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Significant predation on micro- and macrobenthos by the crab *Carcinus maenas* L. in the wadden sea

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Abstract

The predatory role of juvenile and adult shore crabs, *Carcinus maenas* L., on tidal flats in the wadden sea near the North Sea island of Sylt has been evaluated with field enclosures. Early benthic stages (2–4 mm carapace width) prey heavily on microfauna (Nematoda, Turbellaria, Ostracoda) and particularly on juvenile macrofauna. When crabs grow up they gradually shift to larger prey and a bifurcation in prey selection occurs: males concentrate on molluscs while females feed preferentially on annelids. Annual consumption expressed as dry organic matter is estimated at $3.6 \text{ g} \cdot \text{m}^{-2}$ for O-group crabs and $1.3 \text{ g} \cdot \text{m}^{-2}$ for adult crabs. *Carcinus maenas* is expected to cause conspicuous impact on zoobenthos in the wadden sea 1. by preying always on the most abundant species, 2. by increasing juvenile mortality of high-biomass macrofauna, 3. by being a predator of highly variable abundance between years.

Introduction

Are numbers of zoobenthos kept within limits by predatory members of the zoobenthos itself? The inspiring model on North Sea fisheries by ANDERSON and URSIN (1977) assumes this to be so, similarly to the way zooplankton grazes on phytoplankton. CASWELL (1978) and GLASSER (1979) discuss the significance of predation in shaping and maintaining the structure of communities. By keeping prey populations below resource limitation, the level of resources is raised, which in turn allows far more species to co-exist. CONNELL (1975) and MENGE and SUTHERLAND (1976) suggested heavy predation in benign and structurally simple habitats.

To consider these suggestions on the significance of predation, we selected a benthic predator living in a structurally simple and seasonally benign environment and investigated its impact on prey populations: the common shore crab *Carcinus maenas* L. which is abundant on tidal flats in the wadden sea.

We tried to answer three questions: Does the prey spectrum remain the same in different habitats? Which species are in particular preyed upon? What is the amount of prey captured by natural populations in the wadden sea?

To evaluate these questions we carried out enclosure experiments on tidal flats, and presented natural and artificially composed prey spectra to the crabs in the laboratory. In addition, we investigated abundance of juvenile and adult *C. maenas*. Based on these observations, we estimated the annual food intake of the entire population.

Carcinus maenas turned out to be a most general predator on zoobenthos, consuming annually zoobenthos equivalent to $5 \text{ g} \cdot \text{m}^{-2}$ of dry organic matter.

Material and methods

We studied a crab population in a sheltered tidal bay of 4 km², Königshafen, near the island of Sylt in the eastern part of the North Sea. Tidal range is 1.7 m. Information on the physiographic regime and on composition of benthos are given by WOHLBERG (1937) and REISE (1978). All caging experiments were done in the interior part of the bay (Möwenbergwatt).

Abundance of large crabs (> 15 mm carapace width) was evaluated with a drag-net (mesh-size = 15 mm) which could be trailed by man-power. The net was towed on a buoyant tow-rope, thus crabs staying in direction of fishing were not disturbed. Speed of hauling was about 50 m·min⁻¹. Abundance of juveniles was estimated from sets of core samples of 100 cm² each taken during low tide.

Cages with enclosed juvenile crabs were constructed out of PVC tubes of 83 cm² cross section and 8 cm height, punched with lateral holes of 34 mm in diameter. The holes, top and bottom were covered with 40 µm mesh gauze. Cages were carefully filled with undisturbed sediment cores of 6 cm height and buried to adjust inner and outer sediment level. Experiments were carried out with 3 enclosures, each including 100 small crabs (2–4 mm carapace width) and 3 control cages containing no crabs. Following six periods of tidal cycle, from each cage 6 samples of 1 cm³ (sediment depth 0–1 cm) were taken with a glass tube. Samples were washed in a glass beaker and fractionated into 8–12 petri dishes. All metazoa were picked out with a pipette under a dissecting microscope. In addition, all the remaining sediment within cages was washed through a 250 µm mesh gauze to obtain small and juvenile macrofauna.

Adult crabs were enclosed in cages along a transect from the high to low water mark. These cages were constructed with 12 mm wire netting. The size of cages was 50·50 cm, height was 15 cm above surface and the wire netting reached 10 cm into the sediment. The epibenthic snails *Littorina littorea* and *Hydrobia ulvae* could pass the mesh and were thus not considered in the field experiments.

At each experimental site two cages were populated with either 25 males or 25 females, a third cage served as control from which crabs were excluded. In addition samples were taken from the undisturbed sediment outside the cages. All experiments were run for 7 days in the time from June to September. Samples to estimate prey density were taken with glass corers of 10 cm² cross section to a depth of 6 cm. In the laboratory the sediment cores were washed through a 250 µm mesh. Residues were washed into white dishes from which all animals were collected. For identification and measurements organisms were narcotized with MgSO₄. Sets of 10 samples were taken to compare crab cages and controls.

Comparisons between treatments were evaluated with the independent homogeneity test developed by KOLMOGOROV and SMIRNOV (SACHS 1971), using 5 % probability levels. Regression lines were calculated following the method of smallest squares (CAMPBELL 1971), regression curves with the „power model” (Hewlett & Packard program).

Results

During winter adult *Carcinus maenas* stay quiescent in subtidal channels. In Königshafen, crabs are back on tidal flats by May and females release planktonic larvae at this time. Settlement of larvae at the sediment surface occurs in pronounced waves. The first three are the strongest and usually occur early in July (i.e. 13.7.1974 and 2.7.1975). Settlement may be delayed in some years (early August in 1980) or missing altogether (summer 1979). In October these juvenile crabs bury on tidal flats

and in mussel banks to hibernate while adult crabs leave for the subtidal channels. In the first year of their life juveniles may reach a carapace width of up to 20 mm ($\bar{x} = 10.0 \pm 6.0$ mm, $n = 42$, hibernating crabs buried on tidal flats in winter 1973/74). In their second year they may reach 50 mm. The largest crabs measured in Königshafen had 75 mm carapace width.

Both juveniles and adults search for their prey by ploughing the substratum gently with their dactyli and sometimes with their chelae. Having detected a prey object they unearth it, pick it up with their chelae to the maxillipeds and eat it. In case of molluscs they either crack the shell by mere force or – if shells are too thick and solid – try to insert their chelae in even the smallest apertures and chip away small pieces of the shell to expose their prey. O-group crabs of 2–4 mm carapace width often systematically rework the upper layer of sediment producing meandering ditches which tend not to be crossed again.

At high tide ± 10 min the adult population density on 200 m² was 2 ± 2 in *Corophium* beds of the upper intertidal, 11 ± 7 in seagrass beds and 22 ± 16 on the extensive sand flats ($n = 30$ tows). Because of water depth and mussel banks it was impossible to drag a net in the mud flat areas. According to several observations from a boat we assume a population density higher than on sandy flats, probably about 30 crabs on 200 m². To get an estimate of the total population in the Königshafen, densities have to be calculated according to the dimensions of the four tidal habitats (*Corophium* beds 0.5 km², seagrass beds 0.5 km², sand flats 1.5 km², mud flats with mussel banks and channels 1.5 km²). During summer 1978, there were about 425,000 adult *C. maenas* in Königshafen (4 km²).

O-group crabs were most abundant in areas which provide shelter, i.e. seagrass beds and mussel banks. In the seagrass bed 1974 abundance per m² was 500 ± 141 (July), 267 ± 151 (August) and 181 ± 177 (September). Maximum settling density in July was $2,000 \cdot \text{m}^{-2}$. On exposed flat surfaces, abundance was rather irregular as response to currents and wave action. To be conservative, we assumed zero abundance for these areas and obtained an average of 125 O-group crabs $\cdot \text{m}^{-2}$ from July to September for Königshafen.

Table 1

Three enclosures were stocked with 100 *Carcinus maenas* (2–4 mm) for 6 tidal cycles in July 1977. Cannibalism reduced crab number to 43%. Remaining zoobenthos is compared to that of 3 control cages. From each cage, 6 samples of 1 cm³ were taken before the entire sediment was washed through a 250- μm mesh. Numbers are mean \pm S.E.

prey	crab cage individuals $\cdot \text{cm}^{-2}$ ($n = 18$)	control cage
Nematoda	26.4 ± 18.0	123.6 ± 41.9
Turbellaria	0.2 ± 0.4	6.9 ± 5.9
Ostracoda	3.7 ± 3.7	18.7 ± 13.0
Copepoda	1.9 ± 3.2	6.9 ± 4.3
	individuals $\cdot 83 \text{ cm}^{-2}$ ($n = 3$)	
<i>Hydrobia ulvae</i> (juv.)	18.0 ± 11.3	190.7 ± 54.2
<i>Scoloplos armiger</i> (5–10 mm length)	13.3 ± 8.5	104.3 ± 31.3

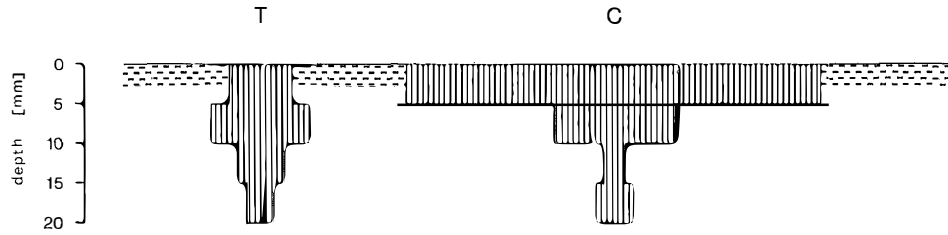


Figure 1

Vertical pattern of Nematoda below 2 cm² of a sandy flat, left when predated by O-group *Carcinus maenas* (2–4 mm), right in the absence of epibenthic predators. Crabs do not capture nematodes deeper than 5 mm in the sediment.

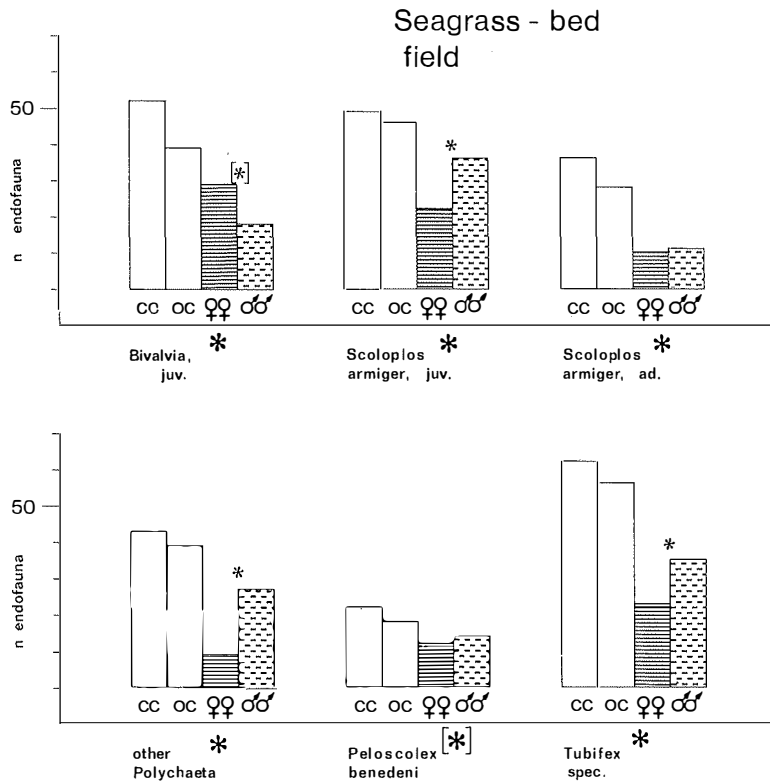


Figure 2

Crab enclosure experiment in the seagrass bed. Indicated is number of prey organisms under 100 cm² left after 7 days of experiment. CC = cage control, crabs are excluded; OC = zero control, normal sediment outside cages, not manipulated; ♀♀ = cage with 25 females (25–35 mm carapace width) enclosed; ♂♂ = cage with 25 males (35–45 mm carapace width) enclosed. Large asterisks indicate significant differences between enclosure cages and controls, small ones between females and males on the 5%-niveau (in brackets 10%-niveau). Molluscs are particularly decimated by males, soft-bodied prey by females. (Bivalvia, juv. = *Cerastoderma edule* and *Macoma baltica*; 'other polychaetes' = *Pygospio elegans*, *Capitella capitata* and *Tharyx marioni*).

On a sandy tidal flat juvenile crabs of 2–4 mm carapace width were allowed to prey in enclosures (Table 1). Crabs significantly reduced all microfaunal taxa as well as juvenile macrofauna. There is no evidence of prey selection; however, feeding is restricted to the upper 5 mm of sediment (Fig. 1). Tests in aquaria with crabs of increasing size (5, 15, 20 and 35 mm carapace width) indicated a gradual shift from small to larger prey.

Cage experiments with adult crabs were run in a seagrass bed, a sand flat and a mud flat. In the *Corophium* bed crabs did not survive seven days enclosed in a cage. Adult *C. maenas* prey upon all macrofaunal species occurring in significant numbers on the

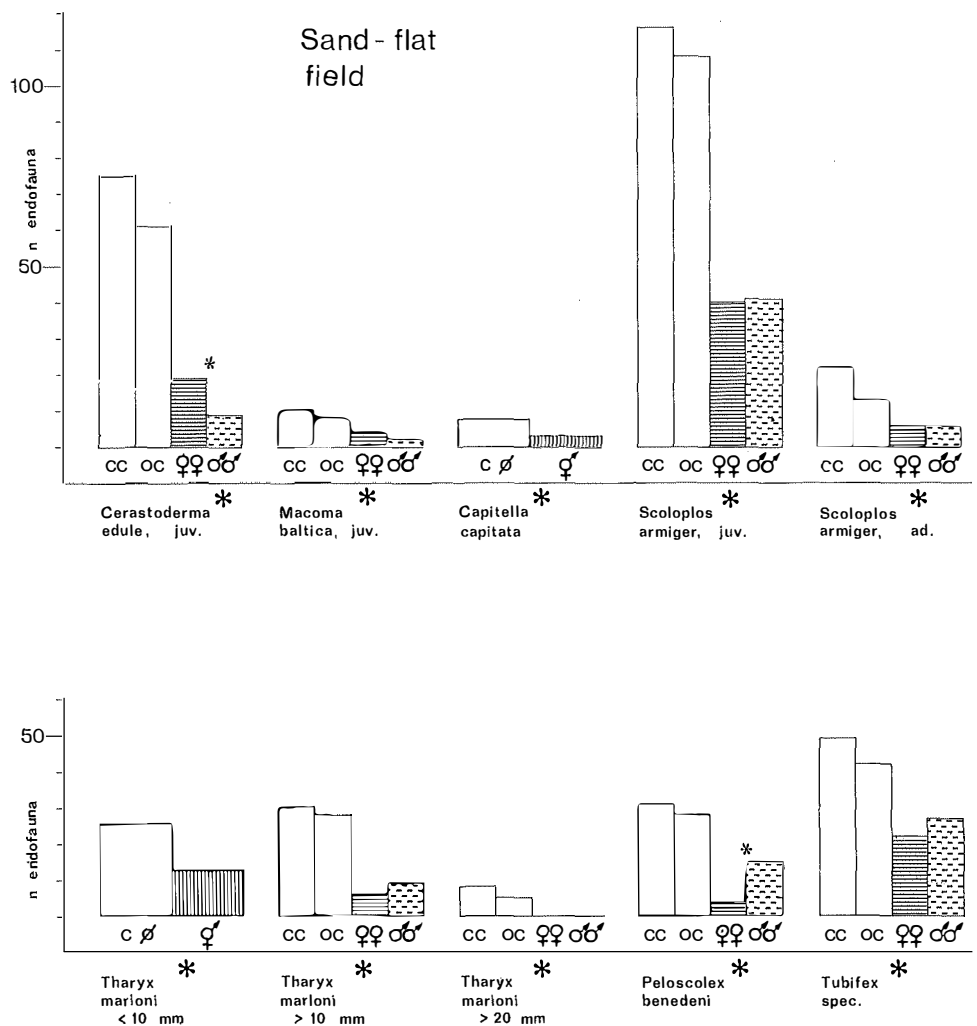


Figure 3

Crab enclosure experiment on the sand flat. Indicated is number of prey organisms under 100 cm² left after 7 days of experiment. For more detailed information see legend to Fig. 2. C Ø = mean of controls, ♀♀ = mean of female and male enclosure cages.

flats. In the seagrass bed crabs feed on young mussels, clams and *Tubifex* sp. in particular (Fig. 2). On the sand flat heaviest predation was on *Scoloplos armiger* (Fig. 3), and on the mud flat they obtained large numbers of *Tharyx marioni* (Fig. 4). Crabs always preyed most heavily on those species with the highest population density. Feeding efficiency was dependent on habitat. On undisturbed natural

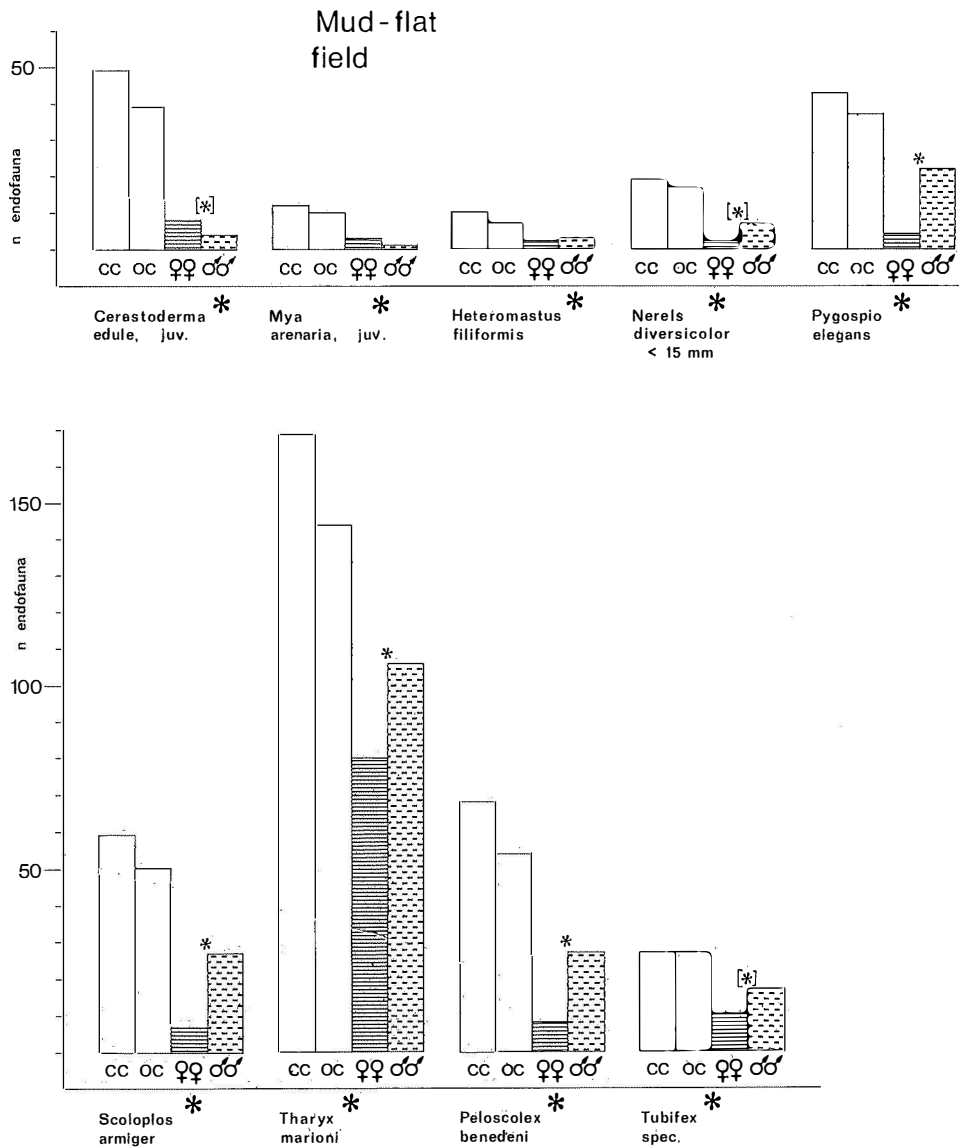


Figure 4

Crab enclosure experiment on the mud flat. Indicated is number of prey organisms under 100 cm² left after 7 days of experiment. For more detailed information see legend to Fig. 2.

sediment blocks in aquaria percentage of captured organisms increases from seagrass bed to sand and then to mud. The period of submersion seems to be of minor importance compared with sediment structure. Prey spectra of male and female crabs were different (Fig. 2–4 and 6). In all experiments the diet of male crabs contained a larger fraction of molluscs. Females concentrated on annelids. The total amount of food consumed by males is less than in females (Fig. 5).

Experiments in aquaria with artificially stocked sediments gave further information on food preferences of males and females (Fig. 6). With exception of the small snail *Hydrobia ulvae*, all species and size classes of molluscs were in particular decimated by males, significantly less so by females. Under artificial arrangements with an excessive supply of easy to catch prey, females apparently prefer molluscs too, but are not able in the same way as males to feed on larger ones.

Male and female crabs of identical size were compared in their ability to feed on different size classes of the prosobranch *Littorina littorea*. Differences in the ability to crack shells can be described as regression curves:

$$\text{males} \quad y = 57,95 \cdot x^{-1,01}; r^2 = 0,96; \text{st. error} = 0,13; n = 30$$

$$\text{females} \quad y = 36,22 \cdot x^{-0,94}; r^2 = 0,98; \text{st. error} = 0,13; n = 15$$

where y is the number of snails cracked, and x the carapace width per shell height.

Hence male crabs catch more and larger winkles than females do. To mimic natural conditions one would have to compare larger males with smaller females of the same

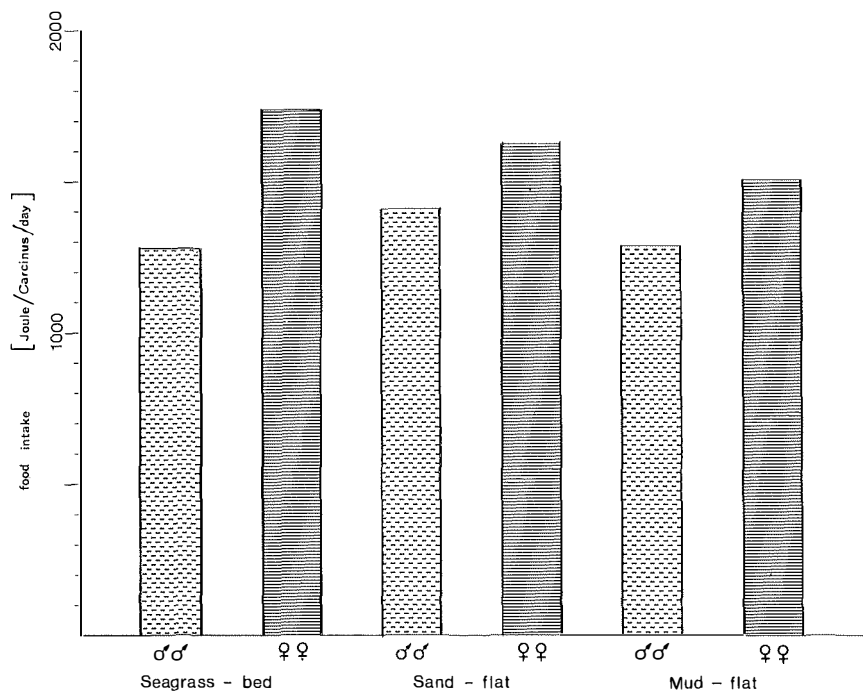


Figure 5

Energy content of the mean daily food intake of adult male and female *C. maenas* in seagrass bed, sand flat and mud flat. Energy intake is always less in males than in females.

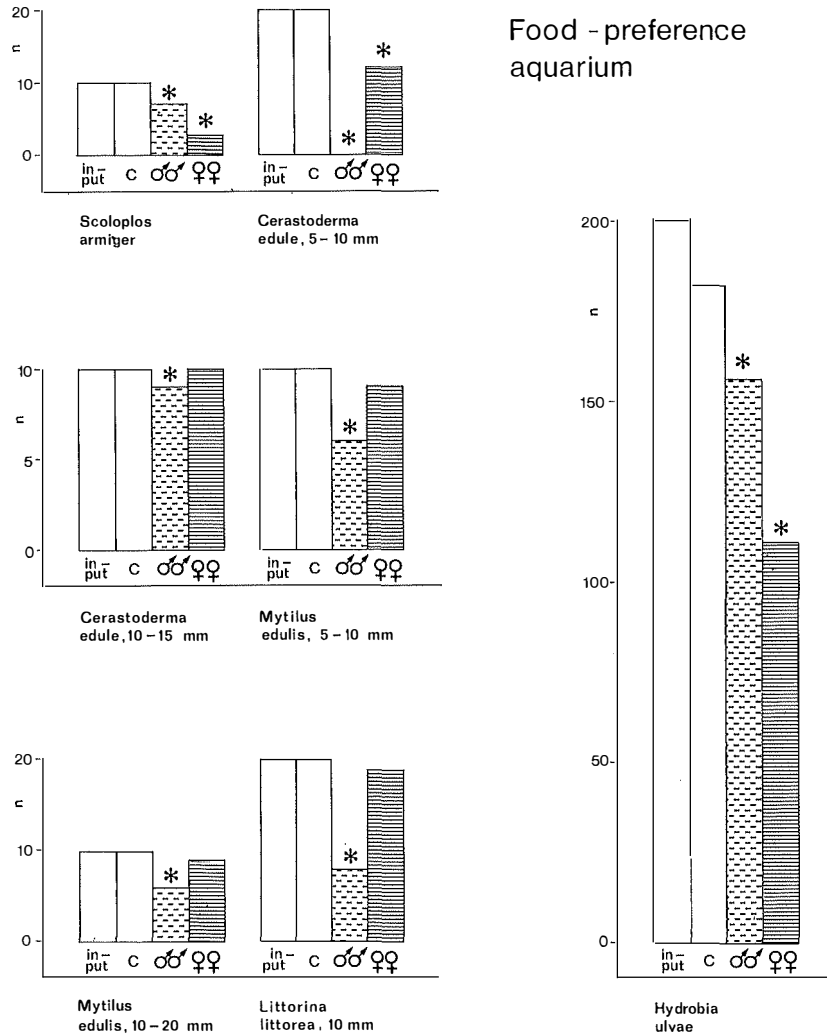


Figure 6

Food preference experiment on artificially stocked sediment in the aquarium. Indicated is total number of prey organisms left after 3 days of experiment: (1) input, (2) C = control, with no crabs, (3) ♂♂ = aquarium with a male crab of 45 mm carapace width (mean of two parallels), (4) ♀♀ = aquarium with a female crab of 40 mm (mean of two parallels). Significant reductions are marked with asterisks (5 %-niveau). All species and size-classes of molluscs with exception of *Hydrobia ulvae* are particularly decimated by males.

age which would enhance the difference. These sex determined differences in food intake are in accordance with a sexual dimorphism in construction of chelae. Dentition in female chelae is sharp, while male chelae are stronger and have a knotty dentition.

Discussion

Compared to previous investigations on *Carcinus maenas*, our procedure differed 1. in the method of obtaining abundance data, 2. prey spectra and preferences were

determined in choice experiments, 3. feeding efficiency and food intake were evaluated under field conditions. In shallow water the man-powered drag-net should be preferred to conventional motor-fishing because we observed crabs being highly disturbed by wake and shadow of the boat. To determine prey spectra we put the natural array of potential prey organisms at the crab's disposal. Prey spectra of O-group crabs were investigated by sorting the unsieved sediment, prey spectra of adults by sieving with a 250 μm mesh. Thus we avoided truncation of prey spectra which is likely to occur 1. if potential prey is selected by preconception, 2. if gut contents are analyzed (a procedure biased towards hard-structured prey), 3. if sieving is done with a coarse mesh. We found that even adult crabs feed to a considerable proportion on small soft-bodied prey. DARNELL (1958) and ROPES (1968) stressed the importance of clams and other bivalves as prey.

In our field experiments, crabs always turned to the most abundant prey species. This behaviour may well prevent habitat monopolization by a few infaunal species. REISE (1978) presented evidence that cockle populations, *Cerastoderma edule*, are kept within limits by such predation. Feeding efficiency varies with habitat structure (REISE 1977 b; this study) and predation pressure is less in the upper intertidal than on the lower flats and in channels. Thus *C. maenas* will contribute to the differential distribution of zoobenthos in relation to sediment and tidal zone.

For comparisons we converted our food intake data into energy units and g dry organic matter, using figures in ANKAR and ELMGREN (1976), BEUKEMA (1976), BURKE and MANN (1974), ELNER (1978), GRAHAME (1973), McINTYRE (1977), MUUS (1967), KLEIN-BRETELER (1975), SIMON and DAUER (1977) and SMIDT (1951). On the average, an adult *C. maenas* consumed about 1500 Joule $\cdot\text{day}^{-1}$. Adults populate the flats approximately 150 days $\cdot\text{yr}^{-1}$ (June-October). The entire adult population in Königshafen comprised in 1978 about 425 000, equal to an average of one crab to 10 m^2 . Accordingly, annual consumption is 24 $\text{KJ}\cdot\text{m}^{-2}$ or 1.3 $\text{g}\cdot\text{m}^{-2}$, expressed in dry organic matter.

Our experiment with O-group crabs does not allow a straightforward estimate of food intake because considerable cannibalism occurred among the enclosed crabs. Of 300 crabs only 136 survived enclosure. Assuming 2.4 J per lost crab of moulting stage I-II (see KLEIN-BRETELER 1975) in addition to other prey consumed, we estimate a daily consumption of 9 J per crab of 2–4 mm carapace width. In the laboratory, KLEIN-BRETELER (1975) observed a consumption of 12 $\text{J}\cdot\text{day}^{-1}$ in similar sized crabs (see also ERIKSSON and EDLUND 1977). Based on a presence of 60 days $\cdot\text{yr}^{-1}$ (July–September) and an average abundance of 125 $\cdot\text{m}^{-2}$ we calculate an annual consumption of 67.5 $\text{KJ}\cdot\text{m}^{-2}$ or 3.6 $\text{g}\cdot\text{m}^{-2}$ for these small crabs. This is calculated for 1974, a year with successful settlement of spat. In other years, consumption may be considerably less.

Taken together, the entire *C. maenas* population consumes annually about 5 $\text{g}\cdot\text{m}^{-2}$ of zoobenthos expressed in dry organic matter. This is in the same order of magnitude as DeVLAS (1979) found for plaice in the Dutch wadden sea (5.6 $\text{g}\cdot\text{m}^{-2}$). KLEIN-BRETELER (1976) estimated 1.5 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ consumption of O and I group *C. maenas* in the same area. The difference to our estimate is in part explained by a higher proportion of high-density areas and partly by more adult crabs in Königshafen.

Our high estimate of consumption does not fit into BEUKEMA's (1981) general scheme of total annual predation pressure in the wadden sea: 4 (birds) + 5 (fishes) + 3 (invertebrate predators) = 12 $\text{g}\cdot\text{m}^{-2}$ of dry organic matter. However, BEUKEMA considers macrozoobenthos only (organisms retained by a 1-mm mesh), while our

estimate refers to the entire size range of zoobenthos. Our results strongly suggest that future studies on trophic links in the benthos should not be limited to certain size categories. Previous field experiments, excluding epibenthic predators in Königshafen, similarly demonstrated that most intense predation pressure is exerted on small and juvenile zoobenthos which generally passes a 1-mm sieve (REISE 1977a, 1978, 1979). Predation causing high mortality in early benthic stages of macrobenthos obviously has tremendous effect on final population size and distribution, provided mortality at later stages is low. This is the case in many bivalves and larger polychaetes which contribute the bulk of benthic biomass in the wadden sea.

Predation by *C. maenas* certainly effects the entire benthos considerably. Microfauna and juvenile macrofauna suffer heavy predation by O-group crabs from mid-July to September. However, PAINE's term "keystone species" probably does not apply to the shore crab because other predators, shrimp (*Crangon crangon*), gobiid fish (*Pomatoschistus microps*), plaice (*Pleuronectes platessa*) and various shore birds largely overlap with the crab's prey spectrum. All of these are general predators and their rank of importance will vary regionally and from year to year. Nevertheless, the highly variable success in O-group development of *C. maenas* between years is likely to have pronounced effects on the survival of other zoobenthos of the wadden sea.

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