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Predator exclusion experiments in an intertidal mud flat

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ABSTRACT: The intensity of predation pressure exerted on the macrofauna in muddy sediments was investigated in Königshafen (island of Sylt, eastern North Sea). Tests in aquaria revealed shrimp *Crangon crangon*, juveniles of the shore crab *Carcinus maenas*, and gobiid fish *Pomatoschistus microps* as the most important local predators. Their high abundance from July to September led to the hypothesis, that predation pressure on the infauna will be most intense during that period. Cages were set up to protect the infauna against these predators. No protective effect was achieved with cages constructed of 20-mm mesh nylon net; however, cages with screen wire and gauze of 5-mm mesh and smaller resulted in a considerable increase of the infauna. In cages of 1-mm mesh gauze, set up from March to June, the macrofauna reached an abundance of four times the control density. In the period from July to October, the factor of increase was as high as 23. Species density was 28 400 cm^{-2}, as compared with only 7 in the control. Species which colonized the mud flat during spring and early summer established dense settlements inside the cages, but failed to do so in uncaged mud-flat areas. It is concluded that predation by young crabs, shrimp and gobies determines to a large extent the structure and dynamics in the local intertidal macrofauna.

INTRODUCTION

Research on biological interactions as determinant of species abundance patterns has become a thriving branch in marine ecology. Predation, an essential component of biological interactions, has been evaluated under field conditions by three basic experimental procedures: (a) removal of predators, (b) introduction of predators, and (c) transplantation of prey organisms into areas of varying predator abundance.

In the present study, predators are separated from their prey by using exclosures. This technique has turned out to be very successful in demonstrating the role of predation in the rocky intertidal zone (Connell, 1970; Dayton, 1971; Paine, 1974). For intertidal soft-sediment environments, however, no predator-exclusion experiments have been reported. These field experiments should be regarded as disturbances of interrelationships among co-occurring organisms (Goodman, 1975); nevertheless, the resulting initial changes in abundance and species number of potential prey provide a rough estimate of the eliminated predation pressure.

In an intertidal mud flat in Königshafen, a sheltered bay of the island Sylt (German Bight), predators – feeding on the macrofauna when the tide is in – were excluded from small plots for intervals of three months. The resulting changes in macrofaunal composition were recorded.

MATERIALS AND METHODS

Close to the low-water mark, mussel beds covered with *Fucus* species occur in discrete patches, allowing the accumulation of soft, fine silt and clay on the flats between the banks. These sediments are exposed for only 2 h during low tide and remain water-saturated. By virtue of their sheltered position the mud flats are not subject to disturbance by gales.

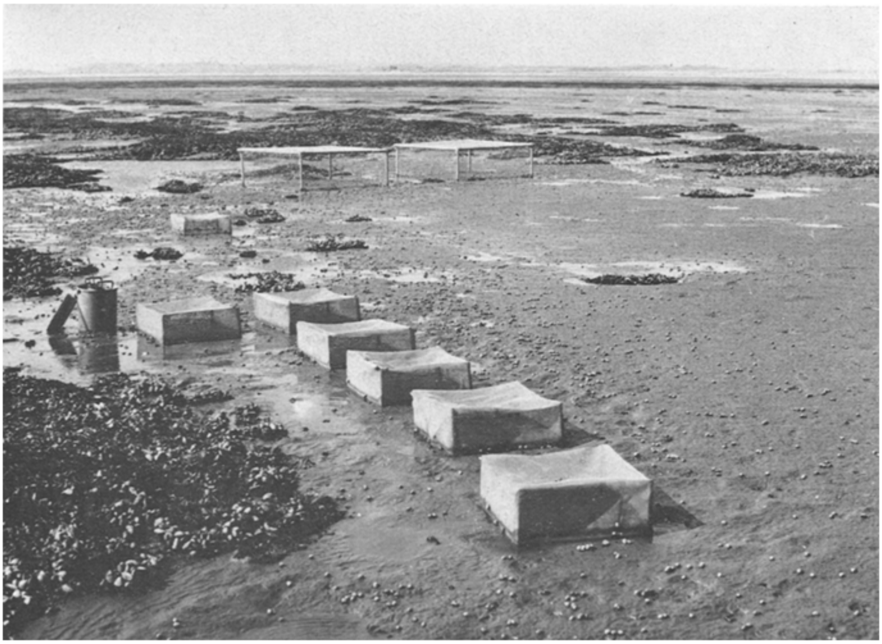

Fig. 1: Mud flat in Königshafen (Island Sylt) with predator exclosures

Samples were collected by pushing a 100-cm^2 steel frame 20 cm into the sediment. The sediment core was divided into fractions of 0–2, 2–5 and 5–20 cm depth. Organisms were extracted with sieves of 0.25, 0.5 and 1.0-mm mesh size, respectively. The sieve contents were washed in white dishes, where all animals collected were sorted while still alive. Cages were used to exclude predators (Fig. 1). They were constructed of 0.5, 1, 2, 5 and 20-mm mesh gauze, screen wire and nylon net attached to iron rods or a tubular steel frame. The cages of up to 5-mm mesh covered an area of 0.25 m^2. They were 15 cm high and penetrated 10 cm into the mud. Cages with 20-mm mesh covered 2.25 m^2. Clogging of gauze was prevented by introducing 20 periwinkles *Littorina littorea* into each cage, which removed all diatoms and other settling algae by grazing preferably on the gauze. Eight samples were taken from each cage to estimate the abundance and species composition of the macrofauna. Four were processed as described above, the others were "puddled" through a 1-mm sieve on site, in order to obtain further counts on the larger animals. In the comparison of abundances, the test on homogeneity developed by Kolmogoroff & Smirnoff was applied (Sachs, 1969).

RESULTS

Three species are particularly abundant among the infauna of the mud flat: the oligochaete *Peloscolex benedeni* (D'Udekem) and the capitellid *Heteromastus filiformis* (Clap.), both being subsurface deposit feeders, and the spionid *Pygospio elegans* Clap., which lives in a tube and feeds on the sediment-water interface. The total abundance is highest in summer, followed by a minimum in autumn. The same applies

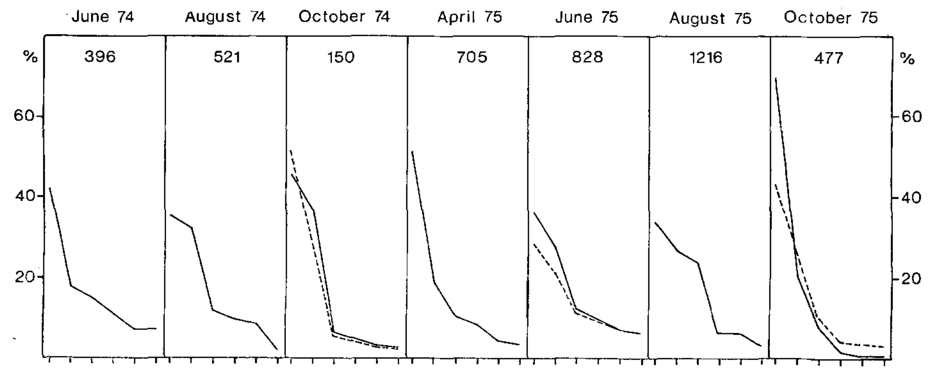

Fig. 2: Dominance-curves for the macrofauna of an intertidal mud flat from sampling periods between June 1974 and October 1975. Only the 6 most abundant species at each period are represented. The percentage of the total macrofauna is given on the ordinate, the species sequence on the abcissa. The total numbers of individuals 400 cm^{-2} are listed in the top. Dominance-curves for caged areas after a period of 3 months are added as broken lines

to the number of species. The maximum in early summer is caused to a large extent by settling juveniles. This species-rich assemblage of juveniles decreases rapidly with the approach of autumn and is replaced by a monotone *Peloscolex-Heteromastus* association. This phenomenon is demonstrated by simple dominance-curves in Figure 2.

The scattered mussel beds give shelter to numerous shore crabs *Carcinus maenas* (L.) and gammarids (two species) which make feeding trips to the mud flats when the tide is in. Shrimp *Crangon crangon* (L.), gobiid fish *Pomatoschistus microps* (Kröyer) and mysids *Praunus flexuosus* Müll. move in with the tide and stay in the sublittoral zone or in little streamlets during low tide. Three of these species, *C. maenas, C. crangon* and *P. microps,* were identified as predators (Fig. 3). In aquaria, they significantly reduced the macrofauna offered to them in the natural sediment. Their presence on the mud flat during the course of a year is shown in Figure 4. An important event is the first arrival of settling young shore crabs (i.e. 13. VII. 1974 and 2. VII. 1975).

In July, I found up to two juveniles 10 cm^{-2}. As judged from the combined presence of all three predators mentioned above, the expected period of most intense predation will be from July to September.

To test this hypothesis, predators were excluded with 1-mm mesh cages, which were placed on the mud flat from June 13 to October 9, 1974 (117 days), March 31 to June 20, 1975 (81 days), and July 1 to October 11, 1975 (103 days).

Table 1

Abundances and species number of macrofauna within 400 cm^2 of caged and uncaged areas in an intertidal mud flat after intervals of three months

Species	June/Oct. 74		March/June 75		July/Oct. 75	
	uncaged	caged	uncaged	caged	uncaged	caged
Macrofauna (total)	150	3459	828	3332	477	4937
Cerastoderma edule (L.) (spat)	2	189	20	307	3	513
Peloscolex benedeni (D'Udekem)	65	1792	180	373	328	1222
Tharyx marioni (Saint-Joseph)	9	889	63	203	3	2129
Pygospio elegans Clap.	1	157	237	706	7	140
Polydora sp.	—	71	15	104	—	213
Macoma baltica L. (spat)	1	5	28	939	—	2
Scoloplos armiger (Müll.)	—	1	22	206	—	1
Capitella capitata (Fabr.)	7	32	41	222	37	56
Heteromastus filiformis (Cl.)	52	45	47	25	96	89
Number of species	12	22	21	25	7	28

Striking differences in the macrofauna between the caged and uncaged areas resulted after each interval (Table 1). In October 1974 and 75, the total abundance was higher within the exclosures by factors of 23.1 and 10.4, respectively. In June 1975, the factor was only 4.0. During the summer, when the overall abundance in the mud flat is high, the fauna is little altered by the cages. Whereas in autumn, when the unprotected fauna is reduced considerably, the difference in abundance is enormous. The annelids *Peloscolex benedeni, Tharyx marioni, Pygospio elegans, Polydora* sp., and many other species, as well as spat of the cockle *Cerastoderma edule,* confirm this general result. In addition, *P. benedeni* and *T. marioni* show only a slight increase in the summer cage, but increase tremendously in the autumn cages. In the case of *T. marioni* there is an increase of 710 times the normal density!

A few species do not show these tendencies. There is no change from summer to autumn, but the populations increase sharply from spring to summer. *Macoma baltica* and *Scoloplos armiger* reproduce only in the spring, thus they can not invade the autumn cages. No explanation can be given for the varying responses of *Capitella capitata* to the presence of cages. The only species which showed no increase within the exclosures is the deep dwelling *Heteromastus filiformis.* Apparently this capitellid remains unaffected by such predators as crabs, shrimp and small fish.

The increase in species number during spring and summer in the mud flat is only slightly intensified by protecting cages. However, from summer to autumn this high species number is preserved within the cages, while in the surrounding mud flat a sharp decline occurs in late summer. As a result, one cage contained in autumn 4 times the uncaged species density. The species rich assemblage during early summer is caused by settling juveniles of species, the adults of which do not occur in the mud flat area. These juveniles established dense settlements when protected by cages. Among them are the polychaetes *Scoloplos armiger*, *Arenicola marina* (L.), *Lanice conchilega* (Pal-

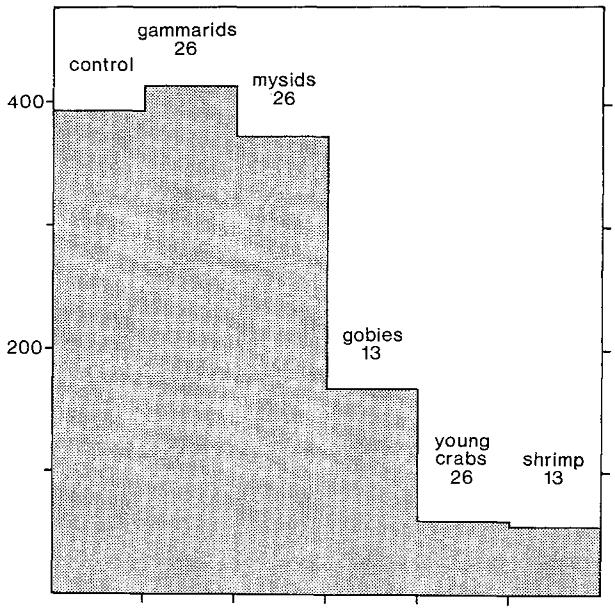

Fig. 3: Test on predation: sediment samples obtained from a mud-flat area were placed in aquaria. For periods of 3 days, test-species were allowed to prey on the infauna. The quantity of surviving macrofauna (indiv. 200 cm^{-2}) is shown

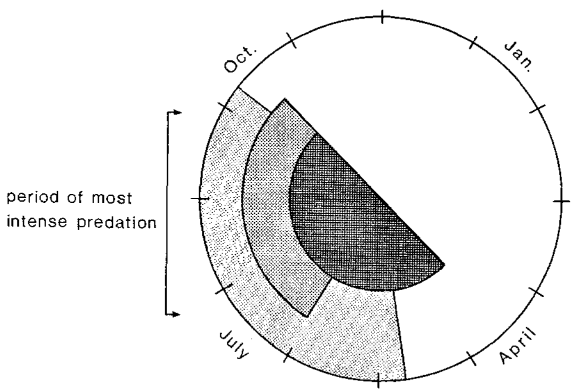

Fig. 4: Presence of *Carcinus maenas*, *Crangon crangon* and *Pomatoschistus microps* in the mud-flat area of Königshafen (Island Sylt) in 1975. Light shade: shrimp and gobiid fish, intermediate shade: young crabs (first arrival at 2–7–75) heavy shade: older crabs

las), *Spio filicornis* (Müll.) and others. Spat from bivalves matured in the cages, whereas the adults do not occur in the intertidal zone, but are restricted to the sublittoral. Examples of this are *Spisula subtruncata* Da Costa, *Mactra corallina* Montagu, *Venerupis pullastra* Montagu and *Abra alba* (Wood).

Despite these apparent changes in abundance and species number, diversity indices (i.e. Shannon index) based on numbers of individuals and species failed to show any significant increase. This is also demonstrated by the broken lines in Figure 2. However, although diversity and diversity-trends indicate no particular difference between the fauna under predation-free conditions and that of the untouched mud flat, the composition of the assemblage did change considerably. For example, when the six most abundant species in each interval are ranked according to their relative individual numbers, positions are altered almost entirely (Table 2). These changes are partially due to the fact that young bivalves, which play no role in the unprotected mud flat, join the higher ranks. In addition, species feeding on the sediment-water interface increase in the cages relative to the deeper dwelling species.

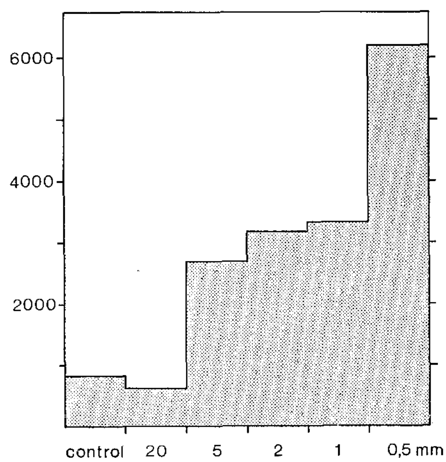

Fig. 5: Total macrofauna abundance (indiv. 400 cm^{-2}) within the uncaged area and in those caged with 20, 5, 2, 1 and 0.5 mm mesh net, screen wire and gauze respectively, after about three months (April to July 1975)

A sequence of cages with 0.5, 1, 2, 5 and 20-mm mesh were set up to find out which size range of predators had the greatest influence (Fig. 5). No protection was achieved with the 20-mm net; 5 mm and smaller, however, caused conspicuous changes in the infauna; 0.5-mm gauze, apparently, was attractive to tube-building polychaetes and some bivalve spat (i.e. *Mytilus edulis* L., *Mya arenaria* L.) and trapped young mud snails [*Hydrobia ulvae* (Pen.)]. From this and the other experiments outlined above, it becomes evident that young shore crabs, shrimp and gobies are responsible for major changes in the composition of the mud flat macrofauna. Birds and large fish in turn seem to be negligible.

Table 2

Ranks of the six most abundant species of the infauna within uncaged (U) and caged (C) areas of an intertidal mud flat after intervals of about three months

October 1974	U	C	June 1975	U	C	October 1975	U	C
Peloscolex benedini	1	1	*Pygospio elegans*	1	2	*Peloscolex benedeni*	1	2
Heteromastus filiformis	2		*Peloscolex benedini*	2	3	*Heteromastus filiformis*	2	
Tharyx marioni	3	2	*Hydrobia ulvae*	3		*Capitella capitata*	3	
Capitella capitata	4		*Tharyx marioni*	4		*Pygospio elegans*	4	
Cerastoderma edule	5	3	*Heteromastus filiformis*	5		*Tharyx marioni*	5	1
Microphthalmus sp.	6	5	*Capitella capitata*	6	5	*Cerastoderma edule*	6	3
Pygospio elegans		4	*Macoma baltica*		1	*Polydora sp.*		4
Abra alba		6	*Cerastoderma edule*		4	*Corophium volutator*		5
			Scoloplos armiger		6	*Malococeros fuliginosus*		6

DISCUSSION

The protective effects of the exclosures are very remarkable, and the resulting densities of up to 12 individuals cm^{-2} are unparalleled for the macrofauna in soft sediment environments. Whereas the increase in abundance and species number is certainly due to a lack of predation within the cages, it is likely that the relative proportions of the species to one another are influenced by competition. Because almost all species increased in individual numbers, when protected by an exclosure, competition was probably not very important in the initial phase of faunal change. Predatory species of the infauna became more abundant within the cages as well. However, they apparently had no distinct effect on the overall change in abundance of the remaining infauna. Both, the co-occurrence of relatively large numbers of young crabs, shrimp and gobies, and the sharp decline of infaunal species abundance from July to September – at which time the highest relative increase within the exclosures was observed – indicate that the overall abundance pattern of the mud flat community can be attributed to the influence of predators. Even the species composition is altered under predation-free conditions. Nevertheless, diversity indices and dominance-curves show no apparent differences between protected and unprotected infauna. Either this is an inherent feature of possible community structures in this mud flat or, in this context, these measurements are simply useless.

These short-term exclusion experiments showed that predation pressure determines, to a large extent, the structure and dynamics of the macrofaunal assemblage in this intertidal mud flat. This is in contrast to hitherto expressed views (Dörjes, 1970; Eltringham, 1971; Woodin, 1974), assuming predation to be of minor importance or considering shore birds to be the most important predators on intertidal flats. Sanders' (1968) hypothesis that intertidal communities are physically controlled is too general in its scope and a more restricted form, stressing biological interactions, ought to be formulated. In general, these results are well in line with the concept of community interactions on marine rocky intertidal shores as proposed by Connell (1972). It is concluded that the structure and dynamics in this intertidal macrofauna community are, to a large extent, determined by predation pressure.

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LITERATURE CITED

Connell, J. H., 1970. A predator-prey-system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol. Monogr. **40**, 49–78.

— 1972. Community interactions on marine rocky intertidal shores. Ann. Rev. Ecol. Syst. **3**, 169–192.

Dayton, P. K., 1971. Competition, disturbance and community organisation: the provision and subsequent utilisation of space in a rocky intertidal community. Ecol. Monogr. **41**, 351–389.

Dörjes, J., 1970. Das Watt als Lebensraum. In: Das Watt, Ed. by H. R. Reineck. Senckenberg, Frankfurt, 71–105.
Eltringham, S. K., 1971. Life in mud and sand. Crane, Russak & Comp., New York, 218 pp.
Goodman, D., 1975. The theory of diversity-stability relationships in ecology. Q. Rev. Biol. **50**, 237–266.
Paine, R. T., 1974. Intertidal community structure. Oecologia **15**, 93–120.
Sachs, L., 1969. Statistische Auswertungsmethoden. Springer, Berlin, 677 pp.
Sanders, H. L., 1968. Marine benthic diversity: a comparative study. Am. Nat. **102**, 243–282.
Woodin, S. A., 1974. Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. Ecol. Monogr. **44**, 171–187.

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