HELGOLÄNDER MEERESUNTERSUCHUNGEN
Helgoländer Meeresunters. 48, 201–215 (1994)

Biomass and abundance of macrofauna in intertidal sediments of Königshafen in the northern Wadden Sea

K. Reise, E. Herre & M. Sturm

Biologische Anstalt Helgoland, Wattenmeerstation Sylt; D-25992 List, Federal Republic of Germany

ABSTRACT: Intertidal sediments of Königshafen (Island of Sylt, North Sea) were sieved for mesofauna (> 0.25 mm) and macrofauna (> 1 mm) in spring and autumn 1990. Although sediments are coarser than in other parts of the Wadden Sea, the macrobenthic fauna was very similar but with a tendency towards higher species density, abundance and biomass. Taking into account the areal size of sandy flats, seagrass beds, mud flats and mussel beds, the average biomass is calculated to be 65 g ash-free dry weight m^{-2}. The lugworm *Arenicola marina* dominates the biomass (28 %), followed by the bivalves *Mytilus edulis* (21 %), *Mya arenaria* (16 %), *Cerastoderma edule* (10 %) and the mudsnail *Hydrobia ulvae* (9 %). While spring and autumn biomass are almost alike, abundance is highly variable and entirely dominated by *H. ulvae*. Mesofauna is mainly composed of oligochaetes, small and juvenile polychaetes. Abundance is similar to that of macrofauna, while biomass is only about 1 g m^{-2}. Macrophyte biomass amounted to 9 % of that of macrofauna. In the course of the century, mussel beds expanded while muddy areas declined. The concomitant effects on biomass presumably compensated each other.

INTRODUCTION

In the European Wadden Sea, 4300 km^2 of sedimentary tidal flats occur, primarily between a chain of barrier islands and the mainland coast. The macrobenthic fauna of this vast intertidal area participates in the mineralization of organic materials imported from the adjacent land and the sea (Wilde & Beukema, 1984). It attracts foraging fish and birds in high numbers to this coastal zone. Macrofaunal biomass and abundance may thus indicate the biotic importance of a particular tidal area.

In the western part of the Wadden Sea, Beukema (1976) showed macrofaunal biomass to be low on the flats farthest offshore (13 g m^{-2}), and highest in the transitional zone between nearshore and offshore flats where silt content and tidal level are intermediate (42 g m^{-2}). Within estuaries, biomass is low in the oligohaline (1 g m^{-2}) and mesohaline (14 g m^{-2}) zones compared to the polyhaline (36 g m^{-2}) zone (Michaelis, 1981; Obert, 1982). Particularly high average biomass (51 g m^{-2}) was found on tidal flats in a landlocked bay in the central part of the Wadden Sea (Michaelis, 1987). To further explore the range of variation in macrozoobenthic biomass within the Wadden Sea, we investigated an embayment on a barrier island in the northern part.

Beukema (1989, 1991, 1992) has documented an increase in zoobenthic biomass and abundance since the 1970s on tidal flats in the western part of the Wadden Sea. This is attributed to eutrophication. In the northern part of the Wadden Sea, a similar trend was inferred from changes in the composition of the benthic fauna (Reise, 1982; Reise et al., 1989; Reise, 1990), while Jensen (1992) found no such evidence. In order to increase the potential to quantify further change, a baseline study on macrobenthic biomass in Königshafen was conducted (this study), in combination with a mapping of species distributions (Reise & Herre, in prep.)

Comparisons between benthic studies are often hampered because of deviations in the methods applied. With respect to the sedimentary fauna, the mesh size of the sieve used to extract the organisms is of particular relevance (cf. Reish, 1959). We, therefore, took subsamples, and retained individuals which passed the 1-mm mesh but not the 0.25-mm mesh. We here term this size-fraction 'mesofauna', and quantify its contribution to biomass and abundance. These figures may be used to estimate the effects of the truncation of the lower size spectrum of the macrofauna by a certain mesh-size.

MATERIAL AND METHODS

Study area

The Königshafen of Sylt is located in the northern part of the Wadden Sea, close to the border between Denmark and Germany. Sand dunes provide shelter against onshore winds and surf. The bay is adjacent to a tidal inlet, and is 12 km off the mainland coast. The area comprises 6.209 km^2 between extreme tide marks (Fig. 1). Sheep-grazed salt marshes cover 10.6 % of the area, bare high sands and beaches 7 %, and a permanent tidal channel meandering in an E-W direction 4.8 %. This leaves 4.816 km^2 of intertidal flats, on which this study focusses.

Tides are semi-diurnal with an amplitude of 1.8 m. Spring and neap tides differ by < 0.2 m, but strong easterly winds (offshore) may decrease low-tide level by 1 m, and westerly gales (onshore) often raise high tide level by > 2 m. Salinity remains close to 30 ‰. Mean annual water temperature is about 9 °C, with a summer average of 15 °C and a winter average of 4 °C. Intertidal sediments of Königshafen are predominantly sand, with a small muddy depression in the western part. Wind-blown dunes have deposited relatively coarse grained sediments. The main modal value is at 2 PHI or 0.25 mm (Austen, 1992). A general description of the area and its biota is given in Wohlenberg (1937) and Reise (1985).

Sampling

Six major intertidal habitats were differentiated, based on aerial photographs taken in 1989 and 1990, on charts of 1 : 10000 provided by the "Amt für Land-und Wasserwirtschaft", Husum 1989, a sediment map by Austen (1992), and on our own qualitative survey on the distribution of macrobenthos conducted in the summers of 1989 and 1990 (Fig. 1). Sampling was done in March/April and repeated in October 1990. According to Beukema (1974), macrofaunal biomass is close to the annual average in these seasons. At another site in the Wadden Sea, Dörjes et al. (1986) observed considerable variation in the seasonality of biomass between years. In most years, they obtained a minimum in March/April and a maximum in late summer to autumn. In Königshafen, 19 sampling sites were chosen (Table 1). Ten were located on the extensive, sandy lugworm flats

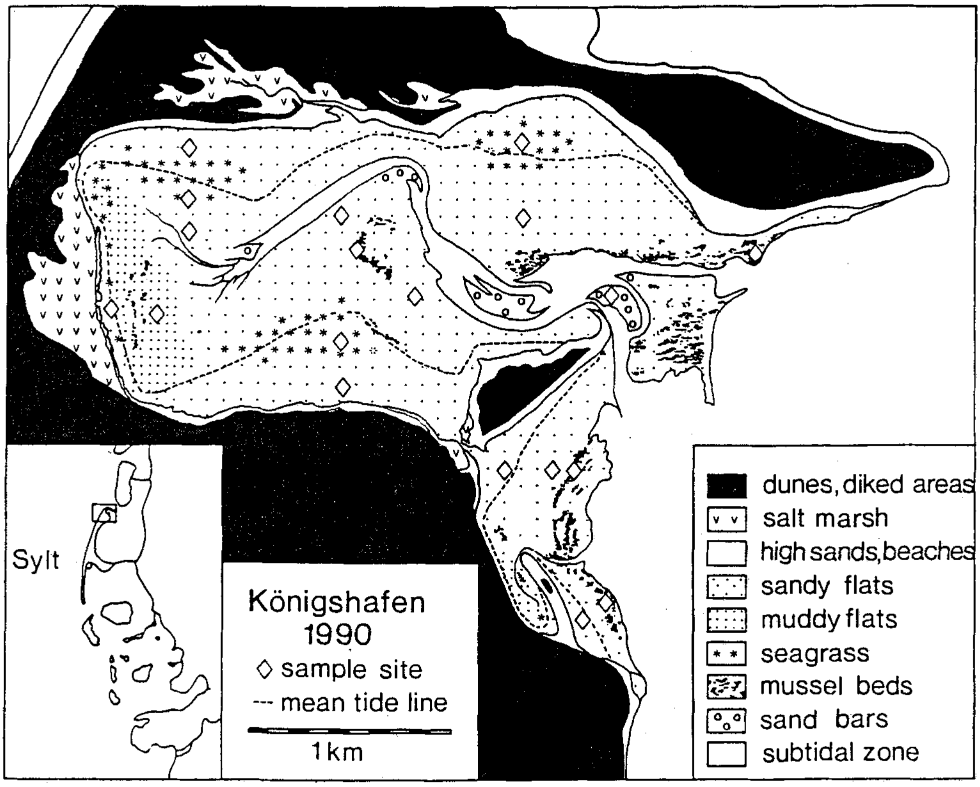

Fig. 1. Intertidal habitats of Königshafen on the island of Sylt in the northern Wadden Sea

Table 1. Areal size and percentage of major intertidal habitat types in Königshafen, and organic content (% of dry weight) and the number of samples from sites in 1990. MTL and LTL are mean and low tide level, respectively

Intertidal habitats in Königshafen	Area ($m^2 \times 10^4$)	Area (%)	Organic content (%)	Number of samples
Sandy flats above MTL no seagrass	123.4	25.6	0.46 (0.20)	50
Sandy flats near MTL with seagrass	59.7	12.4	0.52 (0.05)	30
Sandy flats below MTL no seagrass	242.4	50.3	0.44 (0.10)	50
Mud and muddy sand below MTL	43.1	9.0	1.77	10
Mussel beds near LTL	4.6	1.0	2.82 (1.84)	40
Sand bars near LTL	8.4	1.7	0.28	10

which cover almost 76 % of the entire tidal zone of Königshafen. Although mussel beds comprise only 1 % of the area, four sites were located there because of a disproportionately high biomass. Each of three distinct, sandy seagrass meadows received one sample site. The muddy depression in the innermost part of the bay, and a sand bar adjoining the main tidal channel, were sampled at one site each.

Sample sites were areas of 100 × 100 m. From each, 5 replicate cores of 200 cm^2 cross section and 30 cm depth were taken once in spring and a second time in autumn. A subcore of 10 cm^2 (5 cm depth) was obtained from each replicate. Subcores were first sieved through a 1-mm mesh, and *Hydrobia ulvae* was counted in the residue. Material passing the 1-mm mesh was then sieved through a 0.25-mm mesh. Organisms in the residue (termed mesofauna) were identified and counted. All 200-cm^2 cores were sieved through a 1-mm mesh, and the retained organisms are termed macrofauna. *H. ulvae* was not counted in these large cores.

Biomass was determined from the combined samples of 5 replicates. Mesofauna samples were divided into annelids and small *Hydrobia ulvae*. Macrofauna was divided into annelids < 20 mm length and the various species. In molluscs, size classes of < 5 and > 5 mm, in crabs and shrimp size classes of < 10 and > 10 mm were kept separate. Organisms were dried during 3 days at 80 °C, and burned in a furnace for 12 h at 520 °C. The weight loss of the organisms is considered to be the ash-free dry weight (AFDW). Loss of $CaCO_3$ at combustion temperatures > 450 °C may give an overestimate of organic weight, but this procedure was adopted to allow comparisons with previous studies (cf. Beukema, 1976; Michaelis, 1987). Average values of abundance and biomass per m^2 for the intertidal zone of Königshafen are calculated from the mean of samples taken from particular habitats multiplied by the areal share of that habitat. Thus, these figures approximate conditions for a representative, hypothetical m^2 of Königshafen. In spring, 5 replicates of 10 cm^2 (5 cm depth) were combined from each site for sediment analysis. Median grain size was determined by dry sieving, and weight loss on ignition (520 °C, 6 h) is considered to approximate organic content (Table 1).

RESULTS

A total of 58 invertebrate species were encountered in the combined sample size of 3.8 m^2. Of these, three were only found in the mesofaunal fraction. The number of species in a 0.1 m^2 sample ranged from 7 to 22. The overall average was 13.6 (3.7), with no significant differences between spring and autumn sampling periods, nor between habitat types. The lowest average was found in the sand bars, the highest in mussel beds.

Abundance of macrofauna

Average abundance on the intertidal flats of Königshafen was 5618 m^{-2} in spring and 19 686 m^{-2} in autumn 1990. These figures are primarily determined by the superabundant population of the gastropod *Hydrobia ulvae* (Table 2). This species accounted for 79 and 93 % of all individuals. Excluding *H. ulvae*, respective abundances of all others combined were 1162 m^{-2} in spring and 1330 m^{-2} in autumn. Of these, annelid worms comprised 83 and 74 %, molluscs other than *H. ulvae* 14 and 23 %, and crustaceans < 3 % in both seasons. In spring and autumn, *H. ulvae* was confined to the upper half of the tidal

Table 2. Abundance of macrofauna (> 1 mm) m^{-2} in the intertidal of Königshafen, April/May and October 1990, calculated from 95 + 95 samples of 200 cm^2 taken at 19 sites, weighted by areal size of the respective habitats. + indicates species present with < 1 individual m^{-2}

Species	Spring	Autumn
Hydrobia ulvae (Penn.)	4456	18356
Littorina littorea L.	21	48
Littorina saxatilis (Olivi)	0	1
Littorina mariae (Sac. & Rast.)	+	+
Crepidula fornicata (L.)	0	+
Lepidochiton cinerea (L.)	+	+
Cerastoderma edule (L.)	36	122
Macoma balthica L.	66	94
Abra alba (Wood)	1	2
Venerupis pullastra Mont.	0	+
Ensis americanus (Binney)	0	2
Mya arenaria L.	11	5
Mytilus edulis L.	27	25
Nereis diversicolor Müll.	47	98
Nereis virens Sars	+	1
Nephtys hombergii Sav.	13	32
Aricidea minuta South.	1	0
Harmothoe imbricata (L.)	+	0
Harmothoe sarsi (Klingb.)	+	0
Lepidonotus squamatus (L.)	0	+
Pygospio elegans Clap.	83	53
Spio filicornis Müll.	1	0
Scolelepis foliosa Aud. & M.-Ed.	1	0
Scolelepis squamata Müll.	6	0
Spiophanes bombyx (Clap.)	+	1
Polydora sp.	+	6
Malacoceros sp.	0	+
Magelona papillicornis Müll.	7	1
Capitella capitata (Fabr.)	21	5
Heteromastus filiformis (Clap.)	38	31
Arenicola marina (L.)	63	31
Ophelia rathkei McIntosh	+	1
Eteone longa (Fabr.)	7	9
Phyllodoce mucosa (Oerst.)	3	44
Scoloplos armiger (Müll.)	403	517
Ampharete acutifrons (Grube)	3	+
Tharyx sp.	54	58
Lanice conchilega (Pallas)	8	1
Tubificoides benedeni (D'Udekem)	157	73
Tubificoides pseudogaster (Dahl)	46	24
Lineus viridis (Fabr.)	2	3
Prostomatella arenicola Fried.	0	1
Amphiporus lactifloreus (John.)	1	1
Metridium senile (L.)	+	+
Sagartia troglodytes (Price)	+	+
Balanidae 2 spp.*	11	6
Bathyporeia pilosa Lindström	3	+
Urothoe poseidonis Reibisch	10	3
Gammarus spp.**	+	6
Corophium arenarium Crawf.	4	4
Jaera albifrons Leach	+	+
Carcinus maenas (L.)	2	8
Crangon crangon (L.)	2	7

* *Balanus crenatus* Bruguère and *Semibalanus balanoides* (L.)
** *Gammarus locusta* (L.) and *Chaetogammarus marinus* (Leach)

zone with highest densities in the seagrass beds (Table 3). Most of the numerically dominant species occurred over a wide range of intertidal habitats. *Macoma balthica, Tubificoides pseudogaster, Pygospio elegans, Tharyx* sp. and *Heteromastus filiformis* attained particularly high abundances at the muddy site. Mussel beds were rather distinct by high densities of epifaunal species. In the sand bars adjoining the main tidal channel, abundance was low.

Table 3. Abundance of macrofauna (individuals m^{-2} retained by 1-mm mesh) in 6 habitat types. 'Upper lug.' and 'lower lug.' are sandy lugworm flats above and below mid tide level, respectively. Taxa with > 50 individuals m^{-2} in at least one habitat type are included. Samples from spring and autumn 1990 are combined

Intertidal habitat	Upper lug.	Seagrass bed	Lower lug.	Mud	Mussel beds	Sand bars
Hydrobia ulvae	20163	50233	41	0	0	0
Cerastoderma edule	157	225	8	70	8	0
Scoloplos armiger	535	723	302	60	31	65
Arenicola marina	54	40	52	15	0	40
Nereis diversicolor	75	35	83	80	4	0
Capitella capitata	25	32	3	10	71	0
Tubificoides benedeni	277	123	41	70	149	0
Macoma balthica	89	62	52	265	16	5
Tubificoides pseudogaster	60	22	9	135	35	0
Pygospio elegans	36	28	74	190	3	60
Tharyx sp.	6	2	27	455	5	0
Heteromastus filiformis	9	13	28	165	164	0
Littorina littorea	20	122	15	30	380	0
Carcinus maenas	7	5	2	0	158	0
Balanidae 2 spp.	0	0	3	0	694	0
Mytilus edulis	1	13	1	0	2339	0
Total macrofauna	21606	51733	1000	1735	4270	420
Total macrofauna without *H. ulvae*	1443	1500	959	1735	4270	420

Biomass of macrofauna

Biomass, expressed as ash-free dry weight of all fauna retained by a 1-mm mesh, was 65 g m^{-2} for the intertidal zone of Königshafen. Estimates for spring and autumn were almost alike (Table 4). However, the relative contribution of species differed between seasons. In spring 1990, *Arenicola marina* contributed 37.8 %, *Mya arenaria* 21.4 %, *Mytilus edulis* 17.0 %, *Cerastoderma edule* 8.1 %, *Littorina littorea* 2.9 %, *Hydrobia ulvae* 2.8 % and *Macoma balthica* 2.7 % to the biomass. In autumn, *M. edulis* attained 26.0 %, *A. marina* 18.0 %, *H. ulvae* 15.3 %, *C. edule* 12.8 %, *M. arenaria* 9.8 %, *L. littorea* 3.4 %, *Nereis diversicolor* 3.2 %, *M. balthica* 3.2 %. The biomass estimate for *M. arenaria* is less reliable than for the other species, because the weight of a few large-sized individuals was multiplied with a large areal share (lower lugworm flats). The strong biomass increase in *H. ulvae* from spring to autumn was caused by successful recruitment. In mussels, a slight increase in biomass was associated with a slight decrease in abundance.

Table 4. Biomass of macrofauna (> 1 mm) in g AFDW m^{-2} in the intertidal zone of Königshafen, April/May and October 1990, calculated from 95 + 95 samples of 200 cm^2 taken at 19 sites, weighted by areal size of the respective habitats

Species	Spring	Autumn
Hydrobia ulvae	1.88	9.57
Littorina littorea	1.94	2.15
Cerastoderma edule	5.46	8.03
Macoma balthica	1.82	1.99
Mya arenaria	14.33	6.14
Mytilus edulis	11.42	16.27
Nereis diversicolor	0.59	2.02
Nereis virens	0.04	1.20
Nephtys hombergii	0.23	0.75
Heteromastus filiformis	0.14	0.11
Arenicola marina	25.37	11.28
Scoloplos armiger	1.60	1.62
Phyllodoce mucosa	0.00	0.12
Lanice conchilega	0.49	0.04
Lineus viridis	0.05	0.16
Balanus sp.	0.14	0.07
Carcinus maenas	1.27	0.47
Others (taxa <0.1 g)	0.30	0.65
All macrofauna	67.07	62.64
Zostera spp.	0.69	7.22
Fucus vesiculosus	1.24	2.31

There was almost no recruitment, but individuals gained in weight. Lower biomass of lugworms in autumn is associated with lower abundance. In this species, biomass in autumn may be affected by the preceding spawning period. *L. littorea, M. balthica* and *Scoloplos armiger* showed little change in biomass between spring and autumn. Suspension feeders (44 %) and subsurface feeders (31 %) contributed most to biomass in the Könighafen intertidal. The share of surface deposit feeders and grazers was 9 % in spring and 27 % in autumn. This seasonal increase is mainly attributed to *H. ulvae*.

Although mussel beds covered only 1 % of the intertidal zone, they contributed 20 % to overall biomass. Compared to lugworm flats and sandy seagrass beds, biomass was 26 times higher in beds of mussels (Table 5). This was primarily due to *M. edulis* itself, but *L. littorea* achieved here a biomass equal in magnitude to that of lugworms on the sandy flats. The biomass of *Carcinus maenas* in mussel beds may be enhanced because crabs use this habitat as a refuge at low-tide. Biomass in mud was more than twice as high as in sand. This difference is primarily caused by a high density of large-sized *M. arenaria*. On the lower and higher lugworm flats, *A. marina* dominated the biomass. In the seagrass beds, this species performed less well. Here *H. ulvae* and *C. edule* dominated the biomass. Low biomass was found in the sand bars adjoining the major tidal channel.

Table 5. Biomass of macrobenthos (> 1 mm) in g AFDW m^{-2} in 6 habitat types. 'Upper lug.' and 'lower lug.' are sandy lugworm flats above and below mid tide level, respectively. Taxa with > 1 g m^{-2} in at least one habitat type are included. Samples from spring and autumn 1990 are combined

Intertidal habitat	Upper lug.	Seagrass bed	Lower lug.	Mud	Mussel beds	Sand bar
Arenicola marina	22.80	8.37	20.55	8.89	0.00	18.64
Hydrobia ulvae	11.18	23.00	0.02	0.00	0.00	0.00
Cerastoderma edule	5.77	19.41	2.84	15.84	1.05	0.00
Scoloplos armiger	1.93	3.16	1.42	0.02	0.17	0.35
Macoma balthica	1.06	0.58	1.59	8.55	1.28	0.00
Mya arenaria	0.00	0.34	8.50	65.45	2.90	0.00
Nereis diversicolor	0.76	0.37	1.43	2.96	0.13	0.00
Nephtys hombergii	0.15	0.00	0.39	2.73	0.05	0.46
Littorina littorea	0.92	3.51	1.16	6.15	23.89	0.00
Nereis virens	0.00	0.00	1.13	0.00	5.48	0.00
Lanice conchilega	0.33	0.00	0.33	0.00	1.55	0.00
Balanus spp.	0.00	0.00	0.02	0.00	9.17	0.00
Carcinus maenas	0.56	0.01	1.31	0.00	6.35	0.00
Mytilus edulis	0.71	5.03	0.80	0.00	1264.10	0.00
Others	0.65	0.42	0.53	3.18	2.80	1.09
All macrofauna	46.82	64.20	42.02	113.77	1318.92	20.54
Zostera spp.	1.00	29.00	0.00	0.00	0.00	0.00
Fucus vesiculosus	0.00	0.00	0.00	0.00	177.11	0.00

Biomass of macrophytes

During the sampling period, only seagrass (*Zostera noltii* and *Z. marina*) and *Fucus vesiculosus* made significant contributions to phytomass (Tables 4 and 5). Above-ground growth of seagrass is mainly from July to September in Königshafen. Thus, when sampling was completed in October, biomass had already declined. *F. vesiculosus* is confined to mussel beds in Königshafen, is perennial, and growth occurs throughout summer. Assuming the sampled phytomass comes close to the annual average, plants achieve only 9 % of the macrofaunal biomass. In October, the ratio of zoomass to phytomass is 1.6 to 1 in the seagrass beds, and 6.6 to 1 on mussel beds.

Mesofauna

The small macrofauna or 'mesofauna', defined here as organisms passing a 1-mm mesh and being retained by a 0.25-mm mesh, comprised about as many individuals as the larger macrofauna, while its contribution to biomass was < 2 % of the total macrofauna (Table 6). The mesofauna in spring and autumn was primarily composed of oligochaetes (25 %) and polychaetes (67 %). All species dominant in the mesofauna were also found among the macrofauna, albeit in lower numbers with the exception of *Hydrobia ulvae*. In spring, juveniles of *Scoloplos armiger* made a large contribution to the mesofauna, and in autumn, juveniles of *Tharyx* sp. were highly abundant. The small

Table 6. Abundance (individuals m^{-2}) and biomass (g AFDW m^{-2}) of mesofauna (passing a 1-mm mesh but retained by a 0.25-mm mesh) in the intertidal zone of Königshafen in spring and autumn 1990

Mesofauna m^{-2}	Spring	Autumn
Tubificoides benedeni	787	832
Tubificoides pseudogaster	1483	1262
Scoloplos armiger	6425	292
Capitella capitata	345	83
Pygospio elegans	412	627
Tharyx sp.	220	2921
Nereis diversicolor	433	0
Hydrobia ulvae	439	763
Others (9 spp.)	201	81
Total abundance	10745	6861
Total biomass	0.84	1.21

juveniles of *H. ulvae* were not yet present during the spring sampling period and in autumn most of them were already large enough to be retained by the 1-mm mesh.

Mean individual weights

Seasonal changes in the mean weight of individuals of the zoobenthos populations in Königshafen reflect seasonal recruitment, individual growth and migrations. A comparison of the spring and autumn weights sheds some light on what happened to the populations (Table 7). The low individual weight of mesofauna in spring is a consequence of the high proportion of very small *Scoloplos armiger* which hatched from egg cocoons during this time of the year. In spring, the low individual weight of annelids < 20 mm in length is primarily due to the dominance of oligochaetes. In autumn, there was a higher proportion of juvenile polychaetes which as adults are large-sized. In autumn, these juveniles tend to be larger' than oligochaetes which do not grow beyond this size category.

In *Mytilus edulis* the higher individual weight in autumn reflects growth of individuals already present in spring because abundance did not increase. In *Nephtys hombergii, Nereis diversicolor* and *Hydrobia ulvae* an increase in individual weight goes along with an increase in abundance from spring to autumn (see Table 2). This suggests that adult individuals migrated from non-sampled areas into sampling plots or immigrated into Königshafen from outside. A decrease in individual weight in various other species from spring to autumn reflects the contribution of juvenile populations which were recruited in spring and summer 1990. The lower average individual weight calculated for all macrofauna in autumn is simply the consequence of the increase in the population of the small-sized *H. ulvae* during summer.

Table 7. Mean individual weight (mg AFDW) in populations in spring and autumn 1990, obtained by dividing biomass with abundance estimates for the entire intertidal zone of Königshafen. In the polychaete species listed, weights refer to individuals ≥ 20 mm length only

Group of organisms	Spring	Autumn	Ratio
Mesofauna	0.08	0.18	1:2.25
Annelida <20 mm length	0.29	0.47	1:1.62
Mytilus edulis	422.96	650.80	1:1.54
Nephtys hombergii	19.17	27.78	1:1.45
Nereis diversicolor	19.03	24.34	1:1.28
Hydrobia ulvae	0.42	0.52	1:1.24
Scoloplos armiger	4.68	4.43	1:0.95
Arenicola marina	402.70	376.00	1:0.93
Heteromastus filiformis	4.12	3.67	1:0.89
Macoma balthica	27.58	21.17	1:0.77
Littorina littorea	92.38	44.79	1:0.48
Cerastoderma edule	151.67	65.82	1:0.43
Annelida ≥ 20 mm length	56.35	29.45	1:0.52
All macrofauna	11.94	3.18	1:0.27

DISCUSSION

Bias in the estimates of abundance and biomass

Certain aspects of the sieving procedure, particularly the mesh size, have strong effects on the number of infaunal individuals extracted from sediments. The use of a 0.25-mm mesh, in addition to the conventional 1-mm mesh, resulted in a 2.9- and 1.3-fold increase of abundance in spring and autumn, respectively. The 1-mm mesh is passed by many juveniles of the macrofauna. If sampling had been carried out in summer, more individuals would have been found on the 0.25-mm mesh. This is suggested by samples taken in mid summer 1979 at 66 stations in the northern Wadden Sea (Reise, 1987). Mesofaunal abundance was 140000 individuals m^{-2} on average, with 65 % juvenile *Hydrobia ulvae*, 16 % bivalve spat and 16 % small annelids. This is roughly an order of magnitude higher than the spring and autumn values reported in this study. Juvenile *H. ulvae* and bivalve spat were not yet present in spring, and were already big enough for the 1-mm mesh in autumn. Within short periods of time, juveniles attain a body size large enough to become retained by a 1-mm mesh. This may alter the average abundance of macrofauna by orders of magnitude. Measures of abundance are, therefore, of restricted use in comparisons between surveys, unless samples are taken at short intervals throughout a year.

Biomass may be a better measure for comparative purposes. In this study, the abundant mesofauna contributed < 2 % to the total biomass. The small-sized mudsnail *Hydrobia ulvae* contributed 3 and 15 % to biomass in spring and autumn, respectively. Compared to 79 and 93 % of total abundance, these biomass fractions are small. Thus, the small-sized fauna has a minor effect on biomass. Important are large individuals which change slowly. In the present survey, the spring and autumn biomass differed only by 4 % from their mean.

In biomass comparisons, patchiness and scarcity of large-sized individuals deserve special attention. Biomass on mussel beds was 10 to 50 times higher than in other habitats of Königshafen. In this case, the area of mussel beds is a critical parameter. This was determined by aerial photographs taken in May 1989 and 1990. The two estimates were 4.6 and 3.8 hectares, respectively. Mussel clumps of < 1 m in diameter could not be identified on the photographs. We decided, therefore, on the higher estimate to balance this omission. If the lower estimate had been chosen, the average biomass for Königshafen would have been calculated as 62.3 instead of 64.9 g m^{-2}. Thus, a 0.2 % change in area of the tidal zone causes a change of 3.7 % in biomass. A similar effect may result from scarcity of large individuals. Only 3 large-sized *Mya arenaria* were found in 50 samples taken from the lower lugworm flats which comprise 50 % of the intertidal area. Omission of these clams decreases the average biomass by 4.1 g m^{-2} or 6.3 %. Given the scarcity of these large individuals, it is hardly possible to estimate their abundance properly. The uneven distribution of biomass may give rise to serious sampling errors. Those exemplified here may be combined, thus resulting in a deviation of 10 % from the calculated average biomass. Differences within this range should not be regarded with confidence.

Differences in zoobenthic biomass between consecutive years tend to be in the range of 10 to 30 % of the average amount measured in the intertidal Wadden Sea (see Beukema, 1991: Fig. 1). Thus, a long-term average of biomass for Königshafen may be somewhere between 46 and 84 g m^{-2}. Stronger deviations may only occur subsequent to a severe winter, which was not the case prior to the 1990 survey of Königshafen. Asmus & Asmus (1985) measured in 1980 the mean annual zoobenthic biomass of a seagrass bed (30 g m^{-2}) and a lugworm flat (28 g m^{-2}). These values are 53 % and 40 % lower than the respective habitat values given in Table 5. The difference is primarily caused by a much lower biomass in the lugworm and cockle populations in 1980, while the biomass of *Hydrobia ulvae* is similar. The difference in *Arenicola marina* is odd because the lugworm population has been shown to remain relatively constant over the years, while *Cerastoderma edule* fluctuates strongly in Königshafen (Reise, 1981; 1985). Mussel beds sampled in 1984 showed an average biomass of 1243 g m^{-2} (Asmus, 1987). This deviates only by 6 % from the value found in 1990.

Long-term change in Königshafen

Sediments and the macrobenthos of Königshafen were studied in the 1930s by Wohlenberg (1937). Since then, physical and biotic changes have occurred which presumably have had effects on the zoobenthic biomass. The intertidal area has decreased by about 40 hectares, due to an embankment and the disposal of sand resulting in an island on a former tidal flat. Muddy areas have decreased and sediments have become more consolidated (Austen, 1992). Mussel beds have expanded, small-sized annelids have become more abundant, populations of the amphipod *Corophium volutator* and the tellinid clam *Scrobicularia plana* have vanished (Reise, 1982; Reise et al., 1989; Reise, 1990). The increase in mussel beds and the long-term shift from muddy to sandy areas in Königshafen imply that conditions for suspension feeders have improved while those for deposit feeders have deteriorated. This may have been caused by higher turbulence in the tidal waters. Recordings from a gauge located just south of Königshafen indicate an increase in storm tide frequency since 1900, and an increase in mean tidal range by 25 cm (14 % of the present range) since 1931 (Führböter, 1989).

What are the possible effects on the average zoobenthic biomass in Königshafen? Mud and muddy sand occupied 34 % of the intertidal zone in the 1930s (Wohlenberg, 1937: Fig. 67). Mussel beds covered at the most 0.2 %, which is inferred from maps provided by Nienburg (1927: vegetation map from 1924) and Wohlenberg (1937: maps from 1932–33). These former areal proportions may be used to recalculate biomass with the data given in Table 5, assuming that biomass within habitats has remained similar. Sixty years ago the average zoobenthic biomass of Königshafen may have been 73 g m^{-2}. This deviates only by 12 % from the present average and falls within the range of differences to be expected between consecutive years. The expansion of mussel beds increased biomass while the decline of muddy areas caused a decrease. Therefore, the average was not affected significantly. However, it is not known whether the biomass within these habitat types was the same in the 1930s as it is today.

The long-term increase in small-sized annelids and the loss of populations of *Corophium volutator* and *Scrobicularia plana* may be of minor importance to the average biomass. *C. volutator* was highly abundant in a belt close to high tide level until 1975 (see Wohlenberg, 1937; Reise, 1978). The area of this belt was approximately 20 hectares. With an average abundance of 7725 m^{-2} in spring 1975 (Reise, 1985: Table 5.3), and an individual weight of 0.56 mg (Asmus, pers. comm.), the addition to average biomass is merely 0.2 g m^{-2}. A similar calculation for *S. plana* also yields a value of < 1 g m^{-2}. A recent immigration of *Ensis americanus* (Urk, 1987) added considerably to zoobenthic biomass below the low-tide line but not in the intertidal zone (Reise & Herre, in prep.).

Comparisons within the Wadden Sea

The Königshafen differs with its predominance of medium sand from most other intertidal areas in the Wadden Sea which are composed of fine or very fine sands (Austen, 1992). This aberration is caused by aeolian input from the surrounding dunes, and is not the consequence of sorting by strong currents. This unique sediment composition does not cause the macrozoobenthos to differ from that of other parts of the Wadden Sea. Species composition and dominance in terms of abundance and biomass is very similar to western (Beukema, 1976) and central (Michaelis, 1987) parts of the Wadden Sea. The most common species in Königshafen are also the most common species elsewhere in the Wadden Sea (cf. Smidt, 1951; Jepsen, 1965; Beukema, 1976; Obert, 1982; Michaelis, 1987; Jensen, 1992). An exception is the amphipod *Corophium volutator* which declined from 1975 onwards, and is now virtually absent from Königshafen. The cause is unknown.

Species density is relatively high in Königshafen. While Beukema (1976), Michaelis (1987) and Obert (1982) give an average of 11 species per site (ranging from 0.05 to 0.45 m^2 sample size), the corresponding value for Königshafen is 14 species per site (0.1 m^2). In the adjacent North Sea, species density is 3 to 4 times higher (cf. Duineveld et al., 1990; Kröncke, 1992).

The numerical dominance of *Hydrobia ulvae* in Königshafen is an order of mag-

Table 8. Dominant contributors to biomass (g ash-free dry weight m^{-2}) in macrobenthic surveys in the western, central and northern part of the Wadden Sea. Selected are species with an average of > 1.5 g m^{-2} in the 3 surveys combined

Macrofauna > 1 mm	Western Dutch Wadden Sea Beukema (1989)	Jadebusen Michaelis (1987)	Königshafen This study
Mytilus edulis	0.9	19.6	13.8
Cerastoderma edule	9.5	12.3	6.7
Arenicola marina	6.2	2.2	18.3
Mya arenaria	8.0	5.7	10.2
Hydrobia ulvae	0.8	3.4	5.7
Macoma balthica	5.1	2.6	1.9
Nereis diversicolor	2.2	2.0	1.3
Total macrofauna	38.5	51.4	64.9

nitude higher than in the western part of the Wadden Sea (Beukema,1976; Obert, 1982), but is in agreement with the subtidal zone of the western Wadden Sea (Dekker, 1989), and with tidal zones in the central (Michaelis, 1987) and northern part (Jensen, 1992).

Macrofaunal biomass in Königshafen is higher than in the western Dutch Wadden Sea but similar to that in Jadebusen, a bay in the central part of the Wadden Sea (Table 8). There are two factors which may explain the lower biomass in the western Wadden Sea. First, the areal share of offshore, low-lying tidal flats is particularly high in this region. These tidal flats tend to have a biomass below average (Beukema, 1976). Jadebusen and Königshafen are land-locked bays with few or no low-lying offshore flats. The significant contribution of *Hydrobia ulvae* to the total biomass in these bays is related to a high proportion of nearshore flats and seagrass beds (see Table 5). The biomass of *Arenicola marina* is particularly high in Königshafen. Compared to the western Wadden Sea, average individual weight (0.39 g) is the same, while abundance is 3 times higher. This phenomenon may in part be related to a low abundance of lugworms on low-lying offshore flats. Investigations in Königshafen show that mussel beds are important over-wintering sites for early juveniles (Simon, pers. comm.). It may be hypothesized that the vicinity and abundance of this nursery habitat has a positive effect on adult population density.

The second aspect explaining lower biomass in the western Dutch Wadden Sea is the scarcity of intertidal mussel beds in that region. This may be an effect of enhanced mussel fishery (Beukema, 1992). In the early 1970s, *Mytilus edulis* contributed 23.3 % to the overall average of macrozoobenthic biomass (Beukema, 1976). In 1987, this species contributed only 2.3 % (Beukema, 1989). In Jadebusen and Königshafen, mussel beds cover approximately 1 % of the intertidal area, and contribute 17 and 20 % to the total biomass, respectively (Michaelis, 1987; this study).

Zoobenthic biomass on tidal flats in the Wadden Sea

A comprehensive study of macrofaunal biomass on tidal flats in the Dutch Wadden Sea was conducted between 1970 to 1974 by Beukema (1976). The mean of 27 g m^{-2} has been widely cited since then as a characteristic of the Wadden Sea. However, later surveys documented an increase in biomass by a factor of 2.2 for the western part of the Dutch Wadden Sea (Beukema, 1989) and of 1.6 for the intensively studied Balgzand near Den Helder (Beukema, 1991). As an average, a factor of 1.9 may be used to convert the mean biomass of the early 1970s for the entire Dutch Wadden Sea to an estimate of 51 g m^{-2} applicable to the early 1990s.

Obert (1982) estimated for an extensive tidal area east of the Dutch Wadden Sea an average biomass of 36 g m^{-2}, excluding mussel beds with 609 g m^{-2}. These mussel beds occurred in an area of 11.3% of this intertidal region. Assuming that about 2/3 of this area are interspaces not covered with mussels, the weighted mean for the region is 60 g m^{-2}. For the Jadebusen in the central Wadden Sea, studied by Michaelis (1987) in the period 1975 to 1977, a weighted average of 51 g m^{-2} is obtained, including areas with mussel beds. Together with the presented estimate of 65 g m^{-2} from Königshafen, the range from these 4 areas is 51 to 65 g m^{-2}, and may be regarded as an approximation to the zoomass for tidal flats of the present Wadden Sea. This range is slightly above the 44 g m^{-2} obtained for the subtidal zone in the western part of the Dutch Wadden Sea (Dekker, 1989), and considerably higher than 13 g m^{-2} found in the southern North Sea (Duineveld et al., 1990). However, it should be noted that in a year subsequent to a severe winter, the tidal-flat zoomass of the Wadden Sea will be below the given range (Beukema, 1990).

Acknowledgements. We thank H. Asmus, I. Kröncke and H. Michaelis for helpful comments on the manuscript. This is publication no. 125 of the project "Ecosystem Research Wadden Sea".

LITERATURE CITED

Asmus, H. & Asmus, R., 1985. The importance of grazing food chain for energy flow and production in three intertidal sand bottom communities of the northern Wadden Sea. – Helgoländer Meeresunters. *39*, 273 – 301.

Asmus, H., 1987. Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. – Mar. Ecol. Prog. Ser. *39*, 251–266.

Austen, I., 1992. Geologisch-sedimentologische Kartierung des Königshafens (List/Sylt). – Meyniana *44*, 45–52.

Beukema, J. J., 1974. Seasonal changes in the biomass of the macrobenthos of a tidal flat area in the Dutch Wadden Sea. – Neth. J. Sea Res. *8*, 94–107.

Beukema, J. J., 1976. Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. – Neth. J. Sea Res. *10*, 236–261.

Beukema, J. J.,1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. – Helgoländer Meeresunters. *43*, 405–415.

Beukema, J. J.,1990. Expected effects of changes in winter temperatures on benthic animals living in soft sediments in coastal North Sea areas. In: Expected effects of climatic change on marine coastal ecosystems. Ed. by J. J. Beukema, W. J. Wolf & J. J. W. M. Brouns. Kluwer, Dordrecht, 83–92.

Beukema, J. J., 1991. Changes in composition of bottom fauna of a tidal-flat area during a period of eutrophication. – Mar. Biol. *111*, 293–301.

Beukema, J. J., 1992. Long-term and recent changes in the benthic macrofauna living on tidal flats in the western part of the Wadden Sea. – Publ. Ser. Neth. Inst. Sea Res. *20*, 135-141

Dekker, R., 1989. The macrozoobenthos of the subtidal Wadden Sea. I. Biomass and species richness. – Neth. J. Sea Res. *23*, 57–68.

Dörjes, J., Michaelis, H. & Rhode, B., 1986. Long-term studies of macrozoobenthos in intertidal and shallow subtidal habitats near the island of Norderney (East Frisian coast, Germany). – Hydrobiologia *142*, 217–232.

Duineveld, G. C. A., Wilde, P. A. W. J. de & Kok, A., 1990. A synopsis of the macrobenthic assemblage and benthic ETS activity in the Dutch sector of the North Sea. – Neth. J. Sea. Res. *26*, 125–138.

Führböter, A., 1989. Changes of the tidal water levels at the German North Sea coast.- Helgoländer Meeresunters. *43*, 325–332.

Jensen, K. T., 1992. Macrozoobenthos on an intertidal mudflat in the Danish Wadden Sea: comparisons of surveys made in the 1930s, 1940s and 1980s. – Helgoländer Meeresunters. *46*, 363–376.

Jepsen, U., 1965. Die Struktur der Wattbiozönosen im Vormündungsgebiet der Elbe. – Arch. Hydrobiol. *24*, 252–370.

Kröncke, I., 1992. Macrofauna standing stock of the Dogger Bank. A comparison: III. 1950-54 versus 1985–87. – Helgoländer Meeresunters. *46*, 137–169.

Michaelis, H., 1981. Intertidal benthic animal communities of the estuaries of the river Ems and Weser. In: Invertebrates of the Wadden Sea. Ed. by N. Dankers, H. Kühl & W. J. Wolff. Balkema, Rotterdam, 158–188.

Michaelis, H., 1987. Bestandsaufnahme des eulitoralen Makrobenthos im Jadebusen in Verbindung mit einer Luftbild-Analyse. – Jber. ForschSt. Küste, Norderney *38*, 13-97.

Nienburg, W., 1927. Zur Ökologie der Flora des Wattenmeeres. I. Der Königshafen bei List auf Sylt. – Wiss. Meeresunters. (Kiel) *20*, 146–196.

Obert, B.,1982. Bodenfauna der Watten und Strände um Borkum – Emsmündung. – Jber. ForschSt. Küste, Norderney *33*, 139–162.

Reise, K., 1978. Experiments on epibenthic predation in the Wadden Sea. – Helgoländer Meeresunters. *31*, 55–101.

Reise, K., 1981. Ökologische Experimente zur Dynamik und Vielfalt der Bodenfauna in den Nordseewatten. – Verh. dt. zool Ges. *1981*, 1–15.

Reise, K., 1982. Long-term changes in the macrobenthic invertebrate fauna of the Wadden Sea: Are polychaetes about to take over? – Neth. J. Sea Res. *16*, 29–36.

Reise, K., 1985. Tidal flat ecology. Springer, Berlin, 191 pp.

Reise, K., 1987. Distribution and abundance of small and juvenile macrofauna on the tidal flats in the North Frisian Wadden Sea. – Biologiske Meddr *31*, 7–25

Reise, K., 1990. Historische Veränderungen in der Ökologie des Wattenmeeres. – Vortr. rhein.-westf. Akad. Wiss. (N) *382*, 35–50.

Reise, K., Herre, E. & Sturm, M., 1989. Historical changes in the benthos of the Wadden Sea around the island of Sylt in the North Sea. – Helgoländer Meeresunters. *43*, 417–433.

Reish, D. J., 1959. A discussion of the importance of screen size in washing quantitative marine bottom samples. – Ecology *40*, 307–309.

Smidt, E. L. B., 1951. Animal production in the Danish Waddensea. – Meddr Danm. Fisk.-og Havunders. *11* (6), 1–151.

Urk, R. M. van, 1987. *Ensis americanus* (Binney) (syn. *E. directus* Auct. non conrad) a recent introduction from Atlantic North America. – J. Conch., Lond. *32*, 329–333.

Wilde, P. A. J. W. de & Beukema, J. J., 1984. The role of the zoobenthos in the consumption of organic matter in the Dutch Wadden Sea. – Publ. Ser. Neth. Inst. Sea Res. *10*, 145-158.

Wohlenberg, E., 1937. Die Wattenmeer-Lebensgemeinschaften im Königshafen von Sylt. – Helgoländer wiss. Meeresunters. *1*, 1–92.