

Benthic grazers and suspension feeders: which one assumes the energetic dominance in Königshafen?

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ABSTRACT: Size-frequency histograms of biomass, secondary production, respiration and energy flow of 4 dominant macrobenthic communities of the intertidal bay of Königshafen were analysed and compared. In the shallow sandy flats (*Nereis-Corophium*-belt [N.C.-belt], seagrass-bed and *Arenicola*-flat) a bimodal size-frequency histogram of biomass, secondary production, respiration and energy flow was found with a first peak formed by individuals within a size range of 0.10 to 0.32 mg ash free dry weight (AFDW). In this size range, the small prosobranch *Hydrobia ulvae* was the dominant species, showing maximal biomass as well as secondary production, respiration and energy flow in the seagrass-bed. The second peak of the size-frequency histogram was formed by the polychaete *Nereis diversicolor* with individual weights of 10 to 18 mg AFDW in the N.C.-belt, and by *Arenicola marina* with individual weights of 100 to 562 mg AFDW in both of the other sand flats. Biomass, productivity, respiration and energy flow of these polychaetes increased from the *Nereis-Corophium*-belt, to the seagrass-bed, and to the *Arenicola*-flat. Mussel beds surpassed all other communities in biomass and the functional parameters mentioned above. Size-frequency histograms of these parameters were distinctly unimodal with a maximum at an individual size of 562 to 1000 mg AFDW. This size group was dominated by adult specimens of *Mytilus edulis*. Averaged over the total area, the size-frequency histogram of energy flow of all intertidal flats of Königshafen showed one peak built by *Hydrobia ulvae* and a second one, mainly formed by *M. edulis*. Assuming that up to 10 % of the intertidal area is covered by mussel beds, the maximum of the size-specific energy flow will be formed by *Mytilus*. When only 1 % is covered by mussel beds, then the energy flow is dominated by *H. ulvae*. Both animals represent different trophic types and their dominance in energy flow has consequences for the food web and the carbon flow of the total area. If the energy flow of the macrozoobenthos of Königshafen is dominated by *M. edulis*, then the primary energy has to be gained from the pelagic primary production and the total ecosystem will be dependent on energy input from the North Sea and deeper parts of the adjacent Wadden Sea. In the case of a dominance of *H. ulvae*, the energy flow of Königshafen is mainly based on autochthonous primary production.

INTRODUCTION

Many parameters structuring faunal assemblages show a distinct size distribution. The relation between abundance and body size has been modelled as a power function. From terrestrial populations, some authors have reported negative exponents (Brown & Maurer, 1986; Damuth, 1987; 1991), while others show exponents not significantly different from zero (Morse et al., 1988). The former implies that in these populations, specimens use equivalent amounts of energy regardless of their body size, while the latter implies an energetic dominance by larger individuals (Griffiths, 1992). The slope of

abundance-size relations may be a test of the hypothesis that energy availability limits the abundance of differently sized organisms. In natural assemblages, this is only true for dominant species (Blackburn et al., 1993). Since the energy supply is also size-dependent, the size distribution has a major impact on respiration (Gerlach et al., 1985), growth processes (Schwinghamer et al., 1986; Edgar, 1990 a; Barry & Tegner, 1990) and, as a result, on the biomass of an animal assemblage (Heip et al., 1984; Boudreaux & Dickie, 1992). Showing the size-dependence of these parameters, it will be possible to obtain information on the effects of animal size within the food web. As a paradigm, predation is strongly related to prey size and, if so, the energy flow from one trophic level to the next will be size-controlled (Cohen et al., 1993).

Structuring the metabolic and growth parameters of an animal assemblage in relation to body size may lead to a way to predict the dynamic role of animal assemblages on the ecosystem level. The importance of body size for productivity of marine fauna is recognized by many authors (Banse & Mosher, 1980; Schwinghamer et al., 1986), mainly from a theoretical point of view. Recent investigations show the practical applicability of making use of the size structure for measurements of secondary production (Edgar, 1990a).

In the tidal flats of Königshafen, macrofauna shows a wide range of sizes from small oligochaetes to large adult mussels and polychaetes. The question arises, whether dominant macrofaunal assemblages show different size-frequency histograms of metabolic and growth characteristics and what the reasons and consequences are for the entire ecosystem.

MATERIAL AND METHODS

Study site

Königshafen is a small intertidal bay (4 km²), situated at the northern tip of the island of Sylt in the North Sea. Sand dunes form a small sandbar which protects the bay in the north and the west from the open North Sea. To the east, the bay is open to the Wadden Sea. The tidal flats are drained by a central channel. The average tidal range is about 1.8 m, with only minor deviations due to neap and spring tides or strong winds. The sediments are mainly sandy with a distinct share of windborne sand from adjacent dunes. Muddy sediments are only found in a sheltered basin in the west. For this investigation, 4 sites were selected which are assumed to be representative of the dominant macrofaunal assemblages. The *Nereis-Corophium*-belt (*N.-C.*-belt) borders the mean high tide line and is 20 to 100 m wide. It is inundated for nearly 2 h during a tidal cycle. The upper part of the sand flat is covered by seagrass-beds which are inundated 4–5 h during a tidal cycle. On sandy sites, the small seagrass *Zostera noltii* is dominant, whereas on mud *Zostera marina* is more abundant. On bare sandflats from the upper shore down to the low-water line, the lugworm *Arenicola marina* shapes the character of the sediment. Because of the wide distribution of this assemblage over a wide range of tidal levels, a study site at mean-tide level (inundation of 6 h per tidal cycle) was selected. This *Arenicola*-flat has the greatest share in the total area of Königshafen. Near the low-tide line, mussels form dense beds. The areal coverage of mussel beds varied in the past particularly due to ice scour during severe winters and dredging by an expanding mussel fishery. The areal extension of the macrofaunal assemblages is shown in Table 1.

Table 1. Areal extension of macrofaunal assemblages of Königshafen in 10^6 m^2 , considering different situations of areal coverage by mussel beds. Mud flats (0.3 to $0.4 \times 10^6 \text{ m}^2$) are not considered

Community	1 %	10 %
<i>Nereis-Corophium</i> -belt	0.34	0.34
Seagrass-bed	0.31	0.46
<i>Arenicola</i> -flat	3.03	2.45
Mussel bed	0.05	0.48

Sampling procedure

Biomass data from macrofauna of the three sand flat communities were obtained during an investigation of productivity and community metabolism in 1980. Two cores (area: $600\text{--}700 \text{ cm}^2$) were examined every month in each of these assemblages in order to measure biomass and secondary production. A subsample of $10 \times 10 \text{ cm}$ surface area was taken from these cores and sieved through a $500\text{-}\mu\text{m}$ mesh sieve. This subsample was used to analyse biomass and abundance of the smaller macrofauna, such as *Hydrobia ulvae*, *Pygospio elegans*, juvenile polychaetes and oligochaetes. The rest of the sediment was sieved through a $1000\text{-}\mu\text{m}$ sieve, to retain the larger macrofauna. Due to the greater variability in the structure of habitat, 6 core samples (surface $10 \times 10 \text{ cm}$) were taken at 6 sites of the mussel bed every month during the whole of 1984. The samples were sieved through $500\text{-}\mu\text{m}$ mesh. From these samples, the total macrofauna was counted at the species level. When animals occurred over a larger size range, different size classes were counted separately.

Determination of biomass and secondary production

The macrofaunal material was separated into species and size groups. These samples were dried at 75°C for about 3 days. After cooling in a desiccator, the samples were weighed. To determine ash free dry weight (AFDW), all samples were burnt in a furnace at 550°C . These data were used to estimate the individual weight as well as the biomass per square metre of species and size groups.

Secondary production was estimated for each species and size group from changes in individual weight and from the mean abundance between two subsequent sampling dates (Crisp, 1984; Asmus, 1987; Brey, 1990). These monthly estimates were extrapolated to one square metre, and added up for a one-year period for species and size classes separately. Summing up yearly production values of all species of a common size group gave the secondary production of this size group. In order to compare biomass and production values with carbon flow, 1g AFDW was assumed to correspond to 0.58 g C (derived from Jannsson & Wulff, 1977; Remmert, 1980).

Respiration measurements

For the dominant macrofauna species, respiration measurements were carried out in closed chambers in the laboratory under in situ temperatures. From these measurements

an allometric regression was calculated between respiration and individual weight for each of the dominant species (Asmus, 1984). Respiration rates of rare species were estimated from the individual sizes, using the allometric regression of the dominant species most similar in taxonomic order and size. Respiration from these experiments was assumed to reflect a mean routine metabolism of the species investigated. Hourly respiration was converted to daily respiration considering the mean inundation time of the community. Respiration during low tide was assumed to be negligible. Most of the investigated species are inactive during low tide, and meet their metabolic requirements by anaerobiosis. This induces an oxygen debt which will be compensated at the beginning of the next inundation. To consider this special activity mode in the respiration measurements, the animals were kept at low-tide conditions before the experiment started. Respiration measurements were carried out for the duration of the mean natural inundation period. For conversion of 1 ml O₂ in g C an oxaloric equivalent of 4687 cal per ml O₂ was assumed, corresponding to 0.38 g C per ml O₂.

The size-specific energy flow of the entire macrofauna was estimated from the sum of both secondary production and respiration per square metre and year for every size range expressed in g C.

RESULTS

Size-frequency histogram of macrofaunal biomass

The size-frequency histogram of macrofaunal biomass showed a bimodal curve in the *Nereis-Corophium*-belt, the seagrass-bed and the *Arenicola*-flat (Fig. 1). Maximum biomass was found in a size group of individual weights of 0.18 to 0.32 mg AFDW in the three communities. This size group consisted mainly of the small prosobranch *Hydrobia ulvae*. In the seagrass-bed, this maximum showed higher biomass values than in both other communities. A second biomass peak was found at individual weights of 10.00 to 17.78 mg AFDW in the *Nereis-Corophium*-belt, at individual weights of 100.00 to 177.83 mg AFDW in the seagrass-bed, and of 316.22 to 562.34 mg AFDW in the *Arenicola*-flat. In the *Nereis-Corophium*-belt, this second peak originated from the polychaete *Nereis diversicolor*. In both other sand bottom communities, *Arenicola marina* contributed most of the biomass within this size peak, showing a shift to a higher individual weight due to the longer inundation of the *Arenicola*-flat. In the mussel bed, the size histogram of biomass was unimodal, showing a maximum at a size group of an individual weight of 0.562–1.0 g AFDW. This maximum was due to adult mussels *Mytilus edulis*. The biomass-size histograms reveal a change in dominance from small sized macrofauna in shallow, shortly inundated parts of the tidal flat to the dominance of larger macrofauna near the low tide level.

Size-frequency histograms of secondary production

Size-frequency histograms of the secondary production show a bimodal pattern in the three sand bottom communities (Fig. 2) similar to the biomass-size spectra. In the *Arenicola*-flat an additional peak is found in the size class of 1.78–3.16 mg AFDW, which was formed by juveniles of the bivalve *Macoma balthica*. The highest production was found at the same individual size as the maximum biomass in the *Nereis-Corophium*-belt

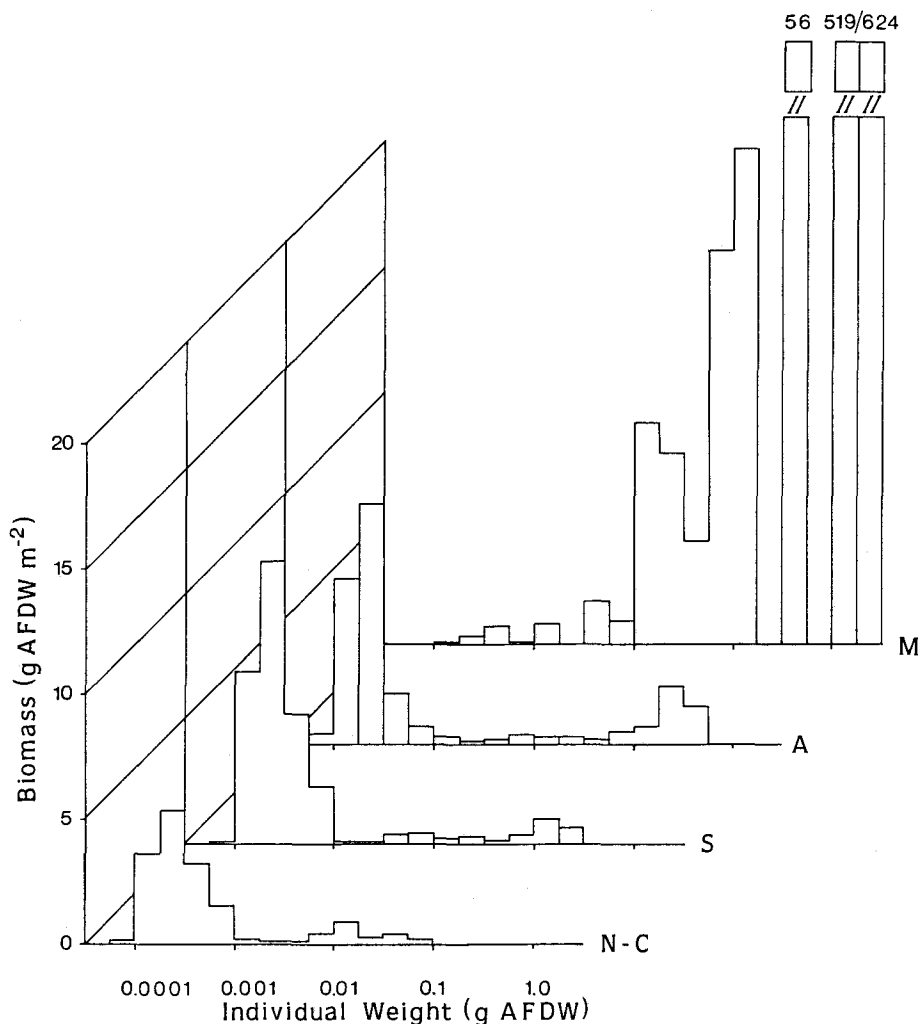


Fig. 1. Size-spectra of macrozoobenthic biomass (g AFDW m^{-2}) and individual weight (g AFDW) of 4 intertidal macrofaunal assemblages of Königshafen. Biomass is indicated as the sum of total biomass of macrofaunal species, averaged over one year, estimated for each size-class. N-C: *Nereis-Corophium*-belt; S: seagrass-bed; A: *Arenicola*-flat; M: mussel bed.

and the seagrass-bed, whereas in the *Arenicola*-flat this was found in a lower size range (0.10 to 0.18 mg AFDW) than that of maximum biomass. This may be due to the greater abundance of juvenile *Hydrobia ulvae*, which tend to grow faster and thus will have a greater production to biomass ratio than older and larger specimens. Maximum production contributed to 51, 61 and 19 % to the total production of the N.C.-belt, the seagrass-bed and the *Arenicola*-flat, respectively. As demonstrated for biomass, the production of this dominant size class was highest in the seagrass-bed. The second peak of the production-size curve was found at an individual weight of 31.62 to 56.24 mg (N.C.-belt),

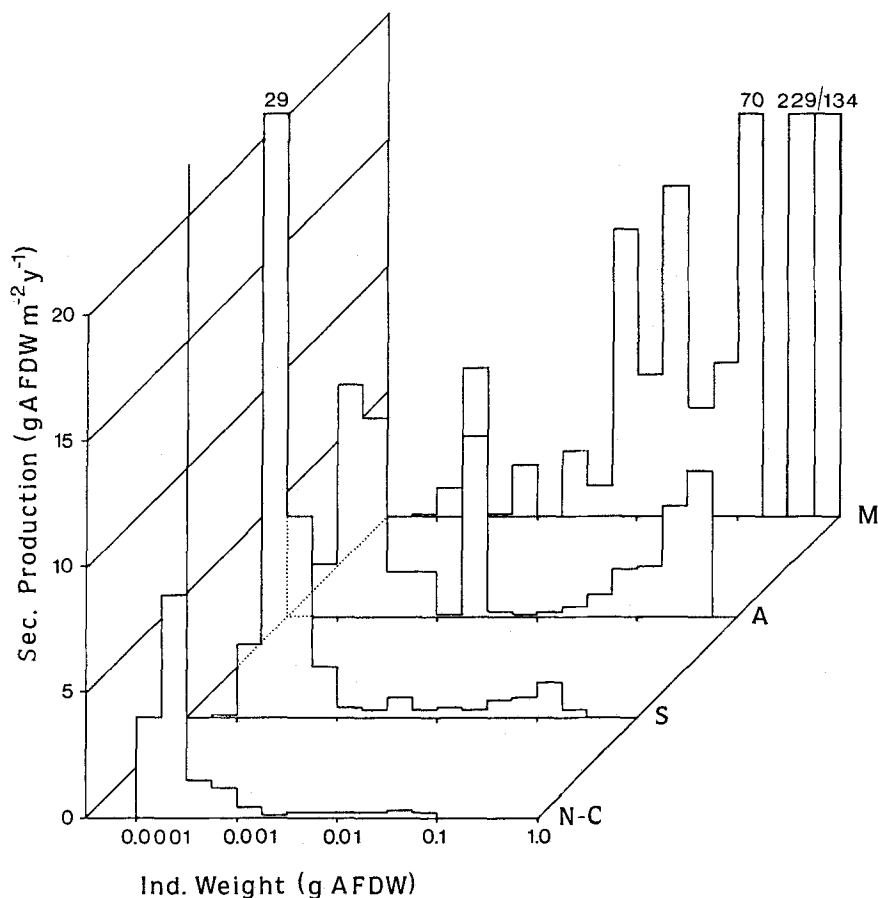


Fig. 2. Size-spectra of macrozoobenthic secondary production ($\text{g AFDW m}^{-2} \text{y}^{-1}$) and individual weight (g AFDW) of 4 intertidal macrofaunal assemblages of Königshafen. Indicated values represent the sum of annual secondary production of each species estimated for each size-class. N-C: *Nereis-Corophium*-belt, S: seagrass-bed; A: *Arenicola*-flat; M: mussel bed.

100.00 to 177.83 mg (seagrass-bed) and 316.23 to 562.34 mg AFDW (*Arenicola*-flat). The longer the inundation time of the community, the higher the individual weight of animals forming this peak. Additionally, the height of production within this peak increases in the same order. In the mussel bed, 47 % of the secondary production is formed by the size group of an individual weight of 562.34 to 1000.00 mg AFDW. This size group consisted mainly of adult *Mytilus edulis*, but these mussels have a lower individual weight than those contributing to maximum biomass. Nevertheless, maximum production is found in the upper range of the whole size spectrum, revealing a unimodal production-size-histogram.

Macrofaunal respiration

The size histogram of macrofaunal respiration reflects similar patterns to those observed in biomass and secondary production. The highest respiration was found at the

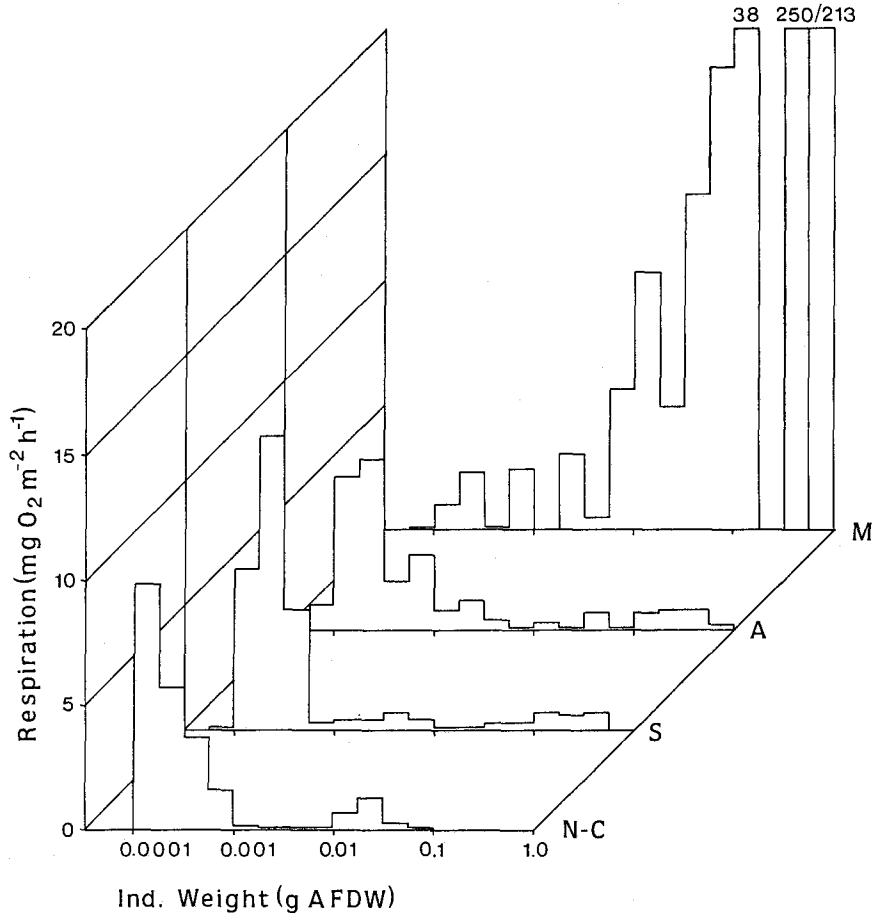


Fig. 3. Size-spectra of macrozoobenthic respiration ($\text{mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$) and individual weight (g AFDW) of 4 intertidal macrofaunal assemblages of Königshafen. The respiration values indicate the sum of the average respiration rate per hour of each species estimated for each size-class. N-C: *Nereis-Corophium*-belt; S: seagrass-bed; A: *Arenicola*-flat; M: mussel bed.

lower size ranges in the three sand bottom communities (Fig. 3). Forty-two % of the total macrofaunal respiration were used by *Hydrobia ulvae* of the size class of 0.10 to 0.18 mg AFDW in the N.C.-belt. In the seagrass-bed and the *Arenicola*-flat, the maximum of respiration (43 % and 27 %, respectively) originated from *H. ulvae* with a size of 0.18 to 0.32 mg AFDW. *Nereis diversicolor* (size range: 17.78 to 31.62 mg AFDW) caused a second respiration peak in the N.C.-belt, and *Arenicola marina* (100.00 to 316.22 mg AFDW) in the seagrass-bed (2.5 %) and in the *Arenicola*-flat (3.2 %). Between maximum respiration at the lower size ranges and the second respiration peak, there was an area of minimum values responding to individual sizes of 1.78 to 10.00 mg AFDW. Maximum respiration (44 % of the total respiration) in the mussel bed was found in the upper size range of adult *M. edulis*. The shape of the size-specific respiration curve was equivalent to that of secondary production. Minimum respiration was found at sizes of less than

0.32 mg AFDW. Total respiration was highest in the mussel bed ($1748 \text{ g C m}^{-2} \text{ y}^{-1}$) followed by the seagrass-bed ($56 \text{ g C m}^{-2} \text{ y}^{-1}$), the *Arenicola*-flat ($39 \text{ g C m}^{-2} \text{ y}^{-1}$) and the *Nereis-Corophium*-belt ($24 \text{ g C m}^{-2} \text{ y}^{-1}$).

Size-specific energy flow

Total net energy flow of the communities decreased from the low-tide line to the upper shore. Highest values were estimated for the mussel bed ($2023 \text{ g C m}^{-2} \text{ y}^{-1}$) and the seagrass-bed ($85 \text{ g C m}^{-2} \text{ y}^{-1}$). In the *Arenicola*-flat ($69 \text{ g C m}^{-2} \text{ y}^{-1}$) and in the *N.C.*-belt ($35 \text{ g C m}^{-2} \text{ y}^{-1}$) energy flow was lower. Size-specific energy flow had a similar bimodal shape as the spectra of biomass, secondary production and respiration for the three sand bottom communities. Energy flow of these communities can be related to two macrofaunal size groups. The first group consisted of small specimens, mainly *Hydrobia ulvae*, with a size range from < 0.10 to 1.78 mg AFDW . Within this group, the energy flow was normally distributed over the entire size ranges. In the *N.C.*-belt, the seagrass-beds and the *Arenicola*-flat, respectively 93 %, 95 % and 78 % of the energy flowing through the macrofauna was concentrated in this group. The share in energy flow of the second group, with a size range larger than 1.78 mg AFDW , was comparably low. The energy flow in this group increased from the *N.C.*-belt to the *Arenicola*-flat, showing the increasing importance of larger animals with longer inundation times.

Mussel beds showed the maximum of energy flow in the upper range of size frequency. Mussel beds may control the energy flow of the total area, because their energy flow per square metre surpassed the other communities by an order of magnitude. This became obvious by a comparison of the total energy flow of the different communities, taking into account their areal extension.

The total energy flow reflected the spatial extension (Table 1). Averaged over the total area of Königshafen, the size-specific energy flow through the macrofauna was dependent on the extension of area covered by mussel beds. Because the area of mussel beds fluctuates from year to year, a comparison of the total energy flow is made between a situation of 1 % (Reise et al., 1994) of the area of Königshafen covered by mussel beds and 10 % coverage by mussel beds (Asmus & Asmus, 1990) (Fig. 4). Both cases showed a bimodal-shaped curve. When 1 % of the area is covered by mussels, the maximum of energy flow is formed by the small macrofauna, the dominant species being *Hydrobia ulvae*. When 10 % of the tidal flats are covered by mussels, the maximum of energy flows through the larger macrofauna, the dominant species being *Mytilus edulis*.

DISCUSSION

Unimodal and bimodal size distribution – What are the ecological effects?

The bimodal pattern of size histograms in the three sand bottom communities was caused by two characteristic, clearly separated species groups. The smaller size group in the range of 0.10 to 1.78 mg was dominated by *Hydrobia ulvae*, representing the trophic type of browsers. *Hydrobia ulvae* mainly grazes on diatoms and other microphytobenthos (Fenchel & Kofoed, 1976; Jensen & Siegismund, 1980), which are produced in the same habitat. The importance of a grazing food chain based on this browsing species for this

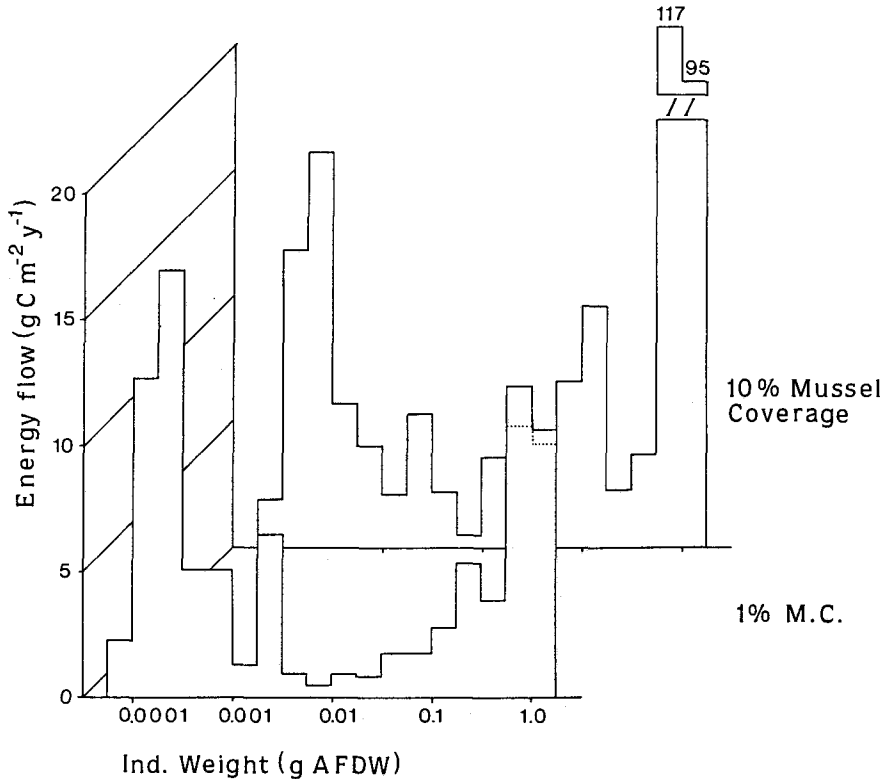


Fig. 4. Total size-specific energy flow of the intertidal macrofauna of Königshafen in relation to the different percentages of areal coverage by mussel beds. The energy flow is estimated from the sum of annual secondary production and annual respiration for each size group and represents the amount of energy assimilated from the macrofauna. For the total energy flow, the per-unit-area values of each assemblages were multiplied by the total areal coverage of the assemblage.

type of sandy intertidal flat was emphasized earlier (Asmus & Asmus, 1985). Extrapolating this to the total tidal flat, Königshafen becomes an ecosystem with a more or less autochthonous energy flow. The energy accumulated in this part of the faunal assemblage is used only by a few epibenthic invertebrate predator species like shrimps (*Crangon crangon*). Many authors describe shrimps feeding on small macrofauna (Plagmann, 1939; Pihl & Rosenberg, 1984; Pihl, 1985; Reise, 1985; Beukema, 1992). Other possible predators are juvenile shore crabs (*Carcinus maenas*) (Reise, 1978; Beukema, 1991) and, to a lesser extent, predatory gastropods (*Retusa obtusa*), nemertines and predatory polychaetes (Reise, 1981).

It is unknown whether small fish like the sand gobies feed on *Hydrobia*, but fish are linked to this small macrofauna group, by feeding on associated small polychaetes (*Pygospio elegans*) and oligochaetes (*Tubificoides benedenii*, *Tubifex* spec.) (Reise, 1978; Wolff & Zijlstra, 1981; Raffaelli & Milne, 1987) and by feeding on its predators, the prawns and amphipods (Raffaelli & Milne, 1987).

Animals in this size range may be too small for an effective predation by most of the

birds visiting the tidal flats. Shelducks (*Tadorna tadorna*) (Goethe, 1980) and avocets (*Recurvirostra avosetta*) are known to feed on *Hydrobia ulvae*, but these birds are rare in Königshafen. Zwarts & Blomert (1992) showed that an effective predation by knots (*Calidris canutus*) starts at sizes in the upper range of the size classes regarded here as the food web based on small macrofauna. Only a few species like the dunlin (*Calidris alpina*) may use the total size spectrum of *Hydrobia* (Ehlert, 1964; Höfmann & Hoerschelmann, 1969; Glutz von Blotzheim et al., 1975; Mouritsen & Jensen, 1992). The quantitative assessment of how much energy is transferred within this food web to higher trophic levels is still unknown, but the number of species which are able to profit from this group of small-sized macrofauna seems to be limited. From the present results, it is possible to estimate the amount of energy and material available from this group of macrofauna to the upper trophic levels. Lauckner (1986) reported that *Hydrobia ulvae* is in some places of Königshafen highly infected by parasites, but a quantification of this probably important branch of energy flow on the ecosystem level was not done.

The second distinctly separated macrofaunal group of the bimodal size histogram of the animal assemblage was dominated by different species depending on habitat. In the *Nereis-Corophium*-belt, this size group was formed by the polychaete *Nereis diversicolor*. This species has a wide range of feeding types, being omnivorous, detritivorous and predatory (Hartmann-Schröder, 1981). Because of its ability to form mucus nets as particle traps, which are fed by the worm when it is filled, *Nereis* has the potential to use the water column as feeding habitat (Riisgard et al., 1992). In both other sand bottom assemblages, the seagrass-bed and the *Arenicola*-flat, *Arenicola marina* dominates this second peak in the size spectrum of the assemblage. *Arenicola* mainly feeds on the upper sediment layer (Fauchald & Jumars, 1979) but is also able to pump water through its burrow (Krüger, 1964; Jacobsen, 1967). The volume of water pumped in this way is small compared to the filtration capacity of a suspension feeder (Baumfalk, 1979), but nevertheless the polychaete may exploit the water column for feeding.

The second peak in the macrofauna size spectrum is dominated by species belonging to another trophic type than those dominating the food web based on small macrofauna. These species are important prey organisms, especially for a large number of wading birds like bar-tailed godwits (*Limosa lapponica*) (Smith & Evans, 1973; Piersma et al., 1980), curlews (*Numenius arquata*) (Boere & Smit, 1980), dunlins (*Calidris alpina*), red-shanks (*Tringa totanus*), and oyster catchers (*Haematopus phaeopus*), that visit the tidal flats of Königshafen frequently. Predation by fish is probably less important for the "large food web", because most of the species are endobenthic, but predation on syphon tips, tail ends and other regenerable parts of the body contribute to a considerable amount to the diet of some predators (de Vlas, 1979). The amount of energy or material available from this part of the faunal assemblages increases with increasing inundation time. Whether this is a consequence of decreasing bird predation, or increasing food supply due to increasing inundation time, is not clear. Considering the trophic role of the Wadden Sea, the larger benthic species are generally regarded as the base of the food web of the ecosystem (Beukema, 1981). However, in the sand bottom habitats of Königshafen, this part of the benthic community contributes only 10 to 30 % to the total energy flow.

Unimodal size-frequency histograms of biomass, secondary production and respiration were found at all sites of mussel beds in Königshafen. The maximum of the size

spectrum was formed by the large *Mytilus edulis* in the size range of 0.56 to 1.00 g. Size spectra of biomass and secondary production are discussed in Asmus (1987). Main predators on mussels in this size-range are oystercatchers (*Haematopus ostralegus*) and Eiderducks (*Somateria mollissima*). Because of the dominance of the blue mussel in this assemblage, suspension feeding is the main mode of energy acquisition for the macrofaunal assemblage. More than the other assemblages, the mussel beds depend on pelagic primary production and pelagic particle import (Asmus & Asmus, 1990). The biomass maximum, as well as the maxima for secondary production and respiration, surpass the biomass peak at a similar size-class of the sand bottom assemblages.

Barry & Tegner (1990) discuss the possible demographic background leading to bimodal or unimodal size-frequency distribution within a population. In a model, they showed that the pattern of a size-frequency histogram is mainly influenced by the mortality rate and the growth rate. Under the assumption that these parameters, as well as the recruitment, are constant, no bimodal or unimodal shapes of the size-distributions are possible. Shifts in the ratio of mortality to growth with age from a growth-dominated to a mortality-dominated population result in a strongly unimodal size-frequency distribution. Stable bimodal distributions require shifts from mortality-dominated to growth-dominated conditions via age-related changes in mortality or growth, or both. Non-equilibrium conditions or events such as pulses in recruitment or mortality can also modify size-frequency distributions, but these effects are usually transient. In contrast to populations, size-specific growth and mortality in assemblages are additionally variable due to different rates of species and ages. These results indicate that inferences concerning the demographic dynamics are more difficult to derive from observing the shape of size-distribution on the assemblage level compared to the population level.

This study demonstrates that on the sandy tidal flats of Königshafen, the macrofaunal assemblage is formed by two separate size-groups with different ecological effects on the total ecosystem, because both groups use different energy sources and direct the energy into different pathways. The habitat of a mussel bed is dominated by suspension feeders occupying the total size-range of the assemblage.

Size-distribution and tidal level: a key to energy use of a community?

The size-distribution of biomass and secondary production varies among the different assemblages of a tidal flat. A simple and widespread explanation is to refer increases in biomass and secondary production of populations – from the high-tide line to the low-tide line – to the increasing energy availability due to inundation. Harvey & Vincent (1990) showed higher growth of *Macoma balthica* at levels with longer inundation times: additional growth differences within the size range of the population were obvious from the high- to low-tide line.

In the present study, the small macrofauna revealed a maximum energy flow in the seagrass-bed ecosystem situated at the upper part of the tidal flat, whereas near the low-tide line, biomass and secondary production of this group were less important. For the food web based on small macrofauna, the energy availability seems, therefore, to be independent of the tidal level, because this food web is based on grazing of micro-phytobenthos, which is higher in seagrass beds by the additional availability of epiphytes. Edgar (1990b) also found an increase in biomass and secondary production due to the

increase of plant material in seagrass-beds, but he related the elevated biomass values to the higher availability of detritus from decaying plants. Most of the seagrass-beds in Königshafen are formed by populations of *Zostera noltii*, growing on sandy sediments with very low shares of plant detritus (Wille, pers. comm.). The higher biomass of small-sized macrofauna in seagrass-beds may be due to better grazing conditions in the first place and secondly to protection from predation (Reise, 1978) and turbulence. Turbulence and currents may be the reason for worse grazing conditions in the deeper tidal levels, because sediment stability is low; thus, growth conditions for microphytobenthos are not as good as in the upper tidal flat (de Jonge, 1992) despite good light conditions.

The large macrofauna shows an increase in biomass, secondary production and energy flow with increasing inundation period. When going down the shore, the dominant species, and accordingly the dominant feeding type, changes from omnivorous to suspension feeding. In mussel beds, biomass and secondary production as well as energy flow show maximum development.

Grazers or suspension feeders: which one assumes the energetic dominance at the ecosystem level?

The grazing food chain is an important energy pathway on the tidal flats of Königshafen (Asmus & Asmus, 1985). Most of the area is dominated by grazing animals like *Hydrobia ulvae*. However, mussel beds surpass these areas by biomass and secondary production per unit-area (Asmus, 1987; Asmus & Asmus, 1990). The energetic dominance of one of these groups depends on the areal extension of the assemblage. Mussel beds show large variations in areal coverage and biomass from year to year (Dankers & Koelemaij, 1989). In Königshafen, mussel beds occupy about 1 % (Reise, pers. comm.) to 10 % (Asmus & Asmus, 1990) of the total area. The net energy flow (assimilated energy) related to the total tidal flat increases with an increasing share of areal coverage by mussel beds from $94 \text{ g C m}^{-2} \text{ y}^{-1}$ at 1 % coverage to $296 \text{ g C m}^{-2} \text{ y}^{-1}$ at a 10 % cover. Additionally, a shift from a weak energetic dominance of small macrofauna to a distinct energetic dominance of large macrofauna is obvious. An increase in energy flow seems to be possible only by a support of food supply from outside Königshafen.

CONCLUSIONS

Macrofaunal assemblages of the *Nereis-Corophium*-belt, the seagrass-bed and the *Arenicola*-flat each consisted of two groups, indicated by corresponding peaks in the size spectra of biomass, secondary production, respiration and energy flow.

The first size-group was mainly made up of *Hydrobia ulvae*. Because of the small size, this part of the assemblage may be effectively utilized by a limited species number of small waders, whereas the main energy flow is directed via predation by shrimps (*Crangon crangon*) to fishes. This food web is based on autochthonous primary production.

The second size group can be directly used by a lot of wading birds as well as by oystercatchers and eiderducks. Biomass as well as secondary production, respiration and energy flow of this food web based on large macrofauna increase from the high-tide line down to the low-tide line. This food web is based on different energy sources from

benthic and pelagic production as well as from detritus input from outside the habitat. Mussel beds are dominated by this food web, surpassing the other benthic assemblages in biomass and energy flow by an order of magnitude. The energy flow of mussel beds is based on energy sources from phytoplankton production and is thus dependent upon input from deeper waters. The amount of total energy assimilated by the intertidal macrofauna of Königshafen depends on the energetic dominance of mussel beds within the macrofaunal assemblages. A high areal coverage by mussel beds increases the energy flow through the macrofauna and induces a shift from autochthonous to allochthonous energy sources.

Acknowledgements. I am grateful for the kind help of my wife Ragnhild Asmus in all stages of this work, from measurements to the final corrections of the manuscript. This work was supported by the Deutsche Forschungsgemeinschaft (As 49/1-1) and by the Federal Ministry for Research and Technology. This is publication no. 129 of the project "Ecosystem Research Wadden Sea".

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