The presence of the bivalve *Cerastoderma edule* affects migration, survival and reproduction of the amphipod *Corophium volutator*

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ABSTRACT: An amensalistic interaction between the common cockle *Cerastoderma edule* (L.) and the amphipod *Corophium volutator* (Pallas) is reported. *C. edule* may attain very high densities in soft-bottom localities. In an intertidal flat in the Danish Wadden Sea densities (1 yr cockles) of about 3500 ind m⁻² were observed. The area fraction occupied by the cockles gives a better indication of their potential impact on coexisting species. Thus, a population in the outer part of the intertidal flat was found to cover 30 to 40 % of the area. Previous observations had indicated that high densities of cockles negatively affect *C. volutator*. Laboratory and field enclosure experiments demonstrate an amensalistic effect by the suspension-feeder *C. edule* on the deposit-feeder *C. volutator*. In *C. volutator* migration rate increases, and survival, growth and reproduction decrease with increasing density of *C. edule*. It is suggested that these effects are caused by the burrowing and ploughing habits of cockles, which inhabit the same upper 3 to 4 cm of sediment as *C. volutator*. Consequences for the distribution of *C. volutator* are discussed. In field experiments, recruitment of the deposit feeding bivalve *Macoma balthica* (L.) was also found to be negatively dependent on area occupied by cockles.

INTRODUCTION

Patterns of distribution and abundance of marine benthic animals have been correlated with various abiotic variables. Recently, however, field and laboratory experiments have emphasized the role of biotic interactions on the distribution of species and on community structure: predation (Paine 1966, Virnstein 1977, Reise 1978, Peterson 1979, Commiato 1982, Kneib & Stiven 1982, Summerson & Peterson 1984), competition (Connell 1961, Underwood 1978, Dayton & Oliver 1980, Schoener 1983) and functional group amensalism (Rhoads & Young 1970, Woodin 1974, 1976, Brenchley 1981, Wilson 1981) have been suggested as important mechanisms.

Hypotheses like the 'trophic group amensalism hypothesis' and later refinements based on interactions between various functional groups (i.e. groups of species which use or alter the environment in a similar way: Weinberg 1984) appear, however, to be too general for predicting association of species in nature (Weinberg 1984). Nevertheless, many biological interactions may be mediated through effects of organisms on the substrate (Brenchley 1981, Wilson 1981,

Probert 1984, Weinberg 1984). Sediment processing by animals includes burrowing, ingestion/defecation, tube-building and biodeposition (Myers 1977a, b).

The Dutch-German-Danish Wadden Sea is characterized by high densities of sediment-reworking species (burrowing polychaetes and bivalves), but the importance of biotic interactions on species distribution has been analysed experimentally only in a few cases (Reise 1978, 1983a, b, Jensen & Jensen in press); however amensalistic interactions may be supposed to be an important mechanism affecting the distribution of species.

Early observations in an intertidal flat in the northern part of the Danish Wadden Sea have indicated that the common cockle *Cerastoderma edule* may influence the distribution of the burrowing amphipod *Corophium volutator* (Thamdrup 1935). After a severe winter causing local extinction of *C. edule*, *C. volutator* spread to areas where it previously had been found only occasionally (Thamdrup 1935). Since cockles often occur in high densities (Dankers & Beukema 1981, Verwey 1981, Møller & Rosenberg 1983, Jensen & Jensen in press), they may be expected to disturb species living in the upper sediment layer due to their

burrowing and ploughing habits. Such an amensalistic interaction between *C. edule* and *C. volutator* may contribute to an understanding of the distribution of *C. volutator*. This possibility is examined in the present study. Over 2 yr a cockle population in the Danish Wadden Sea was studied with respect to density, size distribution and area fraction covered. Laboratory and field experiments were performed to test if *C. edule* could influence migration, survival and reproduction of *C. volutator*.

MATERIALS AND METHODS

Area of *Cerastoderma edule*. Surface area covered by cockles positioned in their usual way in the upper sediment layer with the posterior end upwards and the anterior end downwards were estimated by photographing 35 individuals from their posterior ends. The photographs of the cockles were cut and weighed. A linear regression analysis of area *versus* height of the photographed cockles was performed.

Laboratory experiments. Laboratory experiments were performed at The Netherlands Institute of Sea Research, Texel. Aquaria with a surface area of about 1200 cm² containing sediment (muddy sand sieved through a 1 mm mesh) were separated into 2 sections by a low partition which restricted the cockles to 1 compartment, but allowed *Corophium volutator* to swim freely between both compartments. The preference of *C. volutator* for compartments with various cockle densities was then studied. I used cockle densities of 0, 0.25, 0.50, 1.0 and 2.0 times the natural density (4000 m⁻² for 1 yr old cockles). Mean length and area of the 1 yr cockles were 14.1 mm and 0.82 cm²

respectively. Control cockles were prepared by substituting their flesh with clay and then gluing the shells again. Individuals of *C. volutator* were introduced into the aquaria at a density of 0.8 adult individuals cm⁻² corresponding to 8000 ind m⁻² (mean length 6.6 mm). These experiments were terminated after 3 d. Survival experiments were performed in aquaria with a surface area of 600 cm². *C. volutator* was introduced into aquaria either with natural densities of cockles or without cockles. These experiments lasted for 3 wk. All aquaria were continuously supplied with fresh seawater (33 ‰, 13 °C). Densities of *C. volutator* at the end of the experiments were estimated by random sampling with PVC cores with an area of 9.2 cm². In the survival experiments, numbers of females of *C. volutator* with and without eggs were also counted.

Field experiments. Field experiments were performed in an intertidal flat on the east coast of Skallingen in the northern part of the Danish Wadden Sea. The tidal amplitude is about 1.6 m and the distance between mean high water line and mean low water line in the experimental area is about 400 m. PVC cores with diameter 12.6 cm (area 125 cm²) and height 20 cm were closed with a 10 cm upper part made of 1 mm mesh net and were used in an enclosure experiment. The cores were placed in the sediment with the upper part extending above the surface at a position about 200 m from the high water line. The sediment inside the cages had been sieved through a 0.5 mm mesh sieve to remove larger animals. The sediment has a mean grain size of 0.165 mm and is characterized as muddy sand (Jacobsen 1967). The natural density of *Cerastoderma edule* at the experimental position was 3000 ind m⁻² of 2 yr old cockles

Fig. 1. *Cerastoderma edule*. (a) Relation between height and area as estimated from photographs. (b) Relation between length and height of specimens from Skallingen, the northern part of the Danish Wadden Sea

Fig. 2. *Cerastoderma edule*. Annual variation in density and area fraction covered by a population at Skallingen

with mean length 14.25 mm. Densities of cockles in the cages of 0, 0.25, 0.5, 1.0 and 2.0 times natural density was used. Control cockles were prepared as described above. Adult *Corophium volutator* (mean length 7.2 mm) were added at a density of 0.8 ind cm^{-2} in each cage. The cages were placed in the flat from May 14 to June 5, 1984. At the end of the experiment, the content of each cage was sieved (0.5 mm mesh). All animals including newly settled species were preserved in 4% formaldehyde and counted in the laboratory. The cock-

les were measured and the numbers of male and female *C. volutator* were noted. Dry weight and ash-free dry weight of *C. volutator* males from different cages were also determined.

Statistical treatment. Spearman's rank correlation test was used for analysis of correlations (Siegel 1956). For regression analysis and for a 2-way analysis of variance (ANOVA), SPSS programme was applied. Numbers of individuals were $\log(n+1)$ transformed to normalize the distribution. Regression analyses were used to test the dependence of survival, recruitment, and percentage of pregnant female *Corophium volutator* on area of *Cerastoderma edule*. Two-way ANOVA was used to test the effect of area of cockles and length of male *C. volutator* on dry weight of the males in the cage experiments.

RESULTS

Area fraction covered by *Cerastoderma edule*

Regression of area versus height (Fig. 1a) and height versus length (Fig. 1b) of *Cerastoderma edule* were used for predicting areas in the sediment covered by cockles from either their length or height. The annual variation in density and area fraction by a natural population of cockles inhabiting the intertidal area on the east coast of Skallingen is shown in Fig. 2. As only 1 age class of cockles was present in this period the increase in coverage was due to growth. At this par-

Fig. 3. *Corophium volutator*. Relative density in aquarium compartments as a function of density of *Cerastoderma edule*. The density of *C. volutator* is given relative to the mean numbers per core in the inflow compartment of each experiment (normalized to 100). Bars indicate 95 % confidence limits (the distribution of *C. volutator* was random). Density of *C. edule* is given relative to a natural density of 4000 m^{-2} . C: control cockles

Fig. 4. *Corophium volutator*. (a) Difference in mean numbers between inflow and outflow compartments as a function of density of *Cerastoderma edule*. r_s : Spearman rank correlation coefficient. (b) As (a) for females only. (c) As (a) for males only

ticular station, the area fraction occupied by cockles amounted to about 30 % (1 yr old cockles). However, the area fraction of the cockles increased with inundation time. Thus, the area fraction of cockles at a station closer to the low water line amounted to 40 %.

Laboratory experiments

When *Corophium volutator* were introduced into aquaria without cockles they showed a preference for the outflow compartments (Fig. 3), indicating that a factor correlated with the water flow direction affected

their distribution. For this reason, the cockles were placed in the outflow compartment in each experiment to standardize the effect of water flow. When increasing densities of cockles occurred in the outflow compartments, the preference of *C. volutator* for the outflow compartments was reduced (Fig. 3). The difference in mean density of *C. volutator* in the inflow and outflow compartments correlated with cockle density ($p < 0.01$ according to Spearman rank correlation test, Fig. 4a.). An analysis of sex composition of *C. volutator* in the compartments revealed, however, that only males were significantly influenced by the cockles ($p < 0.01$, Fig. 4b, 4c). Males were moreover found to be over-represented among swimming individuals, compared to the sex composition in the aquaria (Fig. 5). Specimens were picked at random and no attempt to manipulate the sex ratio was made. This behavioural difference between males and females may have caused the differential effect of cockles on the 2 sexes. Whether the effect of the cockles was a result of their ploughing activity or rather of sediment crowding was tested with the control cockles (Fig. 3). In these experiments the preference of *C. volutator* was similar to that observed in aquaria without cockles. This favours the

Fig. 5. *Corophium volutator*. Sex composition of swimmers as a function of percentage of males in each aquarium. The straight line indicates expected sex composition of the swimmers on the basis of sex composition in each aquarium

hypothesis that it was the activity and not the passive occurrence of the cockles that was responsible for the short-term effect on *C. volutator*. Other experiments were carried out to study whether cockles could influence survival and reproduction of *C. volutator* during a 3 wk period. A significantly negative effect of a natural density of cockles on survival of *C. volutator* was found (Table 1). Moreover, a higher percentage of females *C. volutator* carried eggs in the aquaria without cockles compared to aquaria with cockles. At the start of the experiments only 2.7 % of the females carried eggs.

Table 1. Effect of *Cerastoderma edule* (Ce) on survival and reproduction of *Corophium volutator* (Cv) after 3 wk. Area: area fraction covered by *C. edule*; x: mean number 9.2 cm⁻²; cl: 95 % confidence limits; N: population size in aquarium; n: numbers of individuals. Initial density of *C. volutator* was 8000 m⁻² in each aquarium

Experiment	Area	x ± cl	Number swimming	N (cl)	Survival (%)	<i>C. volutator</i> females with eggs (%)
0 Ce + 510 Cv	0	5.25 ± 1.32	38	398 (308–490)	78.0	18.7 (n = 91)
0 Ce + 520 Cv	0	5.3 ± 1.46	44	414 (312–516)	79.6	21.1 (n = 95)
250 Ce + 500 Cv	33 %	2.83 ± 0.97	4	194 (129–259)	38.8	13.8 (n = 58)
250 Ce + 500 Cv	29 %	2.67 ± 0.94	29	209 (146–273)	41.8	6.3 (n = 64)

Table 2. Numbers (mean ± SE) 125 cm⁻² of benthic animals from different experimental treatments at the end of a 3 wk experiment (May 14 to June 5, 1984). ND: natural density of *Cerastoderma edule* (3000 m⁻²); control = 1 × ND of cockle shells containing clay

	0 ND n = 3	¼ ND n = 3	½ ND n = 3	1 ND n = 4	2 ND n = 3	Control n = 2
Oligochaeta						
<i>Tubificoides benedeni</i>	16.7 ± 8.7	8.3 ± 1.2	5.3 ± 2.7	7.8 ± 4.3	15.7 ± 7.4	11.0 ± 2.5
<i>Tubifex costatus</i>	3.7 ± 1.7	2.0 ± 1.2	2.0 ± 0.6	1.3 ± 0.8	1.7 ± 0.9	1.0 ± 0
Polychaeta						
<i>Capitella capitata</i>	17.3 ± 7.8	10.3 ± 2.2	24.0 ± 7.5	12.3 ± 4.3	11.7 ± 3.5	16.5 ± 1.3
<i>Arenicola marina</i>	0	0.3 ± 0.3	0	0	0	0
<i>Eteone longa</i>	0.3 ± 0.3	0.3 ± 0.3	0.3 ± 0.3	0.3 ± 0.3	0	0
<i>Heteromastus filiformis</i>	5.0 ± 0.5	3.3 ± 0.7	3.7 ± 1.2	8.5 ± 1.9	5.7 ± 1.5	9.0 ± 0
<i>Polydora ligni</i>	0.7 ± 0.3	0.3 ± 0.3	0.3 ± 0.3	0	0	0
<i>Manayunkia aesturina</i>	0	1.0 ± 0.3	0	0	0	0
<i>Nephtys hombergi</i>	0	0	0	0	1.0 ± 0.3	0
<i>Nereis diversicolor</i>	33.3 ± 3.7	64.0 ± 7.4	85.7 ± 5.3	61.5 ± 11.9	45.0 ± 10.9	61.5 ± 12.0
<i>Phyllodoce maculata</i>	0	1.0 ± 0.3	0	0	0	0
<i>Pygospio elegans</i>	12.3 ± 1.2	13.3 ± 3.3	25.7 ± 4.8	10.5 ± 3.5	4.7 ± 1.5	8.0 ± 7.0
<i>Tharyx marioni</i>	13.0 ± 3.2	6.0 ± 2.5	7.3 ± 2.6	5.8 ± 2.3	8.0 ± 3.6	4.5 ± 3.5
<i>Scoloplos armiger</i>	7.7 ± 3.0	10.0 ± 2.3	11.7 ± 5.7	6.0 ± 0.9	7.3 ± 3.5	7.0 ± 1.8
<i>Laniche conchilega</i>	0.3 ± 0.3	0.7 ± 0.7	0.3 ± 0.3	0.3 ± 0.3	0	1.0 ± 1.0
<i>Polynoidae</i> sp.	0	0	0	0.3 ± 0.3	0	0
Gastropoda						
<i>Hydrobia ulvae</i>	0.3 ± 0.3	1.3 ± 0.3	1.7 ± 0.9	0.5 ± 0.3	1.0 ± 0.6	0.5 ± 0.5
<i>Retusa obtusa</i>	6.0 ± 0.6	1.0 ± 0.6	3.7 ± 0.7	2.5 ± 1.3	2.0 ± 2.0	2.0 ± 1.0
Bivalvia						
<i>Cerastoderma edule</i>	0	10	19	37	75	40
<i>Macoma balthica</i>	20.3 ± 6.4	16.3 ± 1.5	7.7 ± 3.3	7.0 ± 2.9	4.7 ± 1.5	15.0 ± 13.0
<i>Mytilus edulis</i>	0.3 ± 0.3	0	0	0	0	0
Crustacea						
<i>Corophium volutator</i>	330.3 ± 41.7	334.0 ± 26.3	286.0 ± 68.7	271.8 ± 30.0	170.7 ± 26.2	328.0 ± 19.0
<i>Gammarus</i> sp.	3.3 ± 1.9	0.3 ± 0.3	1.7 ± 0.7	2.5 ± 0.7	3.7 ± 1.7	6.0 ± 5
<i>Iaera</i> sp.	0.7 ± 0.7	0.3 ± 0.3	2.0 ± 0.6	0.5 ± 0.3	0.3 ± 0.3	0.5 ± 0.5

The cockles covered about 30 % of the surface area in these experiments (Table 1).

Field experiments

Results of enclosure experiments with a constant number of *Corophium volutator* (adults) but with different densities of cockles are given in Table 2. During

the 3 wk several species settled in the cages. Two cages (experiments with 0.5 times natural density of cockles) were excluded from the analysis, because they were found to open too widely between the upper part of the cages and the PVC core to keep adult *C. volutator* inside. The enclosure experiments demonstrated that the survival of *C. volutator* was related to the presence of cockles ($p=0.003$, Fig. 6). Juvenile *C. volutator* probably hatched inside the cages since 44 %

Fig. 6. *Corophium volutator*. Survival of adults as a function of area of *Cerastoderma edule* (cage experiments), $r^2 = 0.33$, $p = 0.034$

Fig. 7. *Corophium volutator*. Numbers of juveniles as a function of area of *Cerastoderma edule* (cage experiments), $r^2 = 0.58$, $p = 0.001$

Fig. 8. *Corophium volutator*. Percentage of females with eggs as a function of area of *Cerastoderma edule* (cage experiments), $r^2 = 0.33$, $p = 0.032$

of the females sampled on May 14 carried eggs. The number of juveniles correlated negatively to the area occupied of cockles ($p=0.001$, Fig. 7). Also, the percentage of females with eggs was found to decrease with the area of cockles (Fig. 8).

Among other settled species in the enclosures only the numbers of *Macoma balthica* were related to the area of the cockles ($p=0.007$, Fig. 9). This was probably due to inhalation of settling *M. balthica* larvae by the cockles.

Fig. 9. *Macoma balthica*. Numbers of juveniles as a function of area of *Cerastoderma edule* (cage experiments), $r^2 = 0.41$, $p = 0.007$

Fig. 10. *Corophium volutator*. Weight of males as a function of length and experiment. (●) cages without *Cerastoderma edule*; (□) cages with $2 \times \text{ND}$ of *C. edule*

Length and ash-free dry weight of *Corophium volutator* males from enclosures without and with 2 times the natural density of cockles were compared. A 2-way analysis of variance (ANOVA) of the male weight as a dependent variable, and length and experimental type as independent variables, showed a dependence on both variables (length: $p=0.001$; experiment:

Table 3. Two-way ANOVA of ash-free dry-weight of *Corophium volutator* from cages with 0 $\times$ ND and 2 $\times$ ND of *Cerastoderma edule*; df: degrees of freedom; ms: mean square; ND: natural density

Source	df	ms	F	P
Length	2	3.210	32.209	0.001
Experiment	2	1.710	17.153	0.001
Interaction	2	0.30	0.298	0.743
Residual	104	0.1		

$p=0.002$; Fig. 10, Table 3). This result indicates that cockles have a negative impact on the growth of *C. volutator*.

DISCUSSION

The population of *Cerastoderma edule* studied in the intertidal flat in the Danish Wadden Sea was established in 1982. While cockles had been reported previously from this flat (Thamdrup 1935, Smidt 1951, Jensen 1980), they were totally absent when my sampling started in spring 1982. The preceeding unusually cold winter (ice winter) is presumed to have caused their local extinction (see also Thamdrup 1935, Smidt 1951, Kristensen 1957, Verwey 1981, Möller & Rosenberg 1983). Densities of juvenile cockles observed in July 1982 were among the highest recorded ever. A rapid decline during August was caused by juvenile *Carcinus maenas* (L.). Due to rapid growth, the cockles reached a size refuge from *C. maenas* predation by the end of September (Jensen & Jensen in press). While cockle density remained almost unchanged until at least 1 yr later, their area fraction increased from August onwards. Rather than density, the area fraction of cockles may be an indicator of their significance for other species. Kreger (1940) found a density of 1100 cockles m^{-2} in the Dutch Wadden Sea with a mean length of 35 mm which, translated to area fraction (estimated from Fig. 1a, b), means that they covered about 51 %. Kreger found that these cockles were pressed so tightly against each other that most of the individuals had dented shells.

Populations of cockles are generally found to be dominated by a single age-class. One reason for this may be that adult cockles exert negative impact on settlement of their own larvae (Kristensen 1957, Verwey 1981). Because the field experiments performed in this study were terminated before the onset of settlement of cockle larvae, no intraspecific effect was observed. However, settlement of *Macoma balthica* was affected negatively by the presence of cockles.

In both laboratory and field experiments, *Cerastoderma edule* negatively influenced survival and

reproduction of *Corophium volutator*. In laboratory experiments, *C. volutator* survival in aquaria with a natural cockle density was only 51 % of the survival rate in aquaria without cockles. The corresponding survival rate in the cage experiments was 83 %. Although salinity and temperature differed in laboratory and field experiments, these conditions are not considered important. Cage effects may, however, have induced the differences. A common effect observed in cage experiments is an increase in sedimentation of organic particles (Virnstein 1977, Gray 1981, Eckman 1983). Observations also indicate an increase of deposit feeders inside cages (Gray 1981), probably caused by the increase of food items and augmented settlement due to an effect of the cages on water flow (Eckman 1983). The high survival of *C. volutator* inside the cages may therefore be an effect of increased feeding efficiency. Alternatively, the food conditions may generally be better on the flat than in the laboratory. In both cases the result will be a delay of an effect of cockles on the survival of caged *C. volutator*, compared to survival in aquaria.

The mechanism responsible for the effect of cockles in *Corophium volutator* probably should be sought in the behaviour of the cockles. The cockles inhabit the upper 3 to 4 cm of the sediment. They often change their position (Thamdrup 1935, Smidt 1951, Reise 1983b), and tracks of their movements are visible on the flats at low tide. When moving, the cockles may disturb species inhabiting the upper sediment and destroy tubes and burrows. Reise (1983b) found a negative effect of cockles on *Pygospio elegans* Claparède due to this behaviour of the cockles. *C. volutator* constructs burrows to a depth of about 4 cm, depending on length of the individuals and time of the year. The burrows are very fragile and consequently vulnerable to the cockle activities. This effect is suggested to be responsible for the results of the short-term preference experiments on *C. volutator* in the laboratory. The disturbance reduces the time available for feeding. As a consequence, growth, reproduction and survival is influenced as observed in both field and laboratory experiments.

According to Linke (1939), *Corophium volutator* is found in the marginal areas of the flats. It mainly occurs in the upper part of the intertidal flats nearest the highwater mark or in the inner parts of small and narrow intertidal creeks in the marsh area (Thamdrup 1935, Smidt 1951, Jensen 1980). The distribution of *C. volutator* is independent of inundation time (Linke 1939, Smidt 1951) and sediment type, although it attains particularly high densities in muddy and diatom-rich localities (Gee 1961, Jensen 1980, Dankers & Beukema 1981). Smidt (1951) suggested that *C. volutator* was limited by violent water movements, but

Stopford (1951) found populations along an unsheltered foreshore. Cage experiments, performed by Reise (1978) and in this study, further show that *C. volutator* – at least inside cages – has a potential for surviving in high densities on parts of the flats from which it is normally absent. Thamdrup (1935) ascribed a spread of *C. volutator* to a relaxation of the competition between *C. volutator* and *Cerastoderma edule*, which was decimated during the preceding ice winter. Although amensalistic interaction is a more correct interpretation of the results of the present field and laboratory experiments, this study supports the explanation proposed by Thamdrup (1935). Smidt (1951) suggested that a constant redeposition of bottom material caused by strong water movement was limiting for *C. volutator*. Although he correctly mentioned the negative influence on *C. volutator* of redeposition of bottom material, he failed to recognize that other animals might also have caused a disturbance of the bottom material. The degree of influence on *C. volutator* probably depends on the strength and intensity of sediment reworking.

Observations by Linke (1939) indicate that the lugworm *Arenicola marina* L. may likewise have a negative impact on *Corophium volutator*. Removal of *A. marina* caused the development of a dense diatom mat (Reise 1978). This result suggests that the disturbance of the sediment caused by the activity of *A. marina* also affects *C. volutator*. Localities with high densities of *C. volutator* are often characterized by a very low species diversity (Dankers & Beukema 1981, own obs.). This probably indicates that *C. volutator* is vulnerable to the activities of other species and as a result may be limited to more inferior areas.

In soft bottom communities sediment-reworking organisms may include birds, fishes and various infaunal animals (Dayton & Oliver 1979, Reise 1983a, b, Probert 1984). Effects of bioturbating species include decreased survival and increased migration (Wilson 1981), but also reduced growth, fecundity and foraging time, which all affect population size (Weinberg 1984). However, effects of bioturbators may not exclusively be deleterious for other species. Cases have been observed where bioturbators have promoted coexisting species (Gallagher et al. 1983, Reise 1983a).

The classification of infaunal species into broad ecological categories, such as feeding and mobility types, has been the basis for the hypotheses on functional group amensalism. Feeding types may be relatively well defined, although this is not without exceptions (Probert 1984), but species are difficult to group with respect to mobility, viz. tube-builders may also be mobile (Brenchley 1981). The mobility may vary quantitatively, rendering qualitatively defined groups very crude. Furthermore, bioturbating species do not

rework the sediment in a similar way. The amount of sediment processed may be dependent on both size of organisms and causes of sediment reworking (feeding, burrowing, etc.). Several exceptions to the predictions based on functional group models have indicated the lack of general applicability of these models (Brenchley 1981, Wilson 1981, Weinberg 1984).

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LITERATURE CITED

- Brenchley, G. A. (1981). Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. *J. mar. Res.* 39: 767–790
- Commito, J. A. (1982). Importance of predation by infaunal polychaetes in controlling the structure of a soft-bottom community in Maine, USA. *Mar. Biol.* 68: 77–81
- Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42: 710–723
- Dankers, N., Beukema, J. J. (1981). Distributional patterns of macrozoobenthic species in relation to some environmental factors. In: Dankers, N., Kühl, H., Wolff, W. J. (ed.) *Invertebrates of the Wadden Sea*. A. A. Balkema, Rotterdam, p. 69–103
- Dayton, P. K., Oliver, J. S. (1980). An evaluation of experimental analyses of population and community patterns in benthic marine environments. In: Tenore, K. R., Coull, B. C. (ed.) *Marine benthic dynamics*. South Carolina Press, Columbia, p. 93–120
- Eckman, J. E. (1983). Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.* 28(2): 241–257
- Gallagher, E. D., Jumars, P. A., Trueblood, D. D. (1983). Facilitation of soft-bottom benthic succession by tube builders. *Ecology* 64: 1200–1216
- Gee, J. M. (1961). Ecological studies in South Benfleet Creek with special reference to the amphipod genus *Corophium*. *Essex. Nat.* XX: 291–309
- Gray, J. S. (1981). The ecology of marine sediment. An introduction to the structure and function of benthic communities. Cambridge Univ. Press, Cambridge
- Jacobsen, V. (1967). The feeding of the lugworm, *Arenicola marina* (L.). Quantitative studies. *Ophelia* 4: 91–109
- Jensen, K. T. (1980). Aspekter af *Hydrobia ulvae*'s og *Corophium volutator*'s Økologi i Vadehavet. M. thesis, Department of Ecology and Genetics, Aarhus Univ.
- Jensen, K. T., Jensen, J. N. (in press). The importance of some epibenthic predators on the density of juvenile macrofauna in the Danish Wadden Sea. *J. exp. mar. Biol. Ecol.*

- Kneib, R. T., Stiven, A. E. (1982). Benthic invertebrate responses to size and density manipulations of the common mummichog, *Fundulus heteroclitus*, in an intertidal salt marsh. *Ecology* 63: 1518–1532
- Kreger, D. (1940). On the ecology of *Cardium edule* L. *Archs néerl. Zool.* 4: 157–200
- Kristensen, I. (1957). Differences in density and growth in a cockle population in the Dutch Wadden Sea. *Archs néerl. Zool.* 12(3): 351–453.
- Linke, O. (1939). Die Biota des Jadebusenwattes. *Helgoländer wiss. Meeresunters.* 1: 201–348
- Möller, P., Rosenberg, R. (1983). Recruitment, abundance and production of *Mya arenaria* and *Cardium edule* in marine shallow waters, Western Sweden. *Ophelia* 22(1): 33–55
- Myers, A. C. (1977a). Sediment processing in a marine subtidal sandy bottom community. I. Physical aspects. *J. mar. Res.* 35: 633–647
- Myers, A. C. (1977b). Sediment processing in a marine subtidal sandy bottom community. II. Biological consequences. *J. mar. Res.* 35: 633–647
- Paine, R. T. (1966). Food web complexity and species diversity. *Am. Nat.* 100: 65–75
- Peterson, C. H. (1979). Predation, competitive exclusion, and diversity in the soft sediment benthic communities of estuaries and lagoons. In: *Ecological processes in coastal and marine systems*. Livingston, R. J. (ed.). Plenum Publ. Corp., New York, p. 233–263
- Probert, P. K. (1984). Disturbance, sediment stability, and trophic structure of soft-bottom communities. *J. mar. Res.* 42: 893–921
- Reise, K. (1978). Experiments on epibenthic predation in the Wadden Sea. *Helgoländer Meeresunters.* 31: 55–101
- Reise, K. (1983a). Experimental removal of lugworms from marine sand affects small zoobenthos. *Mar. Biol.* 74: 327–332
- Reise, K. (1983b). Biotic enrichment of intertidal sediments by experimental aggregates of the deposit-feeding bivalve *Macoma balthica*. *Mar. Ecol. Prog. Ser.* 12: 229–236
- Rhoads, D. C., Young, D. K. (1970). The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J. mar. Res.* 28: 150–178
- Schoener, T. W. (1983). Field experiments on interspecific competition. *Am. Nat.* 122: 240–285
- Siegel, S. (1956). Nonparametric statistics for the behavioral sciences. International student edition. McGraw-Hill Book Co., New York
- Smidt, E. L. B. (1951). Animal production in the danish Wadden Sea. *Meddr Kommn Danm. Fisk.-og Havunders. Ser. Fiskeri* 10: 1–125
- Stopford, S. C. (1951). An ecological survey of the Cheshire foreshore of the Dee estuary. *J. Anim. Ecol.* 20: 103–122
- Summerson, H. C., Peterson, C. H. (1984). Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Mar. Ecol. Prog. Ser.* 15: 63–77
- Thamdrup, H. M. (1935). Beiträge zur Ökologie der Wattenfauna auf Experimenteller Grundlage. *Meddr Kommn Danm. Fisk.-og Havunders. Ser. Fiskeri* 10(2): 1–125
- Underwood, A. J. (1978). An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia (Berl.)* 33: 185–202
- Verwey, J. (1981). The cockle *Cerastoderma edule*. In: *Dankers, N., Kühl, H., Wolff, W. J. (ed.). Invertebrates of the Wadden Sea*. A. A. Balkema, Rotterdam, p. 115–116
- Virnstein, R. W. (1977). The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* 58: 1199–1217
- Weinberg, J. R. (1984). Interactions between functional groups in soft substrata: do species differences matter. *J. exp. mar. Biol. Ecol.* 80: 11–28
- Wilson, W. H., Jr. (1981). Sediment-mediated interactions in a densely populated infaunal assemblage: the effects of the polychaete *Abarenicola pacifica*. *J. mar. Res.* 39: 735–748
- Woodin, S. A. (1974). Polychaete abundance patterns in a marine soft-sediment environment: the importance of biological interactions. *Ecol. Monogr.* 44: 171–187
- Woodin, S. A. (1976). Adult-larvae interactions in dense faunal assemblages: patterns of abundance. *J. mar. Res.* 34: 25–41

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