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# The Relative Significance of Biological and Physical Disturbance: an Example from Intertidal and Subtidal Sandy Bottom Communities

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The effects of biological disturbance caused by the lugworm *Arenicola marina* (L.) on the abundance of the macrobenthic fauna were investigated at three subtidal stations (0·5 m, 12 m and 19 m water depth) in Kiel Bay (western Baltic) and on an intertidal flat in the German Wadden Sea. Different effects of biological disturbance were observed (1) between funnel and cast of the lugworm burrow, (2) among stations, (3) between seasons, and (4) among taxa and groups of different living mode of the macrofauna. The strength of the impact of *A. marina* on the abundance of a certain macrobenthic species depends on three factors: (1) species behaviour and living mode, (2) *A. marina* activity, and (3) hydrodynamic conditions. In general, the most distinct effects were observed at the intertidal station during summer, followed by the two deeper subtidal stations. At the very shallow station, only weak effects were detected.

## Introduction

The factors which control structure and dynamics of communities are central themes of theoretical and applied ecology. Besides competition (e.g. MacArthur & Wilson, 1967) and predation (e.g. Paine, 1966), disturbance plays a key role in various theoretical approaches (e.g. Gray, 1984; Huston, 1979; Menge & Sutherland, 1987). The significance of large-scale physical disturbance has already become an integral element of models which try to explain community development and succession (e.g. Connell & Slayter, 1977; Gray, 1977; Sanders, 1968). With respect to marine soft-bottom communities, small-scale disturbance, either physically or biologically induced, was first taken into account by Grassle and Sanders (1973) and has become a focus of interest over recent years (Bell & Devlin, 1983; van Blaricom, 1982; Brenchley, 1981; DeWitt, 1987; Eckman, 1979; Hall *et al.*, 1990; Probert, 1984; Savidge & Taghon, 1988; Smith *et al.*, 1986; Smith *et al.*, 1986; Thrush *et al.*, 1991; Wilson, 1981; Woodin, 1978, 1981, 1985; Zajac & Whitlatch, 1982).

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TABLE 1. Abiotic parameters and sampling regime at the four stations. Salinity and water temperature data from Asmus (1984, WH), Babenerd (1980, GF and BE), and Stienen (1986, KF)

| Station | KF | GF | BE | WH |
|---|---|---|---|---|
| *Water* | | | | |
| Water depth (m) | 0–1 | 12 | 19 | 0–1[b] |
| Salinity[a] (‰) | 10–20 | 16–20 | 9–22 | 26–31 |
| Water temperature[a] (°C) | 2–20 | 2–14 | 2–13 | 1–20 |
| *Sediment* | | | | |
| >0·25 mm | 20·9 | 47·3 | 30·0 | 14·1 |
| 125–0·25 mm | 63·0 | 49·4 | 53·5 | 73·0 |
| 63–125 μm | 14·3 | 3·1 | 12·8 | 6·8 |
| <63 μm | 1·8 | 0·3 | 3·7 | 3·2 |
| *Sampling* | | | | |
| Sampling period | 9/87 and 12/87 | 9/86–6/88 | 2/88–5/88 | 7/87–6/88 |
| No. of sampling dates | 2 | 13 | 3 | 4 |
| No. of samples per day | 5 × 3 | 3 × 3/4 × 3[d] | 4 × 3 | 5 × 3 |
| Total no. of samples | 30 | 126 | 36 | 60 |

[a]Annual variation.
[b]Intertidal, 6-h immersion per 12-h tidal cycle.
[c]Three samples per *A. marina* burrow: funnel, cast and control.
[d]Increase from 3 × 3 to 4 × 3 samples in September 1987.

In shallow water soft-bottom communities, hydrodynamics are the main source of large-scale physical disturbance, whereas bioturbation is one important source of small-scale biological disturbance. Large deposit-feeding infaunal species which deposit their faeces at the sediment surface, e.g. arenicolid polychaetes (summary in Cadée, 1976), holothurians such as *Leptosynapta tenuis* (Myers, 1977*a*,*b*) and *Molpadia oolithica* (Rhoads & Young, 1971) or enteropneusts such as *Balanoglossus auratiacus* (Duncan, 1977), are known as major bioturbators.

The present paper evaluates the significance of biological disturbance caused by the lugworm *Arenicola marina* under different hydrodynamic regimes, i.e. at several sites and in different seasons of the year. The aim was to analyse the interactions between small-scale biological and large-scale physical disturbance and to describe possible synergistic effects on the macrobenthic community.

## Methods

### *Sampling sites*

Samples were taken at four different stations, the subtidal stations KF, GF and BE in Kiel Bay (western Baltic) and the intertidal station WH in the German Wadden Sea. The sediment of all stations consisted of medium and fine sand with a low content of clay and silt (Table 1). Station KF is situated in a particular area of the Kiel harbour constructions, which is silting up continuously due to the local wind and current conditions. The sand bank has a gentle slope (1:15) down to about 1 m water depth, and the upper millimetres of sediment are almost continuously resuspended as a result of ship- and wind-induced waves. Sometimes, during strong southerly winds, the bank becomes completely exposed to the air. Station GF is situated at a subtidal flat north of Kiel lighthouse in 12 m water depth, which is exposed to wave and current activities from all directions. Strong gales lead to wave-induced sand ripple formation, but these events are very rare during summer. The calculations of Boehlich and Backhaus (1987), Schweimer (1976) and Struve-Blanck (1982) indicate that during the summer bottom water current speeds above 10 cm $s^{-1}$ rarely occur at station GF.

Station BE is situated on the slope of the west coast of Kiel Bay at 19 m water depth and is well protected against disturbance due to waves, because most gales in this area are of south-western origin.

Station WH is located in a tidal flat of the German Wadden Sea close to the lighthouse Westerhever; it is immersed for about 6 h per tidal cycle, i.e two times a day.

### *Sampling and sorting*

All samples were taken by hand-operated (KF and WH) or diver-operated (GF and BE) corers (27 $cm^2$, 10 cm sampling depth). Three parallel samples were taken at each *A. marina* burrow which had been selected for sampling: one at the funnel, one at the cast, and one control sample from assumed unaffected area close to the burrow. Between 1986 and 1988, 252 (i.e. 84 × 3) samples were taken (Table 1).

The samples were fixed in a seawater solution of 0·4% formaldehyde and 3% Kohrsolin (see Brey, 1989), stained with Bengal rose, and sieved with 0·50 mm and 0·25 mm mesh size in the laboratory. Animals in the 0·50-mm fraction were identified to species level, whereas the 0·25-mm fraction was separated into molluscs (i.e. mainly O-group animals of the most abundant bivalve species), polychaetes (including oligochaetes) and crustaceans.

Abundance of adult *A. marina* was estimated from the number of casts at the sediment surface. At stations GF and BE a submersible video-camera system (Cyclops™) was used in addition to observations made by divers.

### *Sample analysis*

The samples collected were analysed with respect to two main questions: Do the burrows of *A. marina*, i.e. funnels and casts, affect macrofaunal abundance significantly? Are the effects of funnels and casts different among sampling stations, seasons or macrobenthic groups?

The fauna was grouped into bivalves, gastropods, sessile polychaetes (including hemisessile species such as spionids), motile polychaetes (including oligochaetes) and crustaceans for multivariate tests; univariate tests were applied to different levels from all species combined to single species.

Macrofaunal abundance in funnel, cast and control samples was compared either by ANOVA of the Box–Cox-transformed data or by the non-parametric Kruskal–Wallis test, if the requirements for ANOVA were not fulfilled (Sokal & Rohlf, 1981). Subsequently, a multiple comparison of means or a non-parametric multiple comparison of samples was applied (Sokal & Rohlf, 1981; Sachs, 1982). If more than one station, season or macrobenthic group was included in a test run, abundance data had to be corrected for general abiotic and biotic differences among stations, seasons and faunal groups which were not due to the activity of the lugworms. Within each set of data (i.e. all data within one cell of the type station × season × group), the abundance values of all funnel, cast and control samples were divided by the mean of the control samples; i.e. the mean of the controls was adjusted to one for each data set without changing the relation of the variances among funnel, cast and control samples.

TABLE 2. Appearance of funnel and cast of *Arenicola marina* burrows at the four stations. Types a–c refer to figure 1 in Rijken (1979)

| Station | Funnel | Cast |
|---|---|---|
| KF | Only entrance to burrow visible, no depression of surface | No casts, only a few cm of faeces visible, due to permanent destruction by waves |
| GF | Summer: conical depression of several cm depth entrance to burrow not visible (Type b) Winter: not visible | Summer: flat-rounded casts up to about 10 cm diameter Winter: no casts, only strings of faeces |
| BE | Steep and deep, with well defined brink (between Type b and Type c) | Maximum diameter > 15 cm, higher and with steeper slope compared to GF |
| WH | Flat and shallow, entrance to burrow visible (Type a) | During one low water period growth to 7 cm diameter and 4 cm height on average, complete erosion of casts by each tide |

For the comparison of strength and direction (positive or negative) of funnel and cast effects among stations, seasons and faunal groups, abundance values of funnel and cast samples were transformed to per cent of the corresponding control sample. Different sets of funnel or cast data were compared by the multivariate techniques described above.

*Local migration of* Arenicola marina

Changes in the position of the funnel or the cast of a single specimen were observed in the field as well as in the laboratory. Fourteen animals between 15 and 100 mm length were kept in a circulating seawater system at 12 °C for 10–30 days in a 1250-$cm^2$ tray, which was filled with a 20-cm layer of natural sediment from station GF. Each change in the position of the funnel (if detectable) and the cast was recorded.

## Results

Arenicola marina *abundance and burrow type*

During summer, abundance was estimated from the numbers of inhabited burrows to 2–8 individuals $m^{-2}$ at station KF (September 1987), 5–30 individuals $m^{-2}$ at station GF (summer 1986–88), 5–10 individuals $m^{-2}$ at station BE (May 1988), and 5–15 individuals $m^{-2}$ at station WH (July 1987). During winter, abundance was lower at KF (0–2 individuals $m^{-2}$, December 1987), GF (0–3 individuals $m^{-2}$, February 1988) and WH (0–5 individuals $m^{-2}$ November 1987, March 1988), whereas no decrease was observed at station BE in February 1988.

The visible parts of the burrows (funnel and cast) appeared different at the four stations (Table 2). Only at WH did they correspond to the typical Wadden Sea burrow as described by Rijken (1979) and others.

Arenicola marina *local migration*

Field observations indicated different rates of local migration of *A. marina* at the four stations. At KF, there was no evidence of local migration. At GF, video and diver observations showed clearly that *A. marina* changes its position frequently, at least the position

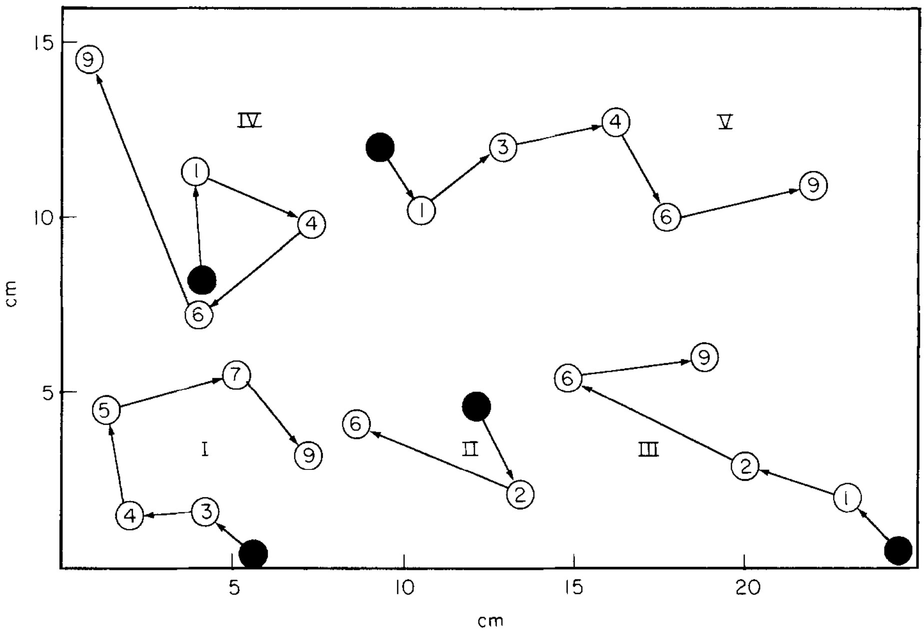


Figure 1. Composite figure of tracks of local migration of five *Arenicola marina* (15–30 mm length) during 10 days. Marks indicate position of cast, funnel usually not visible. ●, Day zero, start of observation. Numbers: first day at position indicated by circle.

of the cast. It is possible to separate casts which are still being added to from casts which are not. Casts which are being produced show freshly produced faecal strings on top; they form well defined mounds and are of bright, whitish colour. Abandoned casts show no faecal strings; with time they become more and more levelled out, and their colour changes towards the ambient greenish sediment surface colour. At BE only a small number of ' old ' casts was observed, indicating that *A. marina* changes its position not as frequently as at GF. At the intertidal station WH, *A. marina* changes the position of the funnels occasionally but most of the casts remain at the same spot during periods of several weeks (information kindly provided by S. Flothmann, Kiel).

In the laboratory experiments, all specimens of *A. marina* changed position about every other day (minimum 0·5 days, maximum 14 days), irrespective of individual length. In 5% of all cases observed ($N=84$) only the position of the funnel changed, whereas in 95% of all cases the positions of cast and funnel (if detectable) changed. The larger animals migrated up to 20 cm on one occasion. Figure 1 shows the migration tracks of five small specimens (15–30 mm length) during 10 days of observation.

### *The macrozoobenthos of the four stations*

At all stations the macrobenthic community (Table 3) is dominated by surface or subsurface deposit feeders and by species which are able to feed from the sediment surface as well as from the water column, such as the bivalve *Macoma balthica* or the spionid polychaete *Pygospio elegans*. Only a few carnivorous species are present, e.g. the polychaetes *Anaitides maculata* and *Eteone longa*. The number of macrobenthic species found was 12 at KF, 43 at GF, 46 at BE, and 21 at WH. The dominant taxa were oligochaetes, *Nereis diversicolor* and *Mya arenaria* at KF, *Pygospio elegans*, *Aricidea jeffreysii* and *Macoma balthica* at GF,

TABLE 3. List of macrobenthic taxa found at the four stations. Mean abundance ($N$ 100 cm$^{-2}$) calculated from all samples

| Taxon | Mobility type | Station KF | GF | BE | WH |
|---|---|---|---|---|---|
| Mollusca | | | | | |
| *Arctica islandica* | S | — | 0·9 | 1·2 | — |
| *Astarte borealis* | S | — | 1·3 | 4·1 | — |
| *Astarte elliptica* | S | — | 0 | 2·2 | — |
| *Cardium edule* | S | 1·4 | — | — | 5·5 |
| *Cardium fasciatum* | S | — | 3·3 | 0·6 | — |
| *Corbula gibba* | M | — | 5·4 | 32·4 | — |
| *Ensis* sp. (juveniles) | S | — | — | — | 0·5 |
| *Macoma balthica* | S | 7·6 | 30·2 | 15·0 | 99·3 |
| *Macoma calcarea* | S | — | — | 3·9 | — |
| *Musculus discors* | S | — | — | 1·2 | — |
| *Musculus marmoratus* | S | — | 0·5 | — | — |
| *Mya arenaria* | S | 39·9 | 2·5 | 1·3 | 10·1 |
| *Mya truncata* | S | — | — | 3·7 | — |
| *Mysella bidentata* | S | — | 19·7 | 57·6 | — |
| *Mytilus edulis* | S | — | 2·4 | — | 0·1 |
| *Phaxas pellucidus* | S | — | <0·1 | — | — |
| *Syndosmya alba* | S | — | 0·5 | 13·3 | — |
| *Acera bullata* | M | — | — | 0·1 | — |
| *Hydrobia* sp. | M | 0·6 | 0·3 | — | 18·9 |
| *Littorina littorea* | M | — | <0·1 | — | — |
| *Onoba striata* | M | — | 1·4 | 1·3 | — |
| *Retusa obtusa* | M | — | — | — | 1·6 |
| *Retusa truncatula* | M | — | 0·4 | 0·9 | — |
| Polychaeta and Oligochaeta | | | | | |
| *Ampharete* sp. | S | — | 0·2 | 0·9 | — |
| *Anaitides maculata* | M | — | 0·5 | 0·9 | 1·2 |
| *Arenicola marina* (juveniles) | S | — | 0·5 | 0·3 | — |
| *Aricidea jeffreissii* | M | — | 34·3 | 2·9 | — |
| *Capitella capitata* | M | 5·3 | 1·9 | 0·6 | 0·5 |
| *Chaetozone setosa* | M | — | 20·6 | 15·0 | — |
| *Eteone longa* | M | 7·3 | 2·0 | — | 1·4 |
| *Euchone papillosa* | S | — | — | 0·6 | — |
| *Fabricia sabella* | S | — | — | — | 25·3 |
| *Fabriciola* sp. | S | — | <0·1 | — | — |

(*Continued*)

*Mysella bidentata, Corbula gibba* and *Chaetozone setosa* at BE, and *P. elegans, M. balthica* and *Corophium volutator* at WH.

Average macrofauna abundance in the 0·50-mm sieve fraction (0·50 mm + 0·25 mm in parentheses) was 540 individuals m$^{-2}$ (810) at KF, 330 individuals m$^{-2}$ (450) at GF, 220 individuals m$^{-2}$ (280) at BE and 590 individuals m$^{-2}$ (860) at WH during the time of investigation. The communities at the four stations are characterized by a low-level trophic structure (*sensu* Menge & Sutherland, 1987), both with respect to the food web and the interaction web (Brey, 1989).

### *Effects of* Arenicola marina *burrows on macrobenthos abundance*

Prior to any detailed analysis, a four-way ANOVA was applied to all data (Table 4) in order to identify general effects of stations, seasons, macrofaunal groups and burrow

TABLE 3. (*Continued*)

| Taxon | Mobility type | Station KF | GF | BE | WH |
|---|---|---|---|---|---|
| *Harmothoe* spp. | M | — | 1·8 | 2·7 | — |
| *Heteromastus filiformis* | M | — | — | 3·0 | 12·1 |
| *Malacoceros tetroceratus* | M | — | <0·1 | — | — |
| *Nepthys* spp. | M | — | 1·9 | 7·3 | — |
| *Nereimyra punctata* | M | — | — | 0·7 | — |
| *Nereis diversicolor* | M | 40·1 | — | — | 9·7 |
| *Ophelia rathkei* | M | — | <0·1 | — | — |
| *Paraonis fulgens* | M | — | — | 0·8 | — |
| *Paraonis gracilis* | M | — | — | 0·5 | — |
| *Pectinaria koreni* | S | — | 1·6 | 7·8 | — |
| *Pherusa plumosa* | S | — | — | 2·4 | — |
| *Pholoe minuta* | M | — | 3·4 | 5·9 | — |
| *Polydora ciliata* | S | 8·6 | — | 2·6 | 1·2 |
| *Polydora quadrilobata* | S | — | 11·4 | 4·7 | — |
| *Pygospio elegans* | S | 1·1 | 131·2 | 1·9 | 305·2 |
| *Scoloplos armiger* | M | — | 10·8 | 7·3 | 7·9 |
| *Sphaerodoridium balticum* | M | — | 0·8 | 0·2 | — |
| *Spio goniocephala* | S | 3·3 | 1·5 | 1·7 | — |
| *Streptosyllis websteri* | M | — | 10·0 | 2·8 | — |
| *Terebellides stroemi* | S | — | — | 1·3 | — |
| *Trochochaeta multisetosa* | M | — | — | 0·6 | — |
| Oligochaeta | M | 421·3 | 3·9 | 1·3 | 30·9 |
| Crustacea | | | | | |
| *Bathyporeia* sp. | M | — | — | — | 6·0 |
| *Caprella* sp. | S | — | 6·3 | 0·6 | — |
| *Carcinus* sp. (juveniles) | M | — | — | — | 0·8 |
| *Corophium insiduosum* | S | 2·2 | 2·4 | — | — |
| *Corophium volutator* | S | — | — | — | 47·3 |
| *Crangon crangon* | M | — | — | — | 0·5 |
| *Diastylis rathkei* | M | — | 3·5 | 3·7 | — |
| *Eudorellopsis deformis* | M | — | 0·1 | 0·1 | — |
| *Gastrosaccus spinifer* | M | — | 0·6 | 0·5 | — |
| *Idotea baltica* | M | — | 0·5 | — | — |
| *Phoxocephalus holboelli* | M | — | 9·2 | 1·3 | — |

S, Sessile (including hemisessile); M, motile.

structures. Bivalves and gastropods were pooled for this analysis due to the low overall abundance and frequency of gastropods. The direct effects of stations, seasons and faunal groups are not significant; they were eliminated by the *a priori* transformation of the data to equal means of controls (see above). *A. marina* funnels and casts affect macrobenthic abundance significantly ($P<0{\cdot}001$). The highly significant interaction terms indicate that the effects of funnels and casts are different among stations ($P<0{\cdot}001$), between seasons ($P=0{\cdot}007$) and among faunal groups ($P<0{\cdot}001$).

Tables 5 to 8 show the results of one-way ANOVAs and subsequent multiple comparisons of funnel, cast and control samples at the four stations, for all seasons as well as for summer and winter separately. All species present were analysed, but those not affected significantly ($a=0{\cdot}05$) are not included in the Tables. At the very shallow station KF (Table 5) only one species (i.e. 8%), the bivalve *Cardium edule*, is affected significantly. Its abundance is zero in the cast samples. At GF (Table 6), 13 species (i.e. 30%) are affected

TABLE 4. Multiple analysis of variance of differences in abundance among samples

| Source | Sum of squares | df | Mean square | $F$ | $P$ |
|---|---|---|---|---|---|
| Station | 0·047 | 3 | 0·016 | 0·173 | 0·914 |
| Season | 0·002 | 1 | 0·002 | 0·021 | 0·884 |
| Group | 0·032 | 2 | 0·011 | 0·120 | 0·948 |
| Burrow | 4·816 | 2 | 2·408 | 26·687 | <0·001 |
| Station × burrow | 3·653 | 6 | 0·609 | 6·747 | <0·001 |
| Season × burrow | 0·913 | 2 | 0·456 | 5·075 | 0·007 |
| Group × burrow | 2·904 | 4 | 0·484 | 5·363 | <0·001 |
| Error | 88·793 | 984 | 0·090 | | |

Abundance data were adjusted to equal means (= 1·0) of control samples in all cells (station × season × group) by the transformation $N_i = N_i/\text{mean}_{\text{control}}$ of all values $N_i$.
Source: Stations, KF, GF, BE, WH; seasons, summer (June–September), winter (October–May); group, molluscs, sessile polychaetes, motile polychaetes, crustaceans; burrow, funnel, cast, control.

significantly. The molluscs are affected more or less similarly at all taxonomic levels. During winter no effects are detectable, whereas during summer abundance is higher at the funnel sites and lower at the cast sites than in the controls. Funnels show stronger effects than do casts. In general, both funnels and casts reduce the abundance of polychaetes (and oligochaetes) in comparison to control sites in summer and winter. Abundance at the funnel sites is higher than at the cast sites for sessile polychaetes, and vice versa for motile species. Crustaceans are affected in the same way as polychaetes, abundance being reduced at funnel and cast sites.

At BE (Table 7) 11 species (i.e. 24%) are affected significantly. Nearly all mollusc species show a strongly increased abundance at the funnel sites, whereas a negative effect of the casts is detectable for all species combined. The abundance of sessile polychaetes is higher at funnel sites and lower at cast sites compared to controls, except in *Terebellides stroemi*, which was found in control samples only. Motile polychaetes show no consistent effects; the abundance of *Aricidea jeffreysii* is lower at funnel sites, but the abundance of *Pholoe minuta* is higher. Crustaceans are affected negatively by funnels and by casts.

At the intertidal station WH (Table 8) seven species (i.e. 33%) are affected significantly. In general, molluscs are negatively affected by casts during summer, whereas funnels only affect the gastropod *Retusa obtusa*. In winter, only *Mya arenaria* is affected weakly. The abundance of sessile polychaetes is reduced by funnels, and more so by casts during summer, but no effect is detectable in winter. Motile polychaetes are not affected at all. Crustaceans show a reduced abundance at the funnel sites in summer and winter, and the amphipod *Bathyporeia* sp. shows a unique distribution in summer, occurring at cast sites only.

### *Seasonal differences in the effects of* Arenicola marina *burrows*

The results of the comparison of funnel and cast effects between summer and winter are shown in the last two columns of Tables 5, 6 and 8 (level of significance: $a = 0{\cdot}05$).

At KF, no significant seasonal differences could be detected. At GF, there are differences between the effects of funnels on all polychaetes, and in *Polydora quadrilobata* between summer (negative) and winter (n.s.). At WH, there is a seasonal difference in the

TABLE 5. Station KF: effects of *Arenicola marina* funnels and casts on the macrobenthos. Only species with significant effects are shown

| Taxon | All seasons | | | | Summer | | | | Winter | | | | $D_{S-W}$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Fu | Ca | Co | MC | Fu | Ca | Co | MC | Fu | Ca | Co | MC | Fu | Ca |
| Molluscs | | | | | | | | | | | | | | |
| All species[a] | 50·6 | 43·4 | 69·6 | – – – | 95·2 | 70·4 | 130·4 | – – – | 6·0 | 16·4 | 8·8 | – – – | – | – |
| All bivalves | 45·0 | 41·9 | 58·8 | – – – | 84·8 | 67·4 | 108·8 | – – – | 5·2 | 16·4 | 8·8 | – – – | – | – |
| *Cardium edule* | **2·3** | **0** | **1·9** | – + + | **4·6** | **0** | **3·8** | – + + | 0 | 0 | 0 | – – – | / | / |
| All gastropods | 1·5 | 0 | 0·4 | – – – | 2·2 | 0 | 0·8 | – – – | 0·8 | 0 | 0 | – – – | – | – |
| Polychaetes and Oligochaetes | | | | | | | | | | | | | | |
| All species[a] | 714·9 | 649·9 | 895·7 | – – – | 1298·8 | 1145·0 | 1668·2 | – – – | 133·0 | 170·4 | 123·2 | – – – | – | – |
| Sessile species | 47·8 | 42·2 | 69·4 | – – – | 80·8 | 72·4 | 126·0 | – – – | 14·8 | 12·0 | 12·8 | – – – | – | – |
| Motile species | 404·8 | 376·1 | 512·9 | – – – | 723·2 | 653·0 | 951·8 | – – – | 86·4 | 99·2 | 74·0 | – – – | – | – |
| Crustaceans | | | | | | | | | | | | | | |
| All species[a] | 3·0 | 1·9 | 3·2 | – – – | 6·0 | 3·8 | 6·4 | – – – | 0 | 0 | 0 | – – – | / | / |
| All taxa | | | | | | | | | | | | | | |
| All species[a] | 768·5 | 695·2 | 968·5 | – – – | 1398·0 | 1220·0 | 1805·0 | – – – | 139·0 | 170·4 | 132·0 | – – – | – | – |

Fu, Ca, Co: mean abundance ($N$ 100 cm$^{-2}$) in funnel, cast and control samples.
Bold figures: significant result of ANOVA or Kruskal–Wallis test ($a = 0{\cdot}05$).
MC: multiple comparison of means or samples: Fu–Co, Ca–Co, Fu–Ca. +, Significant ($a = 0{\cdot}05$), –, not significant.
$D_{S-W}$: test on difference in the effects of funnels and casts between summer and winter [summer: September (5 × 3 samples), winter: December (5 × 3 samples)]. +, significant ($a = 0{\cdot}05$), –, not significant, /, calculation not possible.
[a]Including 0·25 mm sieve fraction.

TABLE 6. Station GF: effects of *Arenicola marina* funnels and casts on the macrobenthos. Only species with significant effects are shown

| | All seasons | | | | Summer | | | | Winter | | | | $D_{S\ W}$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | Fu | Ca | Co | MC | Fu | Ca | Co | MC | Fu | Ca | Co | MC | Fu | Ca |
| Molluscs | | | | | | | | | | | | | | |
| All species[a] | **170·5** | **104·9** | **135·8** | − − + | **244·4** | **146·6** | **185·4** | − + + | 89·2 | 59·0 | 81·2 | − − − | − | − |
| All bivalves | **84·7** | **50·6** | **66·3** | + − + | **94·6** | **54·3** | **75·1** | − + + | 73·8 | 46·7 | 56·6 | − − − | − | − |
| *Macoma balthica* | **38·2** | **24·1** | **28·4** | − − + | **41·7** | **26·2** | **29·0** | + − + | 34·5 | 21·8 | 27·8 | − − − | − | − |
| *Mysella bidentata* | **30·4** | **12·0** | **16·8** | + − + | **35·0** | **10·7** | **18·3** | + + + | 25·3 | 13·4 | 16·3 | − − − | − | − |
| All gastropods | 2·9 | 1·7 | 1·7 | − − − | **4·9** | **1·6** | **2·4** | − − + | 1·1 | 1·9 | 1·1 | − − − | − | − |
| Polychaetes and Oligochaetes | | | | | | | | | | | | | | |
| All species[a] | **286·5** | **192·7** | **357·6** | + + + | **286·1** | **202·1** | **399·7** | + + + | **287·0** | **182·4** | **311·4** | − + + | + | − |
| Sessile species | **155·0** | **89·3** | **197·7** | + + + | **194·6** | **111·0** | **257·1** | + + + | **118·9** | **69·7** | **143·8** | − + + | − | − |
| *Pectinaria koreni* | **2·0** | **0·3** | **2·6** | − + + | **1·9** | **0·2** | **2·8** | − + + | 2·1 | 0·4 | 2·4 | − − − | − | − |
| *Polydora quadrilobata* | **12·7** | **6·0** | **15·4** | − + + | **11·8** | **6·6** | **18·1** | + + − | **13·8** | **5·4** | **12·6** | − + + | + | − |
| *Pygospio elegans* | **138·2** | **78·4** | **177·1** | − + + | **166·2** | **95·2** | **233·9** | + + + | **107·4** | **60·0** | **114·6** | − + − | − | − |
| Motile species | **55·2** | **73·0** | **104·3** | + + + | **43·1** | **67·7** | **89·4** | + + + | **66·2** | **78·0** | **117·9** | + + − | − | − |
| *Aricidea jeffreysii* | **27·5** | **34·5** | **41·0** | + − − | 24·9 | 30·7 | 35·1 | − − − | 30·3 | 38·6 | 47·5 | − − − | − | − |
| *Chaetozone setosa* | **17·9** | **16·9** | **27·0** | + + − | **10·3** | **13·2** | **18·2** | + − + | **26·3** | **20·7** | **36·7** | + + − | − | − |
| *Pholoe minuta* | **6·2** | **0·8** | **3·1** | − − + | 2·5 | 1·2 | 1·8 | − − − | **10·3** | **0·4** | **4·5** | − + + | − | − |
| *Scoloplos armiger* | **11·1** | **8·1** | **15·2** | − + − | 10·0 | 8·9 | 14·0 | − − − | 12·5 | 7·3 | 16·6 | − − − | − | − |
| *Streptosyllis websteri* | **11·5** | **7·0** | **11·2** | − − + | **11·8** | **6·7** | **13·8** | − + + | 11·1 | 7·4 | 8·4 | − − − | − | − |
| Crustaceans | | | | | | | | | | | | | | |
| All species[a] | **23·4** | **14·3** | **31·4** | + + + | **19·3** | **12·0** | **32·1** | + + + | **28·0** | **16·8** | **30·5** | − + + | − | − |
| *Caprella* sp. | **6·9** | **3·0** | **9·0** | − + + | 5·5 | 1·3 | 8·3 | − − − | 8·4 | 4·8 | 9·9 | − − − | − | − |
| *Corophium insiduosum* | 2·5 | 1·5 | 3·2 | − − − | **2·2** | **1·1** | **4·5** | + + − | 3·0 | 2·0 | 1·5 | − − − | − | − |
| *Phoxocephalus holboelli* | **9·2** | **7·0** | **11·2** | − + − | **7·0** | **7·4** | **12·5** | + + − | **11·7** | **6·5** | **9·9** | − + + | − | − |
| All taxa | | | | | | | | | | | | | | |
| All species[a] | **480·4** | **321·2** | **524·9** | + + + | **549·8** | **360·9** | **617·5** | − + + | **404·2** | **258·7** | **423·1** | − + + | − | − |

Fu, Ca, Co: mean abundance ($N$ 100 cm$^{-2}$) in funnel, cast and control samples.
Bold figures: significant result of ANOVA or Kruskal–Wallis test ($\alpha = 0{\cdot}05$).
MC: multiple comparison of means or samples: Fu–Co, Ca–Co, Fu–Ca. +, Significant ($\alpha = 0{\cdot}05$), −, not significant.
$D_{S\ W}$: test on difference in the effects of funnels and casts between summer and winter [summer: June–September (22 × 3 samples), winter: October—May (20 × 3 samples)]. +, significant ($\alpha = 0{\cdot}05$), −, not significant.
[a]Including 0·25 mm sieve fraction.

TABLE 7. Station BE: effects of *Arenicola marina* funnels and casts on the macrobenthos. Only species with significant effects are shown

| Taxon | Fu | Ca | Co | MC |
|---|---|---|---|---|
| Molluscs | | | | |
| All species[a] | **321·9** | **66·1** | **104·1** | + + + |
| All bivalves | **270·8** | **55·2** | **84·6** | + − + |
| *Corbula gibba* | **75·3** | **18·7** | **13·2** | + − + |
| *Macoma balthica* | **20·8** | **10·0** | **14·3** | − − + |
| *Mysella bidentata* | **120·7** | **21·9** | **30·3** | + − + |
| *Syndosmya alba* | **28·5** | **2·8** | **8·4** | + − + |
| All gastropods | 4·4 | 0·3 | 2·2 | − − − |
| *Onoba striata* | **3·4** | **0·3** | **0** | + − − |
| Polychaetes and Oligochaetes | | | | |
| All species[a] | **138·3** | **56·9** | **117·6** | − + + |
| Sessile species | **52·5** | **9·3** | **28·3** | − + + |
| *Pectinaria koreni* | **18·8** | **1·6** | **3·1** | − − + |
| *Pherusa plumosa* | **5·6** | **0·9** | **0·7** | + − − |
| *Terebellides stroemi* | **0** | **0** | **4·0** | + + − |
| Motile species | 56·9 | 35·2 | 45·7 | − − − |
| *Aricidea jeffreysii* | **0·3** | **3·1** | **4·7** | + − − |
| *Pholoe minuta* | **12·8** | **1·3** | **3·8** | − − + |
| Crustaceans | | | | |
| All species[a] | **5·3** | **3·7** | **10·3** | + + − |
| *Diastylis rathkei* | **2·8** | **2·2** | **6·2** | − + − |
| All taxa | | | | |
| All species[a] | **465·6** | **126·7** | **231·9** | + + + |

Fu, Ca, Co: mean abundance ($N$ 100 cm$^{-2}$) in funnel, cast and control samples.
Bold figures: significant result of ANOVA or Kruskal–Wallis test ($a = 0{\cdot}05$).
MC: multiple comparison of means or samples: Fu–Co, Ca–Co, Fu–Ca. +, Significant ($a = 0{\cdot}05$); −, not significant.
[a]Including 0·25 mm sieve fraction.

effect of casts on molluscs at all levels (summer: negative; winter: n.s.) with the exception of *Mya arenaria*. In polychaetes, the effects of funnels and casts are different between summer (negative) and winter (n.s.), except for motile polychaetes. In crustaceans, *Bathyporeia* sp. shows a distinct seasonal difference in funnel and cast effects, but a statistical test could not be applied here (division by zero).

### *Differences in strength and direction of burrow effects among macrofaunal groups*

The *A. marina* burrow effects on abundance were compared among the five macrofaunal groups (bivalves, gastropods, sessile polychaetes, motile polychaetes and crustaceans) at each station and for summer and winter separately (Figure 2). At KF no significant differences could be detected, and thus it is not included in Figure 2. At GF, the funnel effects differ in summer between bivalves (positive) and polychaetes (negative) + crustaceans (negative), and between gastropods (positive) and crustaceans. In winter only bivalves (positive) and sessile polychaetes (negative) are affected differently. All cast effects are negative in summer, but there are differences between crustaceans and bivalves + motile polychaetes, and between sessile and motile polychaetes. In winter there are differences between gastropods (n.s.) and bivalves (n.s.) + polychaetes (negative),

TABLE 8. Station WH: effects of *Arenicola marina* funnels and casts on the macrobenthos. Only species with significant effects are shown

| | All seasons | | | | Summer | | | | Winter | | | | $D_{S-W}$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | Fu | Ca | Co | MC | Fu | Ca | Co | MC | Fu | Ca | Co | MC | Fu | Ca |
| Molluscs | | | | | | | | | | | | | | |
| All species[a] | **383·4** | **124·8** | **602·6** | − + + | **706·1** | **201·7** | **1151·5** | − + + | 62·4 | 47·8 | 53·6 | − − − | − | + |
| All bivalves | **140·6** | **61·2** | **144·6** | − + + | **238·4** | **101·2** | **263·5** | − + + | 42·8 | 21·2 | 25·6 | − − − | − | + |
| *Macoma balthica* | **118·9** | **55·0** | **124·0** | − + + | **202·7** | **90·7** | **224·7** | − + + | 35·1 | 19·3 | 23·3 | − − − | − | + |
| *Mya arenaria* | **15·2** | **4·3** | **11·0** | − − + | **23·4** | **6·7** | **19·6** | − − + | **6·9** | **1·9** | **2·3** | − − + | − | − |
| All gastropods | **21·1** | **13·6** | **26·7** | − + + | **26·6** | **4·0** | **37·3** | − + + | 15·6 | 23·2 | 16·0 | − − − | − | + |
| *Hydrobia* sp. | **20·0** | **13·4** | **23·2** | − + − | **25·1** | **3·6** | **30·4** | − + + | 14·9 | 23·2 | 16·0 | − − − | − | + |
| *Retusa obtusa* | 1·1 | 0·2 | 3·5 | − − − | **1·5** | **0·4** | **6·9** | + + − | 0 | 0 | 0 | / / / | / | / |
| Polychaetes and Oligochaetes | | | | | | | | | | | | | | |
| All species[a] | **362·9** | **288·6** | **656·8** | + + + | **311·9** | **128·8** | **828·2** | + + + | 413·8 | 448·4 | 485·3 | − − − | + | + |
| Sessile species | **252·6** | **227·2** | **550·2** | + + − | **182·2** | **81·0** | **689·2** | + + + | 322·4 | 373·3 | 411·1 | − − − | + | + |
| *Pygospio elegans* | **212·4** | **196·0** | **513·3** | + + − | **157·3** | **66·8** | **669·5** | + + + | 267·4 | 325·2 | 357·0 | − − − | + | + |
| Motile species | 58·9 | 46·3 | 56·5 | − − − | 35·2 | 26·6 | 44·1 | − − − | 73·9 | 60·4 | 59·7 | − − − | − | − |
| Crustaceans | | | | | | | | | | | | | | |
| All species[a] | 32·7 | **60·4** | **74·8** | + − + | **16·0** | **27·1** | **44·2** | + − + | **49·3** | **93·6** | **105·3** | + − + | − | − |
| *Bathyporeia* sp | **2·9** | **12·7** | **2·5** | − + + | **0** | **17·1** | **0** | − + + | 5·8 | 8·4 | 3·9 | − − − | / | / |
| *Corophium volutator* | **25·8** | **47·1** | **69·1** | + − − | **8·5** | **8·9** | **38·2** | + + − | **43·1** | **85·1** | **100·0** | + − + | − | − |
| All taxa | | | | | | | | | | | | | | |
| All species[a] | 779·8 | 473·7 | 1334·1 | − + + | **1034·0** | **357·6** | **2023·9** | + + + | 525·5 | 589·8 | 633·2 | − − − | + | + |

Fu, Ca, Co: mean abundance ($N$ 100 cm$^{-2}$) in funnel, cast and control samples.
Bold figures: significant result of ANOVA or Kruskal–Wallis test ($\alpha = 0·05$).
MC: multiple comparison of means or samples: Fu–Co, Ca–Co, Fu–Ca. +, Significant ($\alpha = 0·05$); −, not significant.
$D_{S-W}$: test on difference in the effects of funnels and casts between summer and winter [summer: June & July (10 × 3 samples); winter: November–March (10 × 3 samples)]. +, Significant ($\alpha = 0·05$); −, not significant; /, calculation not possible.
[a]Including 0·25 mm sieve fraction.

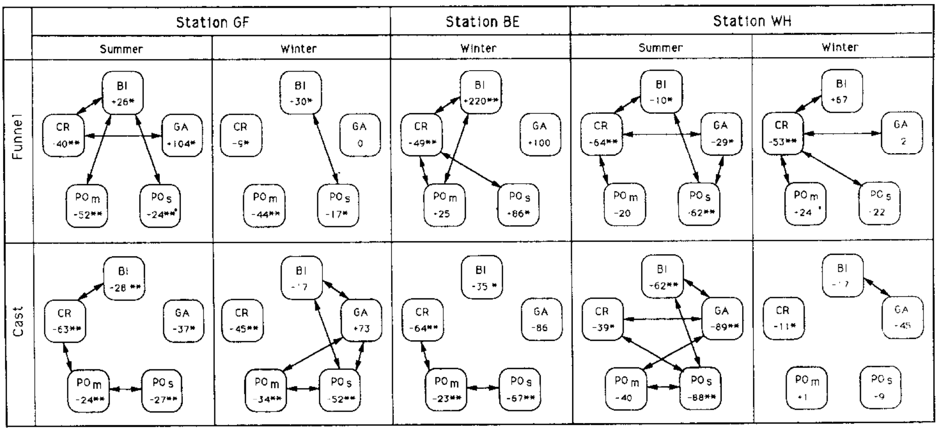

Figure 2. Differences in the effects of *Arenicola marina* burrows among macrofaunal groups. Arrows: significant ($a = 0{\cdot}05$) difference in the effect of funnels or casts. BI, bivalves; GA, gastropods; $PO_s$, sessile polychaetes; $PO_m$, motile polychaetes; CR, crustaceans. Figures indicate average deviation (%) from control abundance. *Significant difference among funnel, cast and control samples (ANOVA). **Significant difference between particular burrow site and control samples.

between bivalves and sessile polychaetes, and between sessile polychaetes and motile polychaetes.

At BE, the effect of funnels is different between crustaceans (negative) and bivalves (positive) + polychaetes (positive), and between bivalves and crustaceans + sessile polychaetes. All cast effects are negative, but different between motile polychaetes and sessile polychaetes + crustaceans.

At WH, the effects of funnels differ in summer between bivalves + gastropods and crustaceans + sessile polychaetes, and between motile polychaetes (n.s.) and crustaceans, although they are negative in all groups. In winter, the crustaceans (negative) differ from all the other groups (n.s.). In summer the cast effects, which are negative in all groups, are stronger in gastropods + sessile polychaetes than in the other groups, whereas in winter only gastropods (n.s.) and bivalves (n.s.) are affected differently.

### *Differences among stations*

Figure 3 shows the results of the comparison of *A. marina* burrow effects among the four stations and with respect to macrofaunal groups and seasons. Gastropods are not included in Figure 3, because no significant differences were detected in this group.

For bivalves, funnel effects are different between KF (n.s.) and GF (negative) in summer, and between BE (negative) and GF (n.s.) + WH (n.s.) in winter. Casts show different effects only in summer, the negative effect being stronger at WH than at GF. For sessile polychaetes, the negative funnel effect is stronger at WH than at GF in summer. In winter there is a difference between BE (positive) and GF (negative). Significant cast effects are always negative; in summer they are stronger at WH than at KF and GF, and in winter they are weaker at WH (n.s.) than at GF and BE.

Different effects on motile polychaetes were found in winter only. The negative funnel effect at GF differs from the weak effects at BE and WH in summer, and the negative cast effect at GF differs from the insignificant effect at WH. For crustaceans, the negative effect of funnels is stronger at WH than at GF in both seasons.

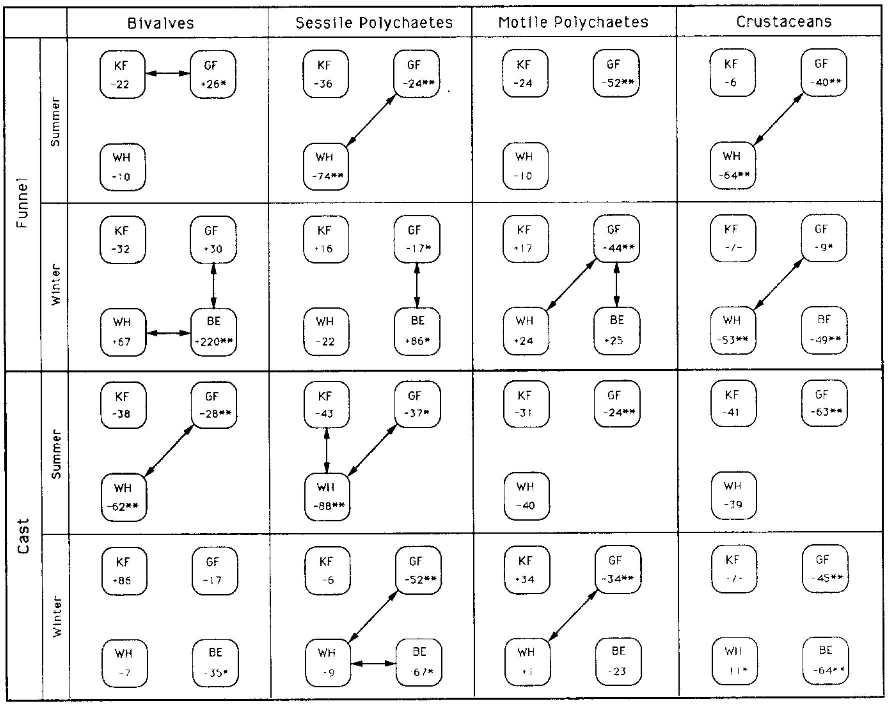


Figure 3. Differences in the effects of *Arenicola marina* burrows among stations. Arrows: significant ($a = 0{\cdot}05$) difference in the effect of funnels or casts. Station BE was not sampled during summer.

## Discussion

### Arenicola marina *local migration*

The frequent change of the position of funnel and cast, which was observed both at station GF and in laboratory experiments using natural sediments from this station conflicts with the observations of Rijken (1979), Schwarz (1939), Thamdrup (1935), Wells (1944) and others. All these authors agree that the position of the funnel may change quite frequently, but the position of the casts usually remains constant over weeks. However, all these observations refer to animals and sediments from intertidal flats with sediments rich in organic content (>1%, see e.g. Cadée, 1976; Linke, 1939), whereas the present observations refer to a subtidal sandy flat with a much lower organic content (about 0·3%).

The combination of a more compacted sediment with the tidal cycle determines the nature of the typical Wadden Sea burrow (station WH, Table 3). Here the funnel is flat and shallow and the lugworm feeds mainly on material from the sediment–water interface, which is very rich in bacteria, microflora, microfauna and detritus. Tides and waves continuously provide new food. In contrast, the less compacted sediment at station GF precludes the formation of stable funnels, and the animal has to feed on the whole sediment column, which is not as rich in food as the sediment–water interface. Therefore it may be that *A. marina* exhausts its food resource at one locality within a few days and has to move to another, unexploited area. At the vacated site, bacterial and microfaunal abundances then presumably recover until colonization by a lugworm occurs again.

*Effects of* Arenicola marina *funnels and casts on macrobenthos abundance*

The Results section outlines the differences in the effects of funnels and casts of *A. marina* with respect to macrofaunal groups and species (Tables 5–8, Figure 2), seasons (Tables 5–8), and stations (Figure 3). To explain these observed effects, qualitative models can be developed, which include the activities of *A. marina*, the macrofauna, and the hydrodynamic conditions.

*The effects of* Arenicola marina *funnels.* The effects of the funnels are not consistent, neither among stations nor among macrobenthic groups. Molluscs, especially small species such as *Mysella bidentata*, show increased abundance at the funnel sites at stations GF and BE. The positive funnel effect on bivalves differs significantly from the effect of funnels on other faunal groups, especially in summer, and also from the effect of funnels on bivalves at other stations, which is not significant in most cases. Sessile polychaetes are affected negatively by the funnels at stations GF and WH. This effect does not differ between seasons at GF, but does at WH, where it is significantly stronger than at GF in summer and not present in winter. At BE the abundance of sessile polychaetes is significantly increased at the funnel sites, except for *Terebellides stroemi*.

The effect of funnels on motile polychaetes is negative at GF but insignificant at the other stations (significant difference between GF and BE + WH in winter). This difference may be related to the dominance of small infaunal species at GF such as *Aricidea jeffreysii* (which is also negatively affected at station BE) and *Chaetozone setosa*. Motile epibenthic species are not affected, e.g. *Anaitides maculata* (GF, BE, WH), or show increased abundance at the funnel sites, e.g. *Pholoe minuta* (GF, BE) and *Streptosyllis websteri* (GF). Crustaceans are affected negatively in both seasons and at all stations with the exception of KF. The strongest effect is found at WH (significantly stronger than at GF), where the tube-building amphipod *Corophium volutator* is the most abundant species.

In order to explain this somewhat confusing picture, three factors must be taken into account: (1) behaviour and living mode of the species considered, (2) *A. marina* feeding activity, and (3) hydrodynamic conditions.

(1) Species behaviour: The crucial point is whether or not an animal is able to select or change its position actively in relation to a funnel site. Recruitment via free-swimming larvae may allow for an active choice of the place of settlement. A motile or hemisessile life-style enables the adult animal to migrate in and out of the funnel site. However, larvae and adults may also be passively redistributed by wave and current impact.

(2) *A. marina* feeding activity: With respect to this factor, a funnel can be interpreted as a flow-through system, through which surface sediment is transported laterally from the edge of the funnel depression to the centre and downward from the centre to the depth of the lugworm itself. This transport also includes those animals which are not able to escape actively.

(3) Hydrodynamic conditions affect the performance of funnels as particle traps (see Aller & Aller, 1986; Savidge & Taghon, 1988) directly via resuspension and sedimentation and indirectly via sediment type and the corresponding funnel type. The latter also affects the lateral/downward transport of surface sediment (see above). The relations between these three factors determine whether the abundance of a certain species at a funnel site is above, below, or equal to control site abundance. Figure 4 illustrates these interactions.

The abundance of motile species will depend on the attractivity of the funnel sites, which may provide more food for scavengers such as *Pholoe minuta* (GF, BE) or *Onoba*

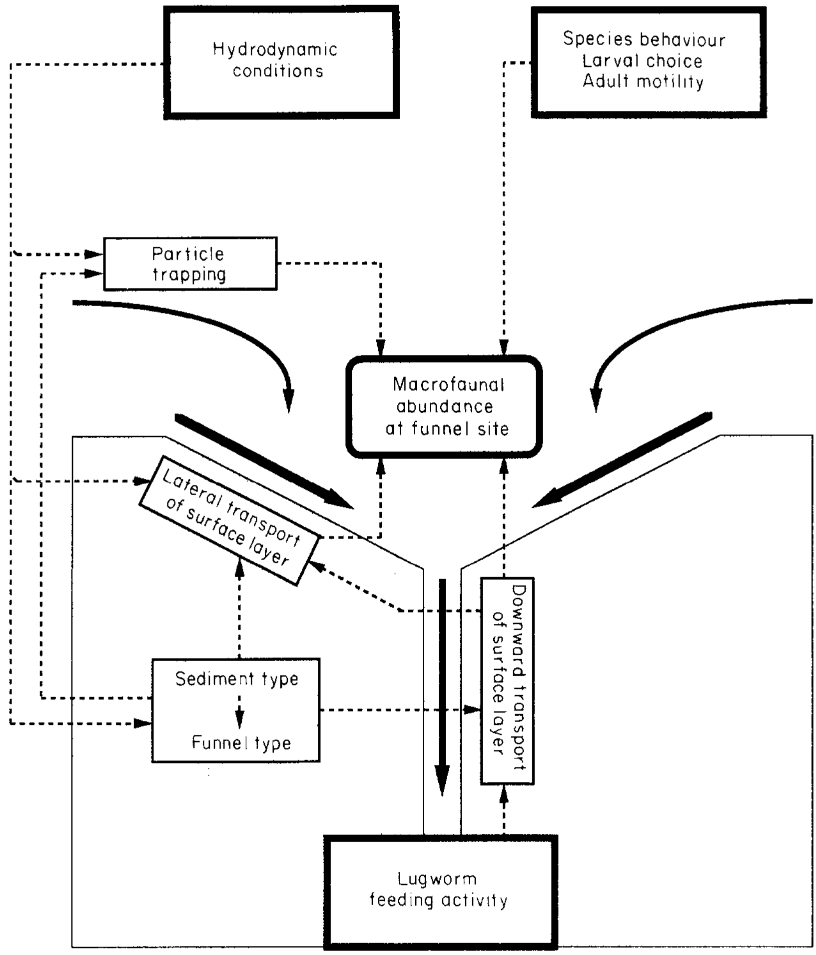


Figure 4. Factors controlling macrofaunal abundance at the site of an *Arenicola marina* feeding funnel. Stippled arrows indicate direction of control.

*striata* (BE) or better shelter from predators. Motile and hemisessile surface and subsurface deposit feeders (e.g. *Aricidea jeffreysii, Chaetozone setosa, Pygospio elegans* or *Corophium* spp.) show reduced abundances at the funnel sites. Adult specimens may avoid the funnels or emigrate, as described by Brenchley (1981) and Wilson (1981), and/or funnel sites may be avoided by settling larvae (Butman, 1987; Woodin, 1985). The sessile polychaete *Terebellides stroemi*, of which very small specimens were only found in the control samples at station BE, may be another example of active habitat selection by settling larvae.

The increased abundance of small molluscs in the funnel samples at the subtidal stations BE and GF (summer only), and of sessile polychaetes at station BE but not at the stations KI and WH (see Figure 3), may be related to the different funnel types. At KF the hydrodynamic conditions prevent the formation of funnel depressions; therefore, the funnels cannot act as particle traps. The deep and steep funnels at stations BE and GF enhance particle trapping, but they reduce the downward transport of surface sediment; thus immotile small macrobenthos is accumulated in the funnels. At the intertidal station

WH the funnels are not so steep-sided and deep as at stations GF and BE, and so they may not be as efficient as particle traps. Additionally, in funnels of this type only the uppermost sediment layer and the animals therein are transported downward. This may lead to a higher mortality rate and may keep the abundance of the accumulated animals below control levels.

The distinct seasonal difference in the funnel effects at station WH, with strong effects in summer and mostly weak or insignificant effects in winter, is due to the distinct seasonal changes in the hydrodynamic conditions. In winter, increased wave and current impact frequently destroy the funnel structures and redistribute small surface-living animals. In contrast, no seasonal differences are detectable at KH because the hydrodynamic impact is strong and independent of the season. At GF, the weak differences in the funnel effects correspond well to the small seasonal difference in hydrodynamic impact. No summer samples have been taken at BE, but it is most likely that at this deep station (19 m), with a more or less constant hydrodynamic regime, the funnel effects are independent of the season.

*The effects of* Arenicola marina *casts.* In general, the casts of *A. marina* have distinct negative effects on the abundance of many macrobenthic groups and species at all stations except at KF. These effects are much stronger in summer than in winter at station WH and slightly different between seasons at GF. In summer, most cast effects are strongest at WH, but in winter some groups are significantly more strongly affected at GF and BE (Figure 3). Within stations, the intensity of the cast effects can differ among macrofaunal groups (Figure 2). Small bivalves such as *Mysella bidentata* (GF) or juvenile *Macoma balthica* (WH, summer), small motile polychaetes such as *Chaetozone setosa* (GF) and tube-builders such as *Pectinaria koreni* (GF, BE), spionids (GF, WH) or *Corophium* spp. (GF, WH) are especially seriously affected, as are some motile epibenthic species also, e.g. the gastropods *Hydrobia* sp. and *Retusa obtusa* (WH) and the polychaete *Pholoe minuta* (GF).

A simple model was developed, analogous to the funnel effects, which combines (1) species behaviour, (2) *A. marina* defaecation activity and (3) hydrodynamic conditions to explain the observed cast effects (Figure 5).

(1) Species behaviour: Again the motility of larval and adult animals is the crucial point (see above).

(2) *A. marina* defaecation: Like a funnel, a cast may be interpreted as a sediment flow-through system. On one side, sediment is imported into this system by the defaecation activity of the lugworm (up to 80 g dry weight day$^{-1}$, see Cadée, 1976). The faeces are deposited at the sediment surface; thus, from a benthic animal's point of view, defaecation by *A. marina* is an extreme type of sedimentation.

(3) Hydrodynamic conditions are responsible for the export of sediment from a cast via erosion. The hydrodynamic conditions affect two parameters of the cast system. These are the export rate, i.e. the amount of sediment which is eroded per unit of time, and indirectly the relation between sediment import by the lugworm and sediment export by erosion, that is the maximum accumulated amount of sediment (i.e. the size of the cast). Many motile species seem to avoid the cast sites, e.g. the polychaetes *Chaetozone setosa* (GF), *Pholoe minuta* (GF, BE) and *Scoloplos armiger* (GF), or the gastropods *Hydrobia* sp. and *Retusa obtusa* (WH). At the cast sites microbial activity (Reichardt, 1988) and meio-faunal abundance (Reise, 1981, 1987) are lower than in flat surface sediments; therefore casts may not offer enough food for animals depending on these sources. At WH all samples were taken during low tide, i.e. the motile animals may have preferred the wet

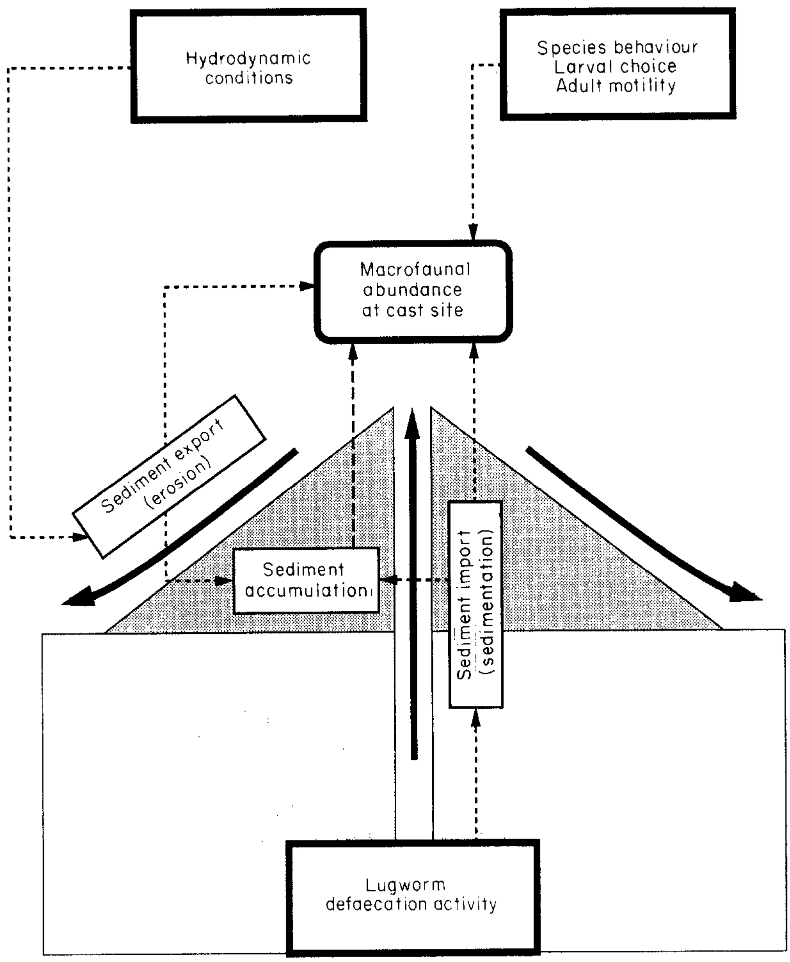


Figure 5. Factors controlling macrofaunal abundance at the site of an *Arenicola marina* defaecation cast. Stippled arrows indicate direction of control.

sediment surface to drier casts. The striking distribution of the amphipod *Bathyporeia* sp., which was found in the cast samples exclusively in summer, may be explained by its behaviour. From personal observations and information kindly provided by F. Buhs (Kiel), *Bathyporeia* sp. crawls around the sediment surface during low tide. A moving shadow, e.g. of a scientist taking samples, induces an escape reaction of the animal into the sediment of the casts.

Sessile and hemisessile species show strongly reduced abundance at the cast sites. Pelagic larvae may avoid the casts actively or may be prevented from settling at this site passively by small-scale hydrodynamic effects of the casts (see Butman, 1987). With respect to demersal recruits and adult specimens, both sediment import (i.e. sedimentation) by the lugworm and sediment export (i.e. erosion) by wave and current action may affect abundance negatively. The observations of Brenchley (1981), Turk and Risk (1981) and Wilson (1981) indicate that especially tube builders and other species of low motility which feed at the sediment surface or from the water column are negatively affected by increased sedimentation. Therefore the defaecation activity of *A. marina* is assumed to be one source of the observed negative cast effects. However, it is most likely that the average defaecation activity of an adult lugworm is the same at the four stations, so defaecation is not sufficient to explain the significant differences among the stations (Figure 3). Therefore, the impact of erosion has to be taken into account, as has been shown for many subtidal and intertidal species (Allen & Moore, 1987).

At KF, each faecal string is eroded the moment it is deposited at the surface. No casts are accumulated and the rate of erosion is equal to the rate of sediment import all the time. At the subtidal stations GF and BE, sediment is accumulated until a certain equilibrium size of the cast is reached. When the lugworm changes position, the abandoned cast is normally eroded slowly, only strong gales quickly eroding the casts at GF (pers. obs.). At the intertidal station WH, sediment is accumulated during low tide and also during high tide if the weather is calm, but during tidal change the casts are completely eroded within an hour. That is, in summer there is a continuous change between 6-h periods of sediment accumulation and short periods of heavy erosion, whereas during winter casts are smaller and irregular large-scale hydrodynamic events occur more frequently.

These differences in cast size (i.e. amount of accumulated sediment) and erosion (i.e. short-term sediment export rates) may explain the different strength of the cast effects among the four stations and between seasons at WH. All those animals which live and/or feed in a relatively narrow sediment horizon, either at the sediment–water interface or in some shallow depth (cm) have to adapt their position continuously to the changing level of the sediment–water interface. The energetic costs of this adaptation may be a serious disadvantage of living at a cast site. Tube builders like *Pectinaria koreni* (GF, BE), spionids (all stations) or the amphipod *Corophium* spp. (GF, WH) have particular problems, because the tubes may be modified or damaged. Jensen (1980) made similar observations on the nematode *Chromadora lorenzeni*, which is also thought to be a tube builder (Jensen, pers. comm.). At a subtidal site in the Øresund (Denmark) the abundance of this species was reduced by 98% at the cast sites (and by 73% at the funnel sites). On the other hand, small free-living specimens such as most of the juvenile molluscs are unable to avoid passive redistribution due to cast erosion.

These changes in the level of the sediment–water interface are most intensive at WH during summer, where casts are produced and eroded in a 6-h rhythm. At the subtidal stations GF and WH the short-term sediment export rates are much lower than at station WH, and only during strong gales are casts eroded completely within a short period of time. Therefore, the negative effect of the casts depends on sedimentation, sediment accumulation and more or less continuous erosion at these stations. In particular small specimens which live in the sediment–water interface may have difficulties in surviving in a site of continuous sedimentation and erosion. However, they are affected to a greater extent by the high short-term sediment export rate at station WH during summer (Figure 3). At station KF, a continuous process of sedimentation and erosion occurs, but the effects on the fauna are very weak. The permanent wave-induced disturbance at this station prevents the formation of casts and the development of strong cast effects. The situation is similar at station WH during winter, when the activity of *A. marina* is lower and direct impact by non-tidal wave and current action is stronger; thus the effects of the casts are masked by hydrodynamic effects.

### *Implications for macrobenthic community structure*

At the stations GF, BE and WH biological disturbance by *A. marina* plays an important role in the development of benthic soft-bottom community structure in space and time.

Funnels and especially casts are patches of reduced macrobenthic abundance and different species composition. The direct effect of *A. marina* on certain species may be amplified by the strong negative effect of *A. marina* on tube builders, which has also been found by Brenchley (1981), Wilson (1981) and Woodin (1981). As shown by Gallagher *et al.* (1983), Neumann and Scoffin (1970), Rhoads *et al.* (1978), Reise (1981) and others, tube builders stabilize the sediment and facilitate colonization by other species. *A. marina* acts as an antagonist to this facilitation effect of tube builders.

The local migration behaviour of *A. marina* at the subtidal stations adds a dynamic component to this system of disturbed and undisturbed patches. The spatial arrangement of these patches is not constant with time, but changes continuously. A system of this kind corresponds well with the model of disturbance-induced small-scale temporal mosaics, which was developed by Grassle and Sanders (1973). A model of community regulation proposed by Menge and Sutherland (1987) predicts a shift from biological control to physical control with increasing environmental stress in communities of low trophic structure. This is in good agreement with the observed differences among stations BE, GF, KF and WH (winter only). The stronger the hydrodynamic impact, the weaker are the effects of bioturbation by *A. marina*. However, biological factors (i.e. bioturbation of *A. marina*) do affect the community significantly at the intertidal station WH during summer, although it is exposed to distinct environmental stress (i.e. disturbance due to tides). In future investigations on the effects of small-scale biological disturbances, the hydrodynamic conditions as well as the living mode of the affected species should be taken into account to avoid generalizations which are based on singular observations.

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