

**Interactions in soft bottom benthic communities:
quantitative aspects of behaviour in the surface deposit
feeders *Pygospio elegans* (Polychaeta) and
Macoma balthica (Bivalvia)***

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ABSTRACT: The surface deposit feeding species *Pygospio elegans* and *Macoma balthica* are dominant members of many sandy bottom communities of northern boreal regions. The feeding mode of both species and the tube-building of *P. elegans* are assumed to affect community structure by interactions with other species. The weight of tubes of *P. elegans* varied between 2 and 13 g DW/100 cm² at the two stations investigated and during the year, which is equivalent to 230–1500 cm of tubes per 100 cm² of sediment surface. Sediment stability may be affected directly or indirectly by the amount of tubes present. *M. balthica* shows a linear relation between the maximum size of particles which can be inhaled and animal length. In Kiel Bay, particles >0.5 mm are out of the range of this species. In summer, the potential feeding area (PFA) of a *P. elegans* population at one station in Kiel Bay was 1.8 times the available surface area. The PFA of three different populations of *M. balthica* in Kiel Bay exceeded the available surface area by factors of 2.6, 2.7, and 3.2. These findings indicate strong intra- and interspecific competition for food. Additionally, the feeding of both species may strongly affect the recruitment of benthic species via pelagic larvae. Experiments are proposed to evaluate the significance of the investigated behavioural aspects for community structure.

INTRODUCTION

Intra- and interspecific interactions and their significance for community structure in soft bottoms have been the subject of many publications during recent years (Bell & Coull, 1980; Black & Peterson, 1988; Blaricom, 1982; Bonsdorff et al., 1986; Gallagher et al., 1983; Hunt et al., 1987; Levin, 1981; Luckenbach, 1987; Olafsson, 1989; Peterson, 1979; Reise, 1983; Whitlatch & Zajak, 1985; Wilson, 1983b; Woodin, 1981; and many others).

Any interaction depends on the effect of one animal on another and vice versa, i.e. interactions are based on certain aspects of the life style or behaviour of the animals. In most cases, we know the mechanisms which cause a positive or negative effect of one animal on another, e.g. protection, predation, territorialism, occupation of space, or disturbance. However, with respect to soft bottom benthic communities, only a few authors have examined the "quantity" of a certain behaviour which an interaction may

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be based on, e.g. the movement of a meiobenthic predator (Watzin, 1985), the sediment turnover of a population of sediment feeders (Cadee, 1976 and references therein), or the pore water transport rates of a population of tube building polychaetes (Aller, 1980).

The aim of this paper is to evaluate some aspects of behaviour which are potential sources of interactions in two surface deposit feeding species, the tube building polychaete *Pygospio elegans* (Claparède) and the bivalve *Macoma balthica* (L.), which are both very common in shallow sandy sediments of the northern boreal regions. In both species, feeding is assumed to affect other animals which live at the sediment surface, either via disturbance and competition for food or via predation (see e.g. Hines et al., 1989; Olafsson, 1989; Wilson, 1981). I have tried to quantify the potential feeding area at the sediment surface, i.e. the area within the range of the tentacles (*P. elegans*) or the inhalent siphon (*M. balthica*) of the animals. Additionally, I investigated the particle size selection of *M. balthica*, which may play an important role for the successful recruitment of species with pelagic larvae (see Hines et al., 1989) and the amount of sediment which is bound in the tubes of *P. elegans*, which are assumed to affect pore water transport and sediment stability.

METHODS

Samples were taken at two stations, the subtidal station "Gabelsflach" (GF) in Kiel Bay (medium/fine sand, 12 m water depth) and the intertidal station "Westerhever" (WH) in the German Wadden Sea (fine sand), during 1986 to 1988 (Fig. 1). Specimens for laboratory experiments were sampled at the station GF with a 0.1 m² VanVeen grab or a 0.09 m² box corer. All other samples were taken by hand (station GF: diver) operated corers (27 cm², 10 cm sampling depth), fixed in a seawater solution of 0.4 % formaldehyde and 3 % Kohrsolin (see Brey, 1986), stained with Bengal rose, and sieved through 0.25 mm in the laboratory.

Pygospio elegans – potential feeding area (PFA)

At the station GF, a 40 × 30 cm PVC tray was filled with a 4 cm layer of natural sediment, which had been sieved through 1 mm previously in order to remove larger animals. On top of this sediment layer I put unsieved sediment from the upper 3–5 cm of the content of two grabs. Afterwards, the tray was filled with seawater. After two days, the specimens of *P. elegans* in the tray had re-established their tubes and were easily recognizable by the area around each tube, which was swept clean of all fine detritus particles. The size of 50 (June 86) and 60 (July 87) randomly selected PFAs was measured.

Pygospio elegans – tubes

The amount of tubes of *P. elegans* was investigated at several dates at both stations. The tubes were collected from core samples, dried at 80°C and weighed. In the laboratory, specimens of *P. elegans* were allowed to build tubes in 15-ml glass tubes filled with azoic sediment and placed in a circulating sea water system at 12°C. Animals and their tubes were measured and weighed.

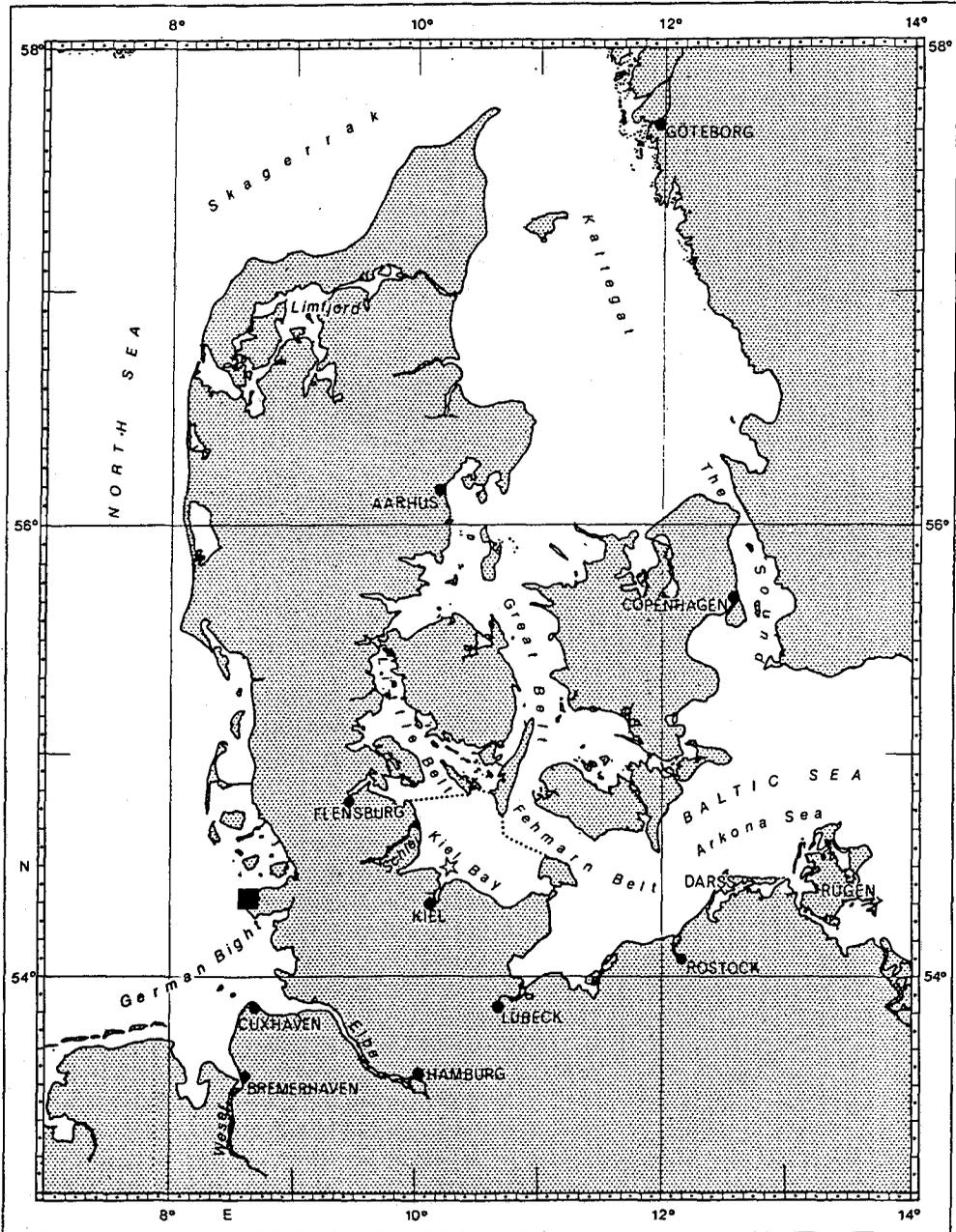


Fig. 1. Location of stations Gabelsflach (GF, star) in Kiel Bay and Westerhever (WH, square) in the German Wadden Sea

Macoma balthica – potential feeding area (PFA)

Single specimens were measured to the lower 0.1 mm, placed in a tray filled with 6 cm natural sediment and kept at 12°C. The animals buried themselves very rapidly and started to suck material from the surface with their inhalent siphon. The area which had been swept clean was measured after 2 and 5 h in a first set of experiments, and after 24 h in a second set.

Macoma balthica – particle selection

Self & Jumars (1988) stated that *M. balthica* does not select particles of a certain size with its inhalent siphon, but there may be an upper limit of particle size which is related to the size of the animal. The maximum size of particles in the mantle cavity of preserved specimens (4–17 mm length) from the station GF was measured under the stereo microscope and correlated with animal length.

RESULTS

Pygospio elegans – potential feeding area (PFA)

Table 1 shows the results of these experiments. The average PFA of *P. elegans* was 57 mm² (June 86) and 91 mm² (July 87), respectively. Figure 2 shows the frequency distribution of PFA in July 87. The minimum distance between two tubes was below 4 mm in both experiments. Direct observations showed that *P. elegans* is able to put the greater part of its body out of the tube, if the range of the tentacles is not sufficient to

Table 1. The average feeding area of *Pygospio elegans* from the station GF in two laboratory experiments. Min. dist.: Minimum distance between two tubes; S.D.: Standard deviation

Date	N m ⁻²	Feeding area			Average area (mm ²)
		Min. dist. (mm)	Mean radius (mm)	S.D.	
19 June 86	4200	3.5	4.26	0.9	57
15 July 87	3800	3.9	5.46	2.0	91

reach a certain spot at the sediment surface. Furthermore, I could not observe any sign of aggressive reactions during encounters of tentacles of different specimens.

The length of the specimens used for feeding area measurements was not determined, but there is a length frequency distribution of *P. elegans* available from the tube samples (see below) of July 87 (Fig. 3). Assuming that the relation between animal length and radius of PFA is linear, the parameters of the corresponding equation may be estimated roughly from the smallest and largest length and radius values (length: 1 mm–9 mm; radius: 1.5 mm–9.5 mm):

$$R_{\text{PFA}} = 0.5 + 1.0 \times L_{\text{Pygospio}} \text{ (mm-mm)} \quad (1)$$

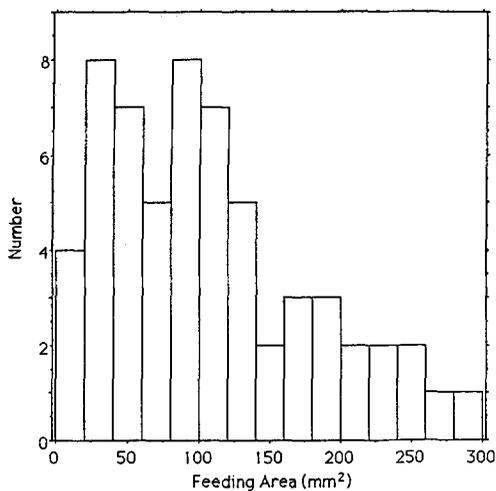


Fig. 2. Frequency distribution of potential feeding areas of *Pygospio elegans* sampled at station GF (10 July 87, N = 60)

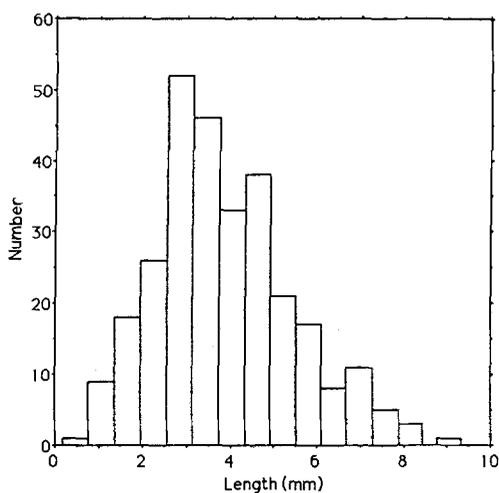


Fig. 3. Length frequency distribution of *Pygospio elegans* at station GF (10 July 87, N = 289)

Pygospio elegans – tubes

The individual tube building was investigated by laboratory experiments. Figure 4 shows the relation between length of *P. elegans* and total length (including branches) of the corresponding tubes. There is a linear relationship between tube length and animal length:

$$L_{\text{Tube}} = 2.275 + 3.567 \times L_{\text{Pygospio}}; \text{ (mm-mm)}$$

$$r^2 = 0.671, N = 127 \quad (2)$$

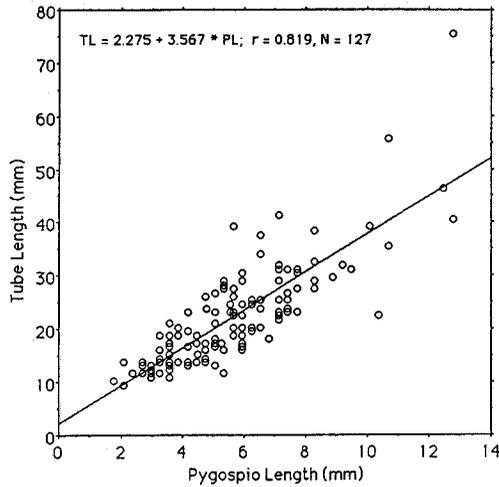


Fig. 4. Relation between animal length and tube length in *Pygospio elegans* (animals from station GF)

By means of the relation between tube length and tube dry weight

$$\begin{aligned} DW_{\text{Tube}} &= -2.152 + 0.864 \times L_{\text{Tube}i} \text{ (mg-mm)} \\ r^2 &= 0.927, N = 94 \end{aligned} \quad (3)$$

and the relation between *Pygospio* length and *Pygospio* dry weight

$$\begin{aligned} \log(DW_{\text{Pygospio}}) &= -2.356 + 1.750 \times \log(L_{\text{Pygospio}i}) \text{ (mg-mm)} \\ r^2 &= 0.992, 21 \text{ length classes, } 187 \text{ specimens} \end{aligned} \quad (4)$$

the empirical relation between *P. elegans* weight and tube weight was established (see Fig. 5):

$$\begin{aligned} DW_{\text{Tube}} &= 7.532 + 97.388 \times DW_{\text{Pygospio}i} \text{ (mg-mm)} \\ r^2 &= 0.677, N = 127 \end{aligned} \quad (5)$$

Figure 6 shows the abundance ($N/100 \text{ cm}^2$) of *P. elegans*, the total amount of tubes ($\text{g DW}/100 \text{ cm}^2$), and the average tube weight per individual at the two stations GF and WH during the year (combination of data from 1987 and 1988). In general, the changes of these parameters in time are similar at both stations. Abundance is low in winter and spring, rapidly increasing towards summer. The amount of tubes is low during winter and spring, but high in summer and autumn. The average weight of tubes per individual, however, is highest in February and March, decreasing towards summer. Figure 7 shows the vertical distribution of tubes in the sediment at both stations in July. At station WH, the tubes reach down to 6 cm depth, whereas at station GF there are no tubes below 4 cm depth.

Macoma balthica – potential feeding area (PFA)

Figures 8 and 9 show the relation between the square of length and PFA in *M. balthica* after 2 h, 5 h, and 24 h, respectively. The corresponding regression equations are:

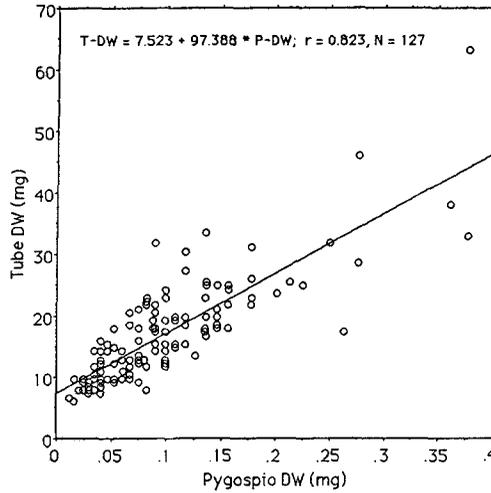


Fig. 5. Relation between animal dry weight and tube dry weight in *Pygospio elegans* (animals from station GF)

$$\text{PFA}_{2\text{h}} = -12.919 + 1.863 \times L_{\text{Macoma}}^2; (\text{mm}^2\text{-mm})$$

$$r^2 = 0.654, N = 30 \quad (6)$$

$$\text{PFA}_{5\text{h}} = -69.559 + 4.354 \times L_{\text{Macoma}}^2; (\text{mm}^2\text{-mm})$$

$$r^2 = 0.740, N = 30 \quad (7)$$

$$\text{PFA}_{24\text{h}} = 689.716 + 31.398 \times L_{\text{Macoma}}^2; (\text{mm}^2\text{-mm})$$

$$r^2 = 0.694, N = 51 \quad (8)$$

Macoma balthica – particle selection

The mantle cavity of 72 specimens of *M. balthica* was examined and the largest particle found (i.e. a sand grain) was measured. The relation between maximum particle diameter (D) and animal length is (cf. Fig. 10):

$$\text{Max. D} = 0.094 + 0.020 \times L_{\text{Macoma}}^2; (\text{mm}-\text{mm})$$

$$r^2 = 0.626, N = 72 \quad (9)$$

DISCUSSION

Pygospio elegans – tubes

The effects of polychaete tubes on sediment stability, pore water chemistry, and the community have been discussed intensively since the 1960's. Field observations and experiments indicated that the presence of tube-building polychaetes stabilizes the sediment and facilitates the settlement of other species (see e.g. Sanders et al., 1962; Fager, 1964; Neumann & Scoffin, 1970; Rhoads et al., 1978; Reise, 1981; Gallagher et al.,

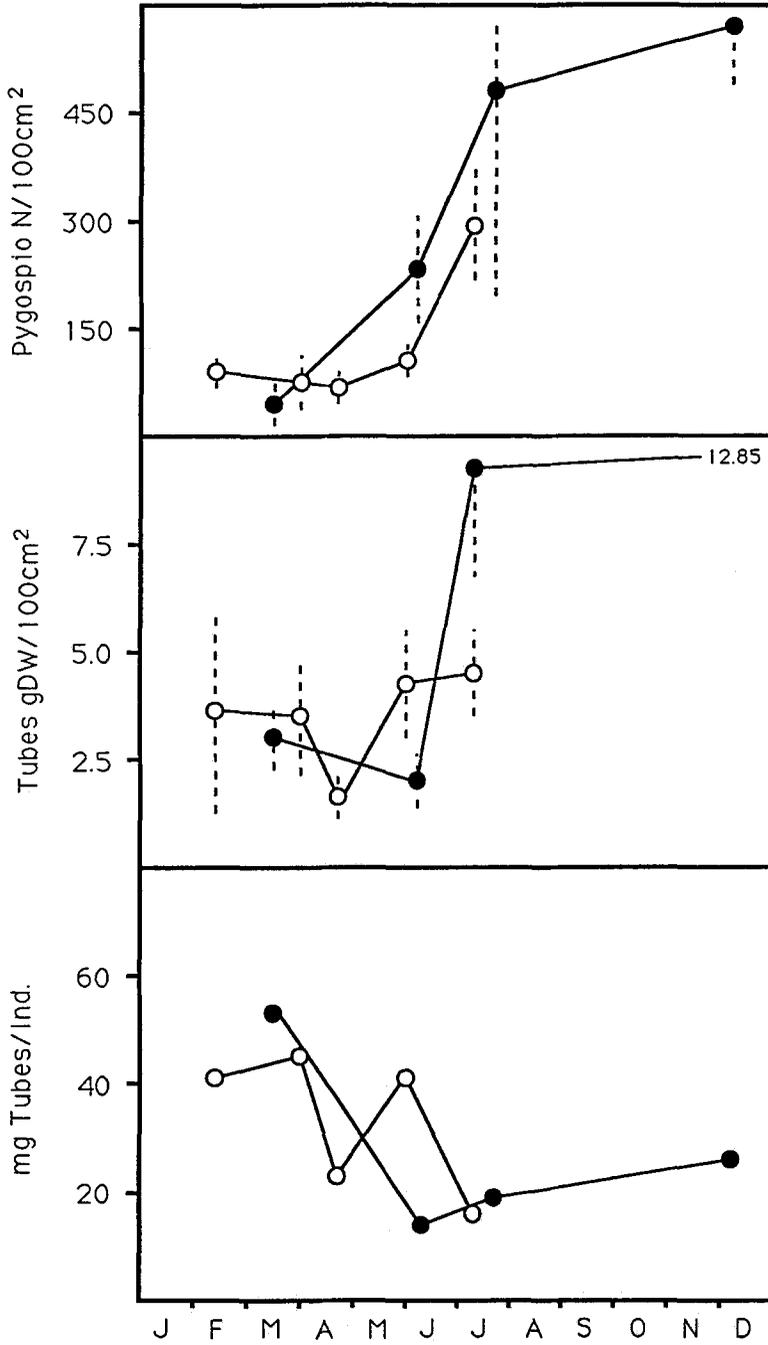


Fig. 6. Seasonal variation in abundance, total amount of tubes and average tube weight per individual in *Pygospio elegans* at the stations GF (circles) and WH (dots). Number of samples/date: 12 (GF) and 15 (WH). Vertical bars: 95% confidence limits of mean

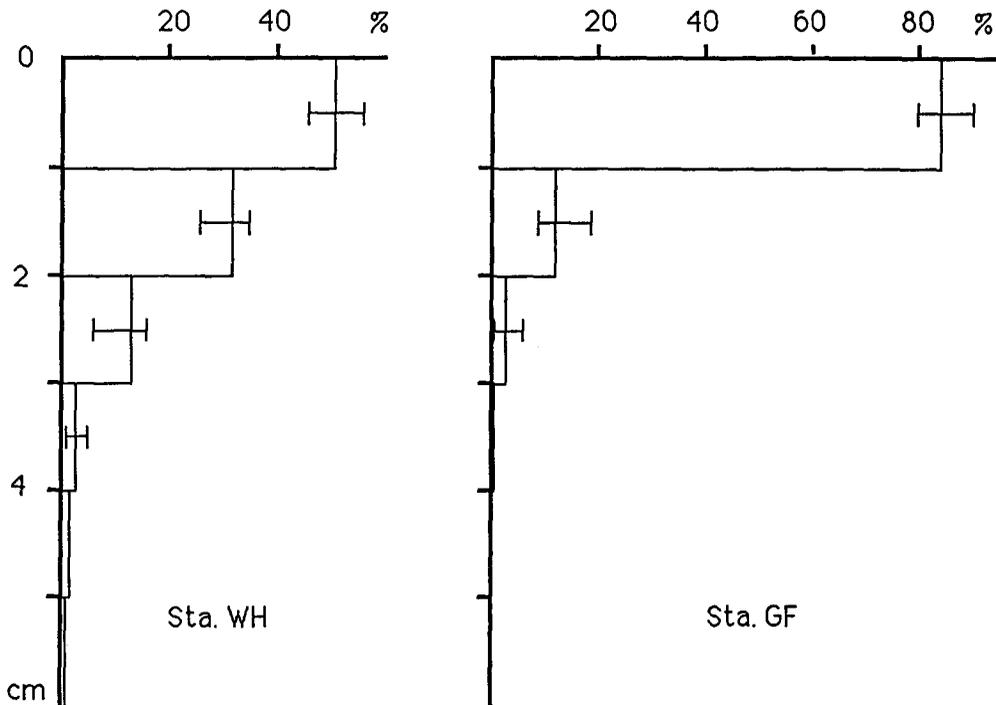


Fig. 7. Vertical distribution of tubes of *Pygospio elegans* at the stations WH (21 July 87) and GF (10 July 87)

1983). Eckmann et al. (1981) showed that tubes do not increase sediment stability due to a reduction of the turbulent flow along the sediment water interface, whereas Führböter & Manzenrieder (1987) could demonstrate that tubes do act as a physical protection against erosion under certain circumstances. As far as we know today, the stabilizing effect of tubes is most likely to be a more indirect one. Tube-builders change the chemical composition of the pore water and affect the vertical transport rates of oxygen and nutrients by the irrigation of their tubes (Aller, 1980, 1983). This may enhance biomass and production of bacteria, diatoms and filamentous algae, which can stabilize the sediment by mucus secretions (see e.g. Aller & Aller, 1986; Holland et al., 1974; Grant et al., 1986; Reichardt, 1986).

With respect to *Pygospio elegans*, the average amount of tubes found was 3.51 g DW/100 cm² at GF and 6.78 g DW/100 cm² at WH. With Eq. (3), these values lead to a total length of all tubes of 410 cm and 780 cm below 100 cm² of sediment surface. This is equivalent to an average tube weight of 26 mg/Ind. (133 Ind./100 cm²) and 20 mg/Ind. (333 Ind./100 cm²), and to an average tube length of 31 mm/Ind. and 23 mm/Ind., respectively. With respect to the maximum amount of tubes found in a single core (8.8 g DW/100 cm² at GF and 18.8 g DW/100 cm² at WH), the maximum total length of tubes was about 1020 cm (GF) and 2180 cm (WH) per 100 cm², and average tube length amounted to 45 mm and 48 mm, respectively. As shown in Figure 6, the total amount of tubes is highest in summer and autumn, whereas the average tube weight per individual

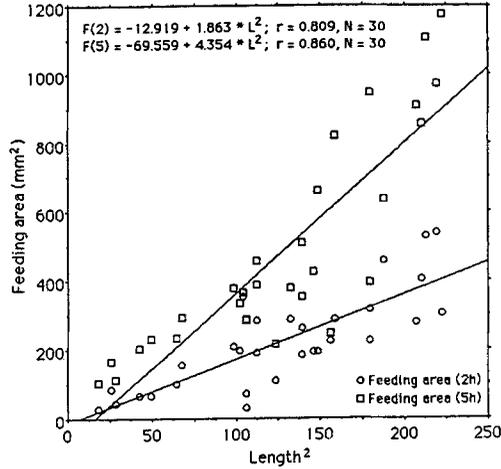


Fig. 8. Relation between potential feeding area and animal length in *Maccoma balthica* after 2 h and 5 h of exposition

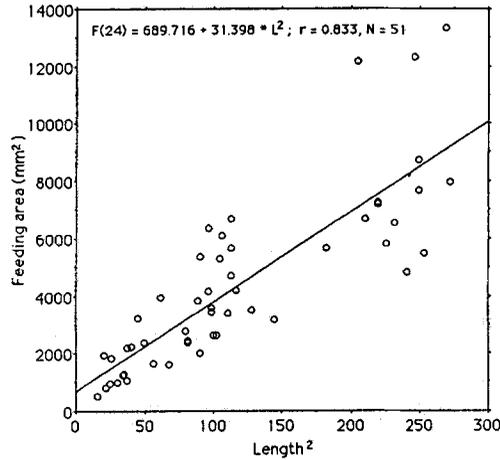


Fig. 9. Relation between potential feeding area and animal length in *Maccoma balthica* after 24 h of exposition

is lowest during this period. These opposite trends are clearly related to the changes in recruitment with time. During summer there is a continuous high reproduction rate, and the populations consist of a few large and many small specimens (see Fig. 3), whereas during winter there are only a few large individuals present. The high values of abundance and tube weight in November at station WH are due to the extraordinary mild autumn 1987 that led to a prolonged recruitment phase in *P. elegans*.

Aller (1980) investigated a population of *Heteromastus filiformis* at a muddy sediment site. According to the average abundance of *H. filiformis* (35 Ind./100 cm²) and

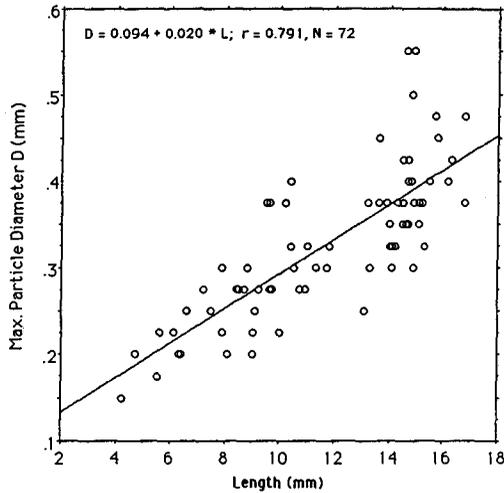


Fig. 10. Relation between length of *Macoma balthica* and the maximum diameter of particles found in the mantle cavity

average tube length (15 cm), total length of all tubes was about 530 cm/100 cm², which is well in the range observed for *P. elegans*. With respect to the upper 5 cm of the sediment only, the amount of tubes is much higher in the *P. elegans* populations than in the *H. filiformis* population. Therefore, the effect of *P. elegans* on pore water transport rates may be even stronger than that of *H. filiformis* in the upper sediment layer.

However, a few calculations show that only a part of all tubes found in a sample may be inhabited. The direct measurements of animal length in July 87 at station GF (Fig. 3) gave an average length of *P. elegans* of 3.7 mm. According to Equations (2) and (3), this corresponds to an average weight of 11.2 mg DW of tubes per animal. The field samples, however, yielded on average a tube weight of 15.5 mg DW at station GF (Fig. 6). That means there are about 30 % more tubes in the natural environment than are predicted by the empirical relations. This difference may be due to empty tubes, which have lost their inhabitant either by emigration (Fauchald & Jumars, 1979; Wilson, 1981, 1983b) or by predation (Poxton et al., 1983; DeVlas, 1979; Woodin, 1984), and which still exist for a certain time.

Pygospio elegans – potential feeding area (PFA)

The total PFA of the *P. elegans* population at station GF in July 87, which can be estimated via the length-frequency distribution (Fig. 3) and the relation between length and radius of PFA [Equation (1)], is about 184 cm²/100 cm², i.e., if all animals utilize their potential range, there is an overexploitation of the available area by a factor of 1.8. This implies intraspecific competition for food, if food is not available in excess. Taghon et al. (1980) could show that the greater part of a *P. elegans* population changes its feeding mode from deposit feeding to suspension feeding if the water current increases above 10 cm/sec, which would reduce direct competition. However, also in spionids, which are able to change their feeding mode, intraspecific competition for food may affect growth

and reproduction, as described by Wilson (1983a) for *P. elegans* and by Zajak (1986) for *Polydora ligni*. Additionally, according to Boehlich & Backhaus (1987), Schweimer (1976) and Struve-Blank (1982) currents above 10 cm/sec do not occur very frequently at station GF during summer, so it is most likely that the animals are deposit feeding most of the time.

The overexploitation of the available surface area by a *P. elegans* population (as well as by other deposit feeding spionids) may have serious effects on the recruitment of other species, because several deposit feeding spionids are known to predate on settling larvae of other species (e.g. Weinberg, 1984; Whitlatch & Zajak, 1985; Wilson, 1981; Tamaki, 1985). As soon as the total PFA of one of those populations is above the available area, there are no refuges left for settling larvae. Reproduction via brooding in many deposit feeding spionid species may be a strategy to overcome the problem of cannibalism.

Macoma balthica – particle selection and potential feeding area (PFA)

Hylleberg & Gallucci (1975) and Self & Jumars (1988) could not find any particle selection prior to inhalation in *M. nasuta* and *M. balthica*, respectively. According to Self & Jumars (1988), the selection of food takes place in the mantle cavity with respect to diameter and specific weight of the particles. The rejected part of the inhaled material is pushed out through the inhalent siphon. However, a passive size selection of the material to be ingested takes place, if the sediment contains particles which are above the diameter of the inhalent siphon. The linear relation between animal length and maximum diameter of particles in the mantle cavity (Fig. 10) shows clearly that this must be the case at station GF. At this station, particles above 0.5 mm are out of the range of the whole population.

The total PFA of a *M. balthica* population can be estimated by a length-frequency distribution and Equation (8). Figure 11 shows the length-frequency distribution and the corresponding length-PFA distribution of the population from station GF ($N = 909$ Ind./m²; total PFA = 27 230 cm²/m²), and from two stations which were sampled during previous research programs in Kiel Bay: station Schleimünde (6 m depth, $N = 2322$ Ind./m²; total PFA = 26 090 cm²/m²) and station Schönberg (12 m depth, $N = 598$ Ind./m²; total PFA = 31 850 cm²/m²). At all stations, the total PFA is far above the available area (factor 2.6, 2.7, 3.2), which indicates strong intraspecific competition for food. However, like *P. elegans*, *M. balthica* is able to switch from deposit feeding to suspension feeding, if the water current exceeds a certain limit (Rasmussen, 1973; Olafsson, 1979). Therefore, competition may not be as strong as indicated by the figures above. However, the fact that total PFA is similar at the three stations, although the length-frequency distributions are quite different, may be a hint on an upper limit of total PFA for *M. balthica*, at least in Kiel Bay. The regular distribution of the related tellinid species *Tellina tenuis*, which has been observed by Holme (1950) on an intertidal sand flat, may be a strategy of minimizing overlap of individual PFA.

The inhalation activity of *M. balthica* is assumed to be the main source of the negative effect of this bivalve on recruitment and growth of the own larvae and larvae of other species (Bonsdorff et al., 1986; Brey, 1989; Hines et al., 1989; Olafsson, 1989), either by disturbance and competition for food, or by inhalation and rejection of larvae, which may have lethal effects (see Mileikovsky, 1974). Most of the pelagic larvae of marine

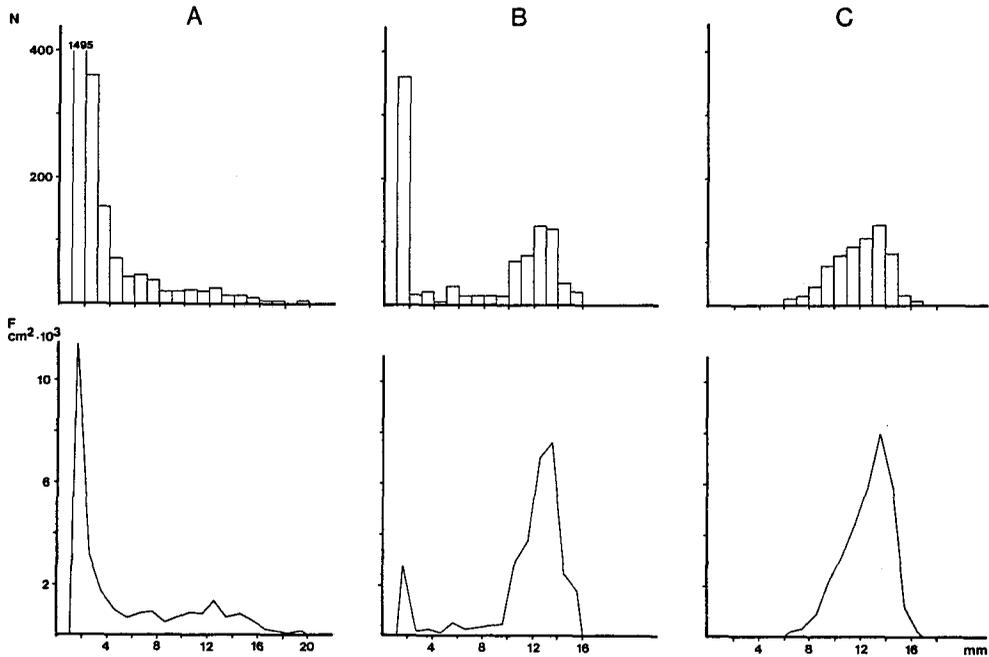


Fig. 11. Length-frequency and PFA-frequency distributions of three different populations of *Macoma balthica* in Kiel Bay. A: Schleimünde, 6 m water depth, $N = 2322$ Ind./m². B: Gabelsflech, 12 m water depth, $N = 909$ Ind./m². C: Schönberg, 12 m water depth, $N = 598$ Ind./m²

invertebrates are between 0.2 and 0.5 mm (see e.g. Muus, 1973) when they settle, i.e. well within the size range of particles which can be inhaled by adult *M. balthica*. Fast growth may be one strategy for larvae to escape this "Macoma-bottleneck" sensu Bell & Coull (1980).

To sum up, the results of the present study indicate that tube-building activities and potential feeding areas may be important structuring factors in the investigated sandy bottom communities. However, more intensive investigations have to be carried out to evaluate the significance of these factors, for example:

- Measurements similar to those of Aller (1980), combined with investigations of the growth of bacteria and microalgae around tubes, could prove the indirect positive effect of the tube-building of *P. elegans* on sediment stability.
- The potential feeding areas of populations of both *P. elegans* and *M. balthica* are assumed to be better indicators for the strength of intra- and interspecific interactions than are pure abundance values. The question of whether or not unaffected areas between individual PFAs act as refuges for freshly settled larvae and juveniles may be tested by an experiment that compares the effects of a population with total PFA < available surface area with the effects of a population with total PFA > available surface area.
- The question of whether competition for food or inhalation of larvae is the more important factor in the interactions between adult *M. balthica* and settling larvae may

be answered by a field experiment that compares the effects of different size classes of *M. balthica* on the recruitment of different species.

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