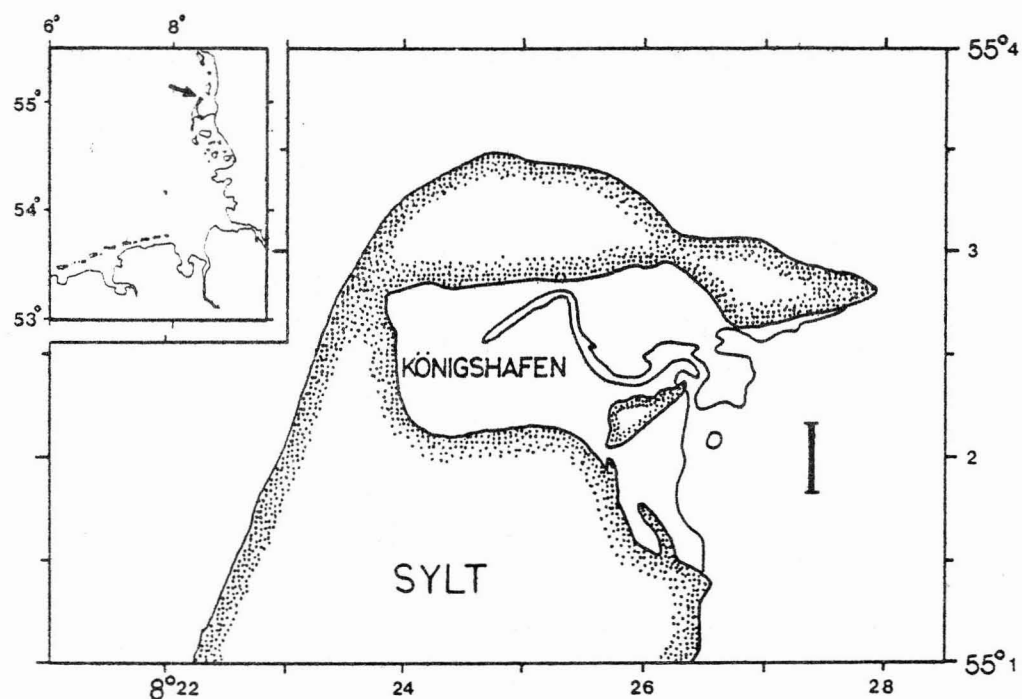
Fig.1: Map showing location of the sampling site in Königshafen, Sylt island, northern Wadden Sea. Thick bar indicates location of tows.
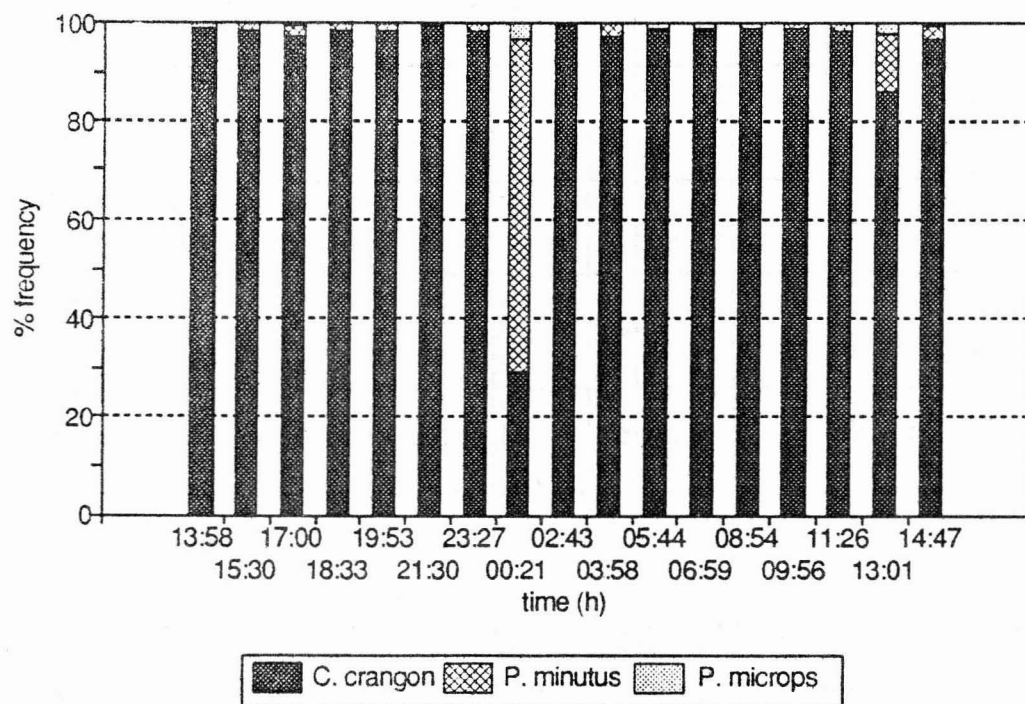

Fig. 2: Relative percentage frequencies of *P. microps*, *P. minutus* and *Crangon crangon* during the 24-h period.
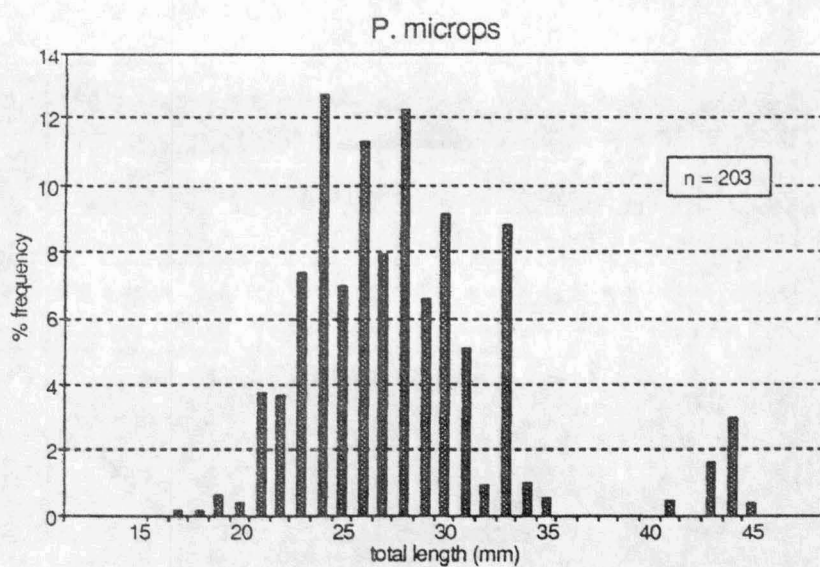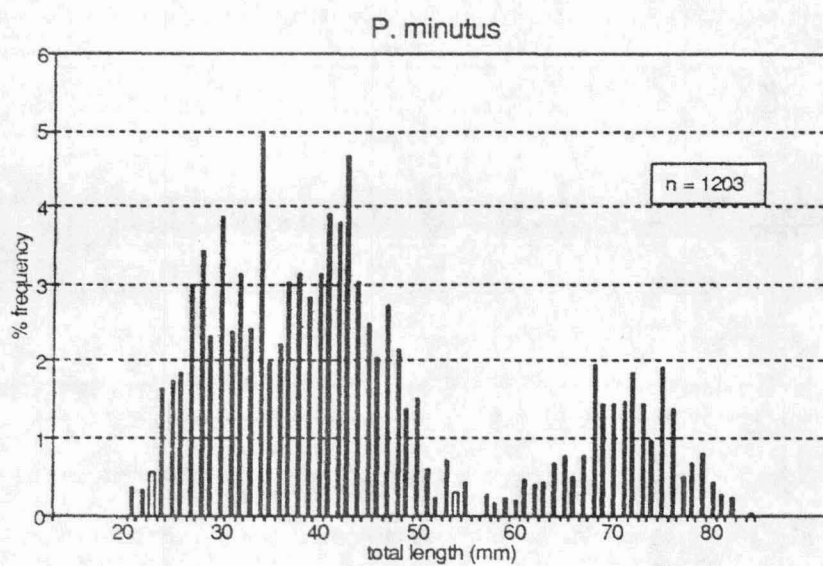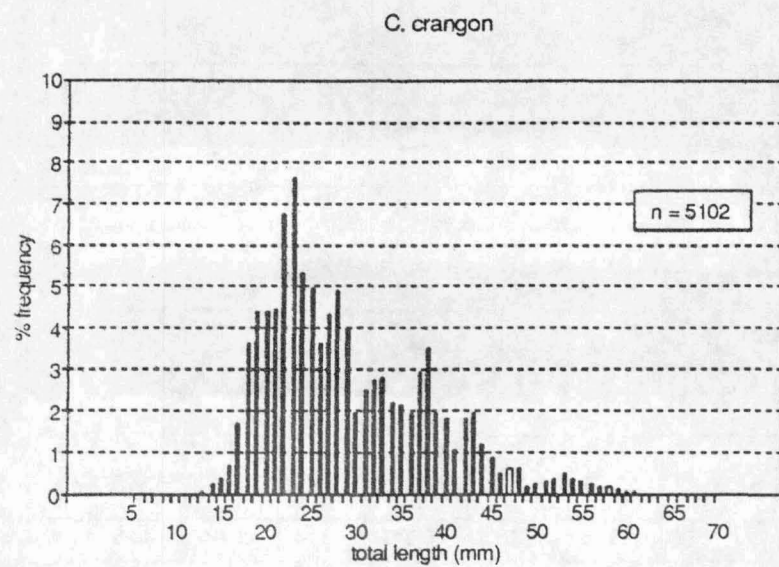
Fig. 3-5: Overall size distributions of *C. crangon*, *P. minutus* and *P. microps*.
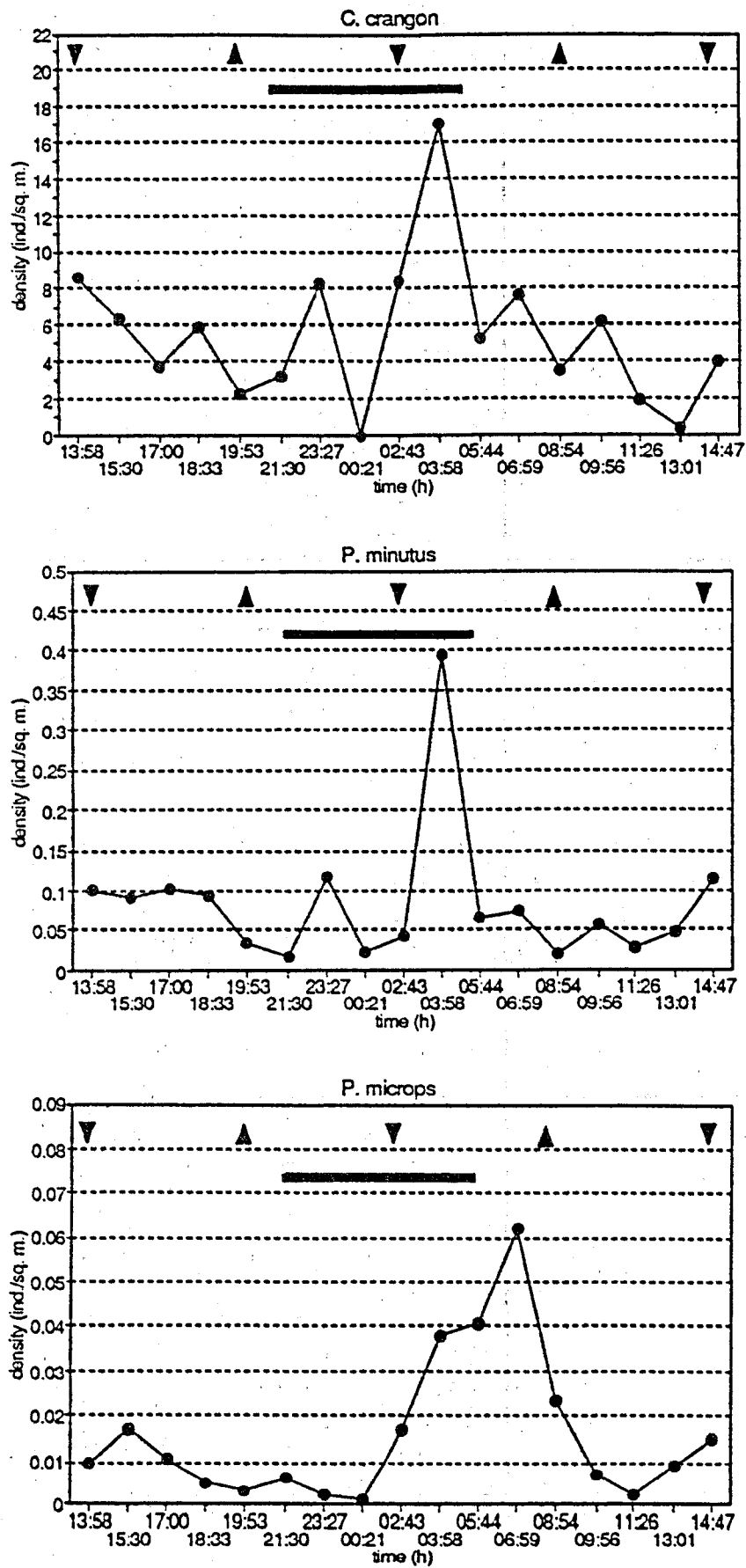
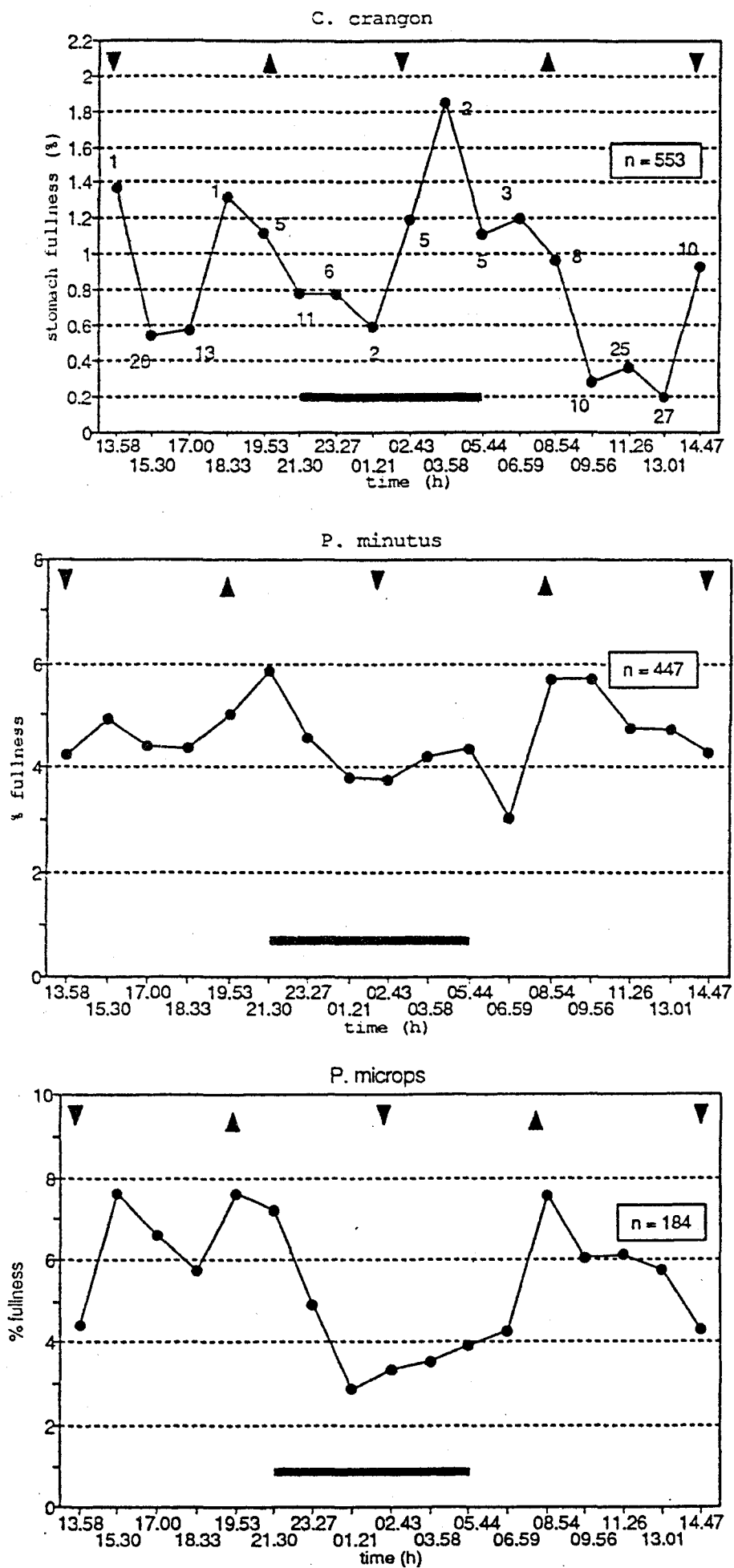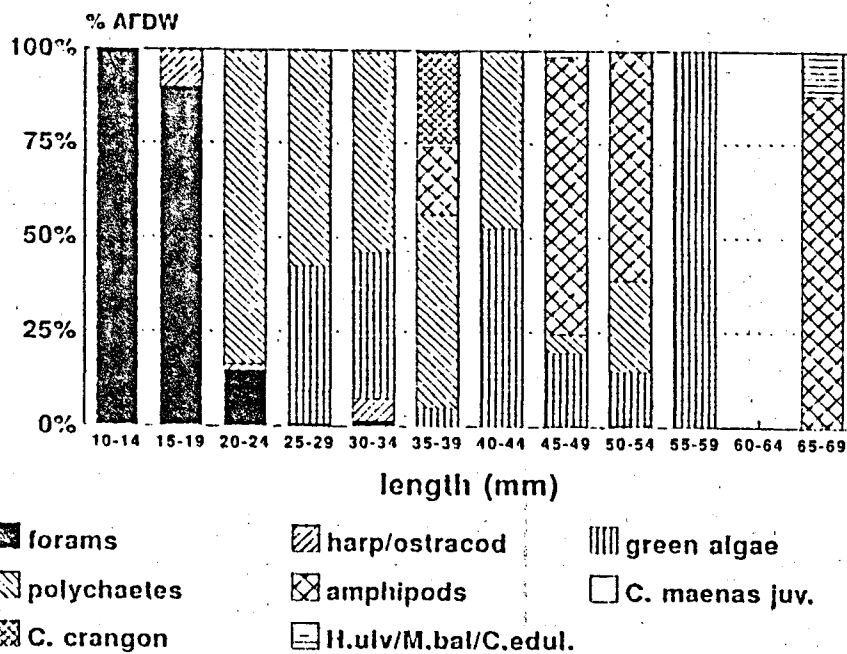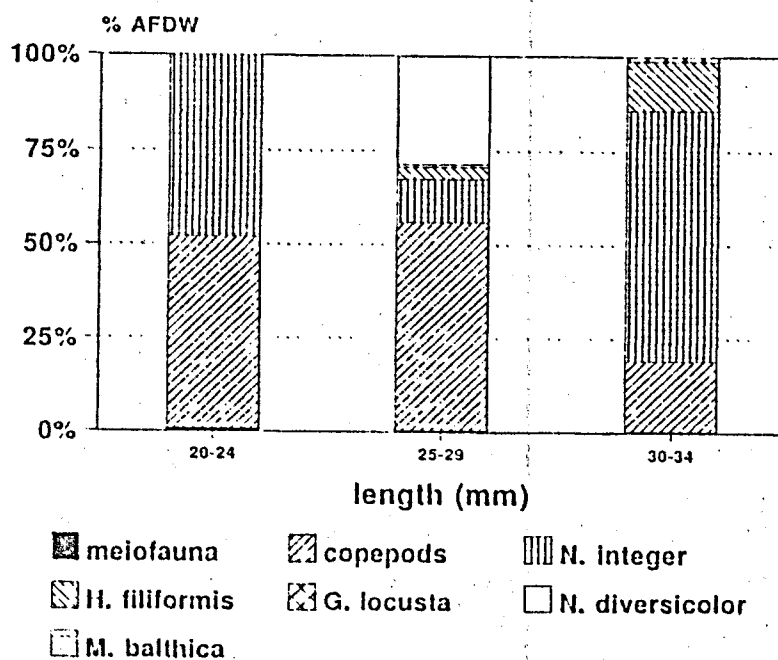Fig. 6-8: Diurnal density patterns of *C. crangon*, *P. minutus* and *P. microps*. Arrows indicate low and high tides, while thick bar indicates nighttime.

Fig. 9-11: Diurnal feeding patterns of *C. crangon*, *P. minutus* and *P. microps*. Numbers next to points in Fig. 9 indicate number of shrimp empty stomachs. Other legends as in Fig. 6-8.
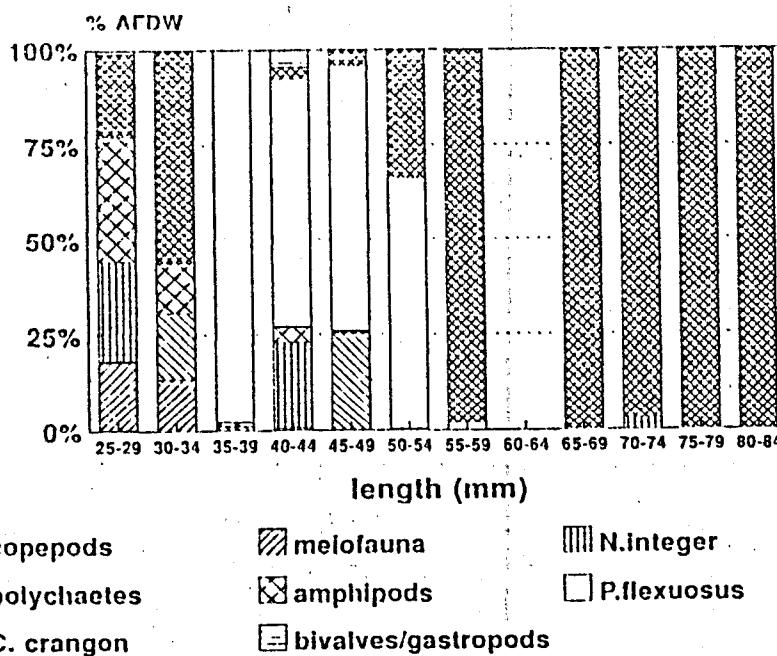
C. crangon

% AFDW

100%

75%

50%

25%

0%

10-14 15-19 20-24 25-29 30-34 35-39 40-44 45-49 50-54 55-59 60-64 65-69

length (mm)

- ▨ forams
- ▨ polychaetes
- ▨ C. crangon
- ▨ harp/ostracod
- ▨ amphipods
- ▤ H.ulv/M.bal/C.edul.
- ▥ green algae
- ☐ C. maenas juv.

P. microps

% AFDW

100%

75%

50%

25%

0%

20-24 25-29 30-34

length (mm)

- ▨ meiofauna
- ▨ H. filiformis
- ▢ M. balthica
- ▨ copepods
- ▨ G. locusta
- ▥ N. integer
- ☐ N. diversicolor

P. minutus

% AFDW

100%

75%

50%

25%

0%

25-29 30-34 35-39 40-44 45-49 50-54 55-59 60-64 65-69 70-74 75-79 80-84

length (mm)

- ▨ copepods
- ▨ polychaetes
- ▨ C. crangon
- ▨ meiofauna
- ▨ amphipods
- ▤ bivalves/gastropods
- ▥ N.integer
- ☐ P.flexuosus

Fig. 12-14: Prey selection by size class of *C. crangon* (n = 39), *P. microps* (n = 14) and *P. minutus* (n = 29) during peak feeding times.
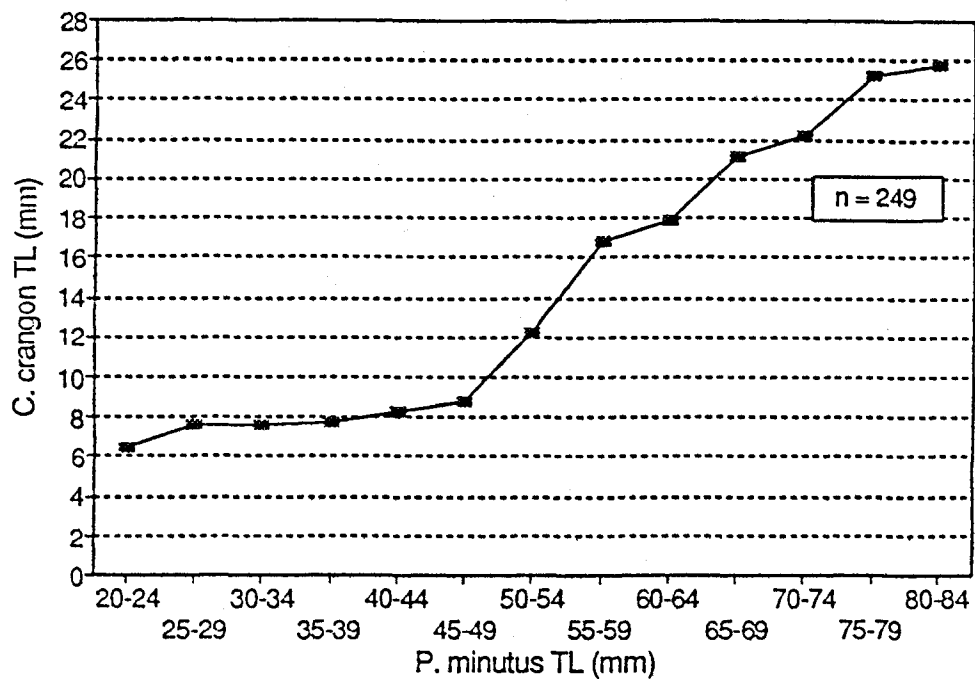
Fig. 15a: Averaged sizes of brown shrimp preyed upon by *P. minutus*, presented according to size of predator.
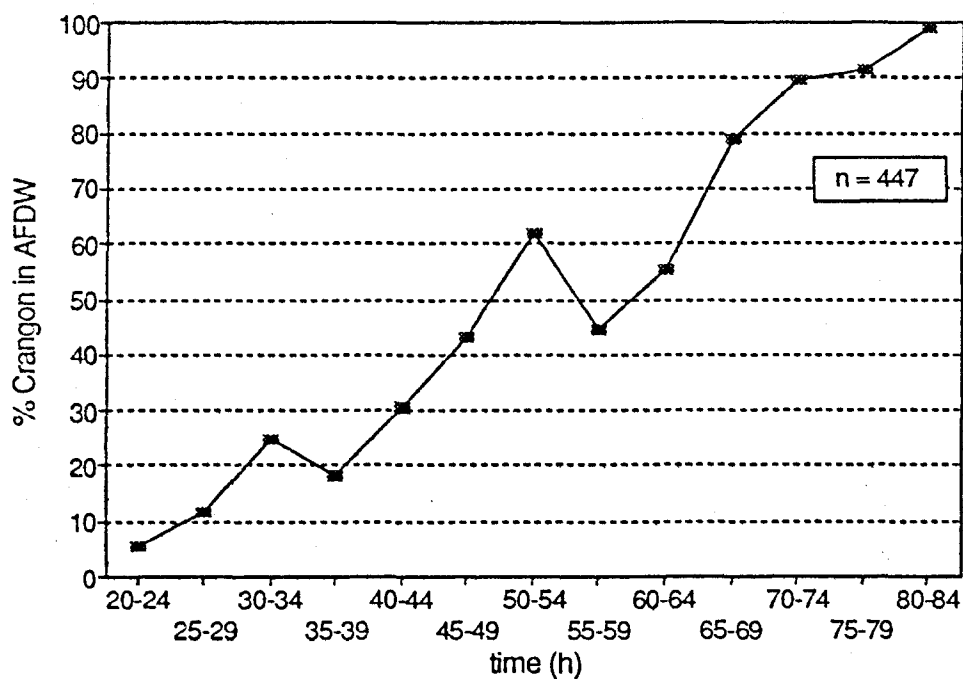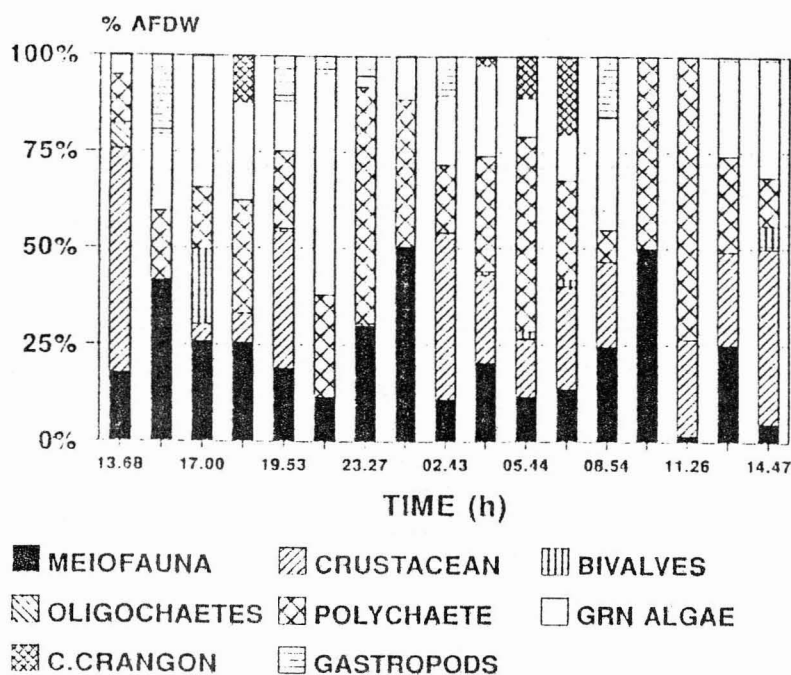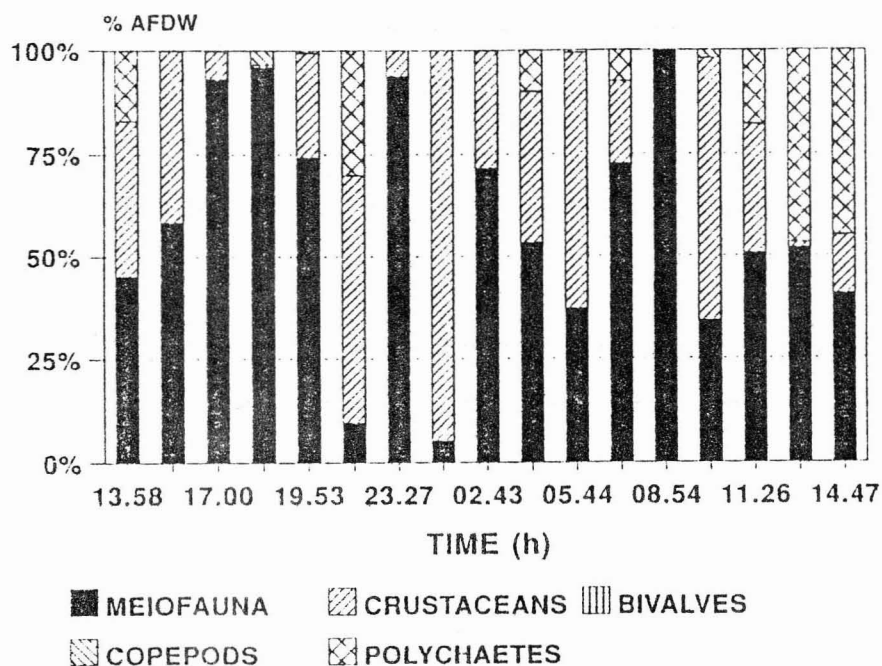

Fig. 15b: Quantities of brown shrimp, as percent AFDW of total gut contents, preyed upon by *P. minutus*, likewise according to size of predator.
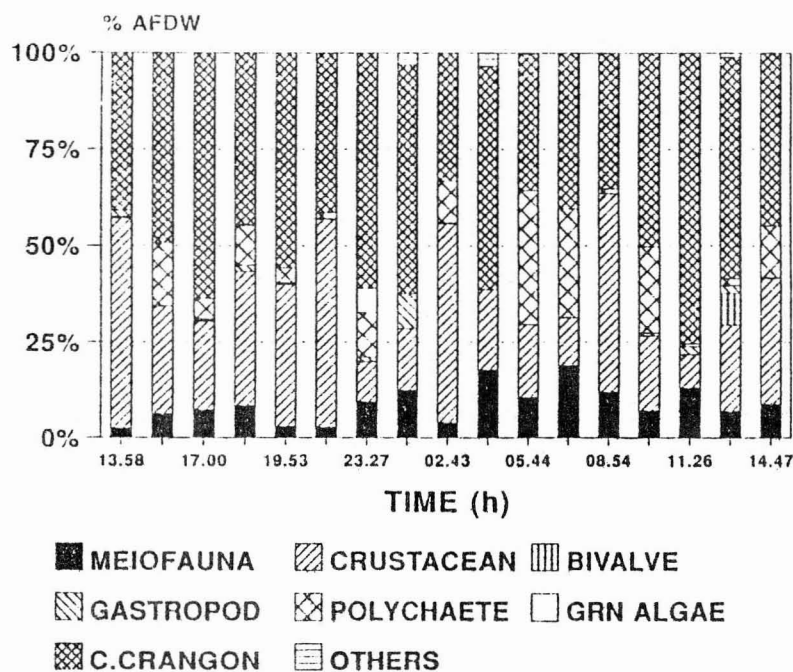
Fig. 16-18: Diurnal prey selection of *C. crangon* (n = 553), *P. microps* (n = 184) and *P. minutus* (n = 447).
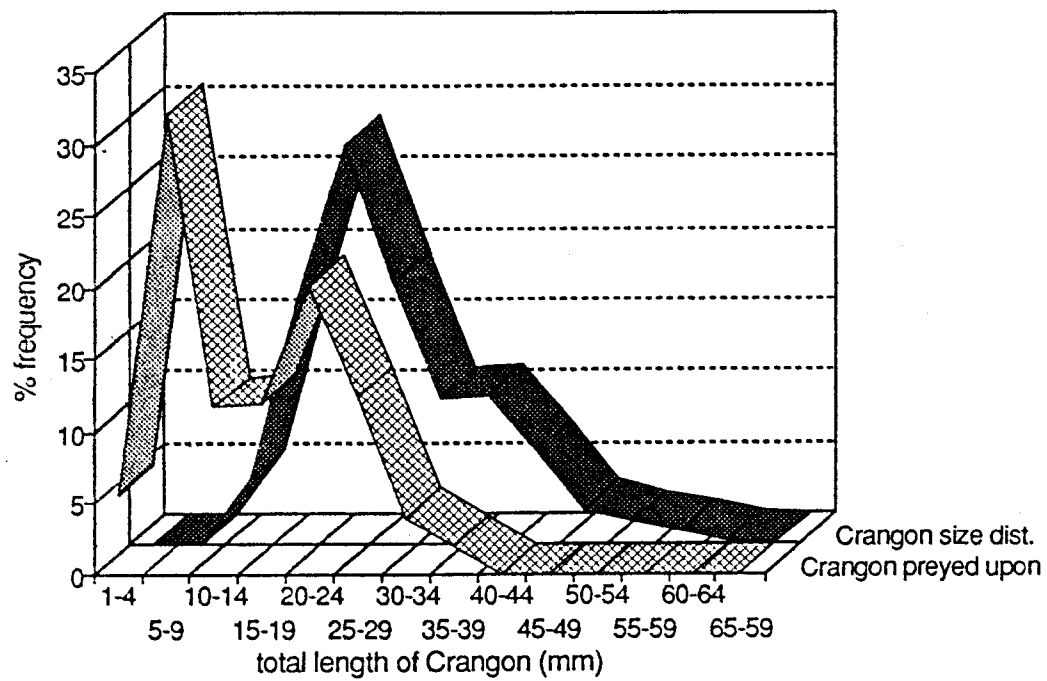
Fig. 19: Comparison of *Crangon* size distribution (available) vs. sizes preyed upon by *P. minutus*.