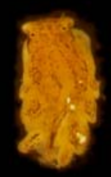
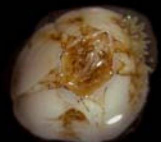
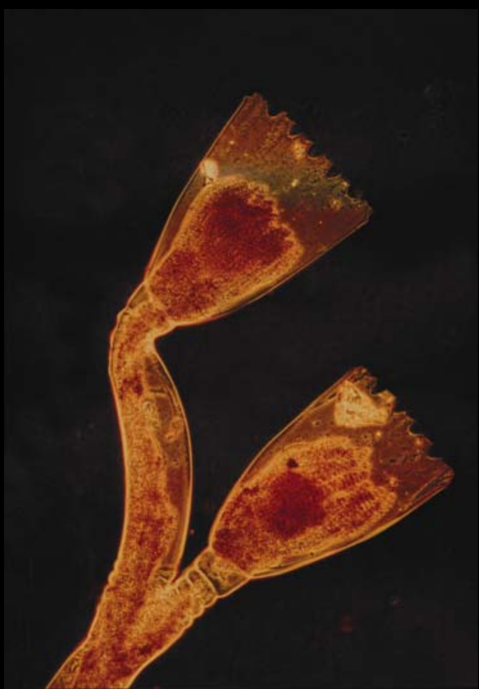






Analysing brackish benthic communities of the Weser estuary: Spatial distribution, variability and sensitivity of estuarine invertebrates.



Jan Witt

Bremen 2004

Alfred-Wegener-Institut für Polar- und Meeresforschung, Bremerhaven

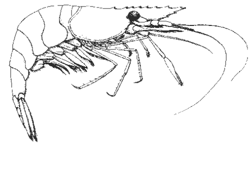
Analysing brackish benthic communities of the Weser Estuary:

Spatial distribution, variability and sensitivity of estuarine invertebrates.

Jan Witt

Dissertation zur Erlangung des akademischen Grades
eines Doktors der Naturwissenschaften (Dr. rer. nat.)

vorgelegt dem Fachbereich 2 (Biologie/Chemie)
der Universität Bremen



Bremen 2004

Advisory Commitee:

1. Gutachter: Prof. Dr. Wolf E. Arntz (AWI Bremerhaven, Universität Bremen)
2. Gutachter: Prof. Dr. Karsten Reise (AWI Bremerhaven, Universität Kiel)
1. Prüfer: Prof. Dr. Juliane Filser (Universität Bremen)
2. Prüfer: Dr. Rainer Knust (AWI Bremerhaven)

CONTENTS

SUMMARY

This study analyses the benthic invertebrate fauna of the brackish-water zone of the Weser estuary from km 45 to km 115, based on personal sampling and observation in the years 1994 to 2002 and additional data from the region since 1980. In order to provide the biological information for an evaluation and the conservation management of the Weser estuary, the spatial distribution of benthic invertebrates and their sensitivity to human interference was investigated in three case studies. Additional external data of benthic invertebrates were added to provide a comprehensive database that allows a transfer of recognized principles from the case studies to a benthic characterisation of the entire estuary.

An inventory of all benthic species recorded 233 species in the brackish-water zone of the Weser estuary. 40 species were identified as genuine brackish-water species, which are restricted to the brackish-water zone and special habitat structures. The compiled database is much more comprehensive than in prior studies because of the integration of supratidal habitats such as reedbeds, saltmarsh ditches and artificial substrates such as groynes. Some species that were considered to be extinct or absent from the Weser estuary by earlier studies, were still frequent in special small-sized biotopes. Others showed a strong decline within a few decades (e.g. *Sabellaria spinulosa*). Similar to other estuaries the brackish-water zone of the Weser can be separated into four major zones by differing benthic communities along the salinity gradient from the oligohaline, through the mesohaline to two polyhaline zones. This zonation was found to be distinct in the subtidal and intertidal areas, but is less obvious towards the supratidal biotopes as salinity drops.

By including the supratidal areas in the analysis, 10 brackish subzones were identified and compared by area and benthic assemblages. In contrast to earlier characterisation by dominant or frequent species, a biotope characterisation by brackish-water species is suggested, which allows the identification of small-structured biotopes.

The analysis of benthic distribution within mesohaline and polyhaline estuary zones at different spatial scales showed similar patterns of benthic colonisation in principle. These patterns are a response to estuarine hydrological features, such as the salinity gradient and the tidal energy. The hydrological parameters result in a specific bottom morphology, sediments and substrates, which are inhabited by certain benthic assemblages. It was found that the salinity gradient across the tidal range, with low salinities in the supratidal habitats, is a major distribution factor similar to the gradient along the estuary.

The strong gradients from land to water and river to ocean result in a variety of special biotopes demanding extreme adaptive skills from benthic inhabitants. A low point diversity, which reflects the strong species selection of such an environment, combined with an increase of species richness on larger scales is found to be characteristic for a transitory environment as represented by an estuary. Some small-scale biogenic biotopes as provided

by structurally important species such as *Mytilus edulis*, *Lanice conchilega* or *Obelia* sp. are the basis for complex and diverse assemblages of associated fauna.
Artificial structures, such as groynes and salt marsh ditches which might negatively influence natural estuarine processes on one hand, were found to provide exclusive habitats for some estuarine species on the other. Such artificial substrates and structures may have a specific function and value as substitutes of former biotopes in technically influenced estuaries.

The identification and characterisation of large salinity zones and small-scale biotopes gives the possibility of an evaluation by area, which was done by a GIS supported calculation. The percentage of polyhaline channels within the total area (91,850 ha), for example is 51.3% while the supratidal marshes only yield 1.6%. Seagrass meadows and mussel beds are special biotopes with only 0.4% each of the total intertidal area. Together with information on decline and threat, as given in the Red Lists of biotopes, a ranking list of most valuable habitats was compiled for the evaluation of the Weser estuary. The strong restriction of certain brackish water species to single habitat structures, e.g. the gastropod *Alderia modesta* that exclusively feeds on certain green algae (*Vaucheria* sp.), demonstrates the sensitive situation to be dealt with.

Sensitivity to impacts depended on certain biological criteria both at the species and the community level. In contrast to short-lived and mobile species that showed high tolerance or even opportunistic reaction to sediment interference, sessile epibionts were sensitive indicators of the impact. Besides mobility, also the anatomy and the feeding strategy differed between sensitive and tolerant species. Indicator species and assemblages for the evaluation of the environmental status of an estuary and for monitoring questions are suggested and discussed. Appropriate methods to assess human interference in estuarine waters, considering the different spatial scales, are proposed.

An efficient conservation and management strategy for estuarine features as recently claimed by the EU directives needs to take into account the observed different spatial scales of individually structured biotopes and the specific sensitivity of estuarine benthic communities to impacts to ensure the continuance of the estuarine environment as an entity.
Separation of areas with economic and environmental priorities within a conservation management based on benthic data is suggested.

ZUSAMMENFASSUNG

In dieser Arbeit wird die benthische Wirbellosenfauna der Brackwasserzone des Weserästuars im Bereich von Stromkilometer 45 bis 115 untersucht. Eigene Untersuchungen von 1994 bis 2002 bilden den Kern der Arbeit, der mit zusätzlichen benthischen Daten der Region bis zurück zum Jahr 1980 ergänzt und erweitert wird. Um mittels benthischer Daten biologische Informationen aus dem Gebiet darzustellen und für eine Bewertung sowie für ein naturschutzbezogenes Management nutzbar zu machen, werden die räumliche Verteilung der benthischen Gemeinschaften und die eingriffsbezogene Sensibilität der Arten in drei Fallstudien analysiert. Zusätzliche benthische Daten aus Studien Dritter werden in die Analyse integriert, um eine Datengrundlage zu erhalten, die eine Übertragung der prinzipiellen Erkenntnisse aus den Fallstudien für eine benthische Charakterisierung des gesamten Ästuars ermöglicht.

Die Inventarisierung aller bisher nachgewiesenen benthischen Arten und eine Analyse von Untergemeinschaften ergibt 233 Arten bzw. Taxa in der Brackwasserzone der Weser. Davon sind 40 Arten zu den echten (genuinen) Brackwasserarten zu zählen, die auf Brackwasserbedingungen und besondere Habitatstrukturen angewiesen sind. Die zusammengestellte Datenbasis ist deutlich umfangreicher als vorhergehende Studien, da supralitorale Biotope wie Röhrichte, Salzwiesengräben und anthropogene Hartsubstrate der Buhnen in die Auswertung eingehen. So können einige Arten, die bereits als ausgestorben oder verschollen galten, an besonderen Strukturen recht regelmäßig nachgewiesen werden. Für andere wird jedoch ein starker Rückgang in nur wenigen Jahrzehnten festgestellt, wie z.B. für den Polychaeten *Sabellaria spinulosa*. Ähnlich wie andere Ästuare kann das Weserästuar für die Aufnahme der benthischen Besiedlung in vier Salinitätszonen eingeteilt werden: in eine oligohaline, eine mesohaline und zwei polyhaline Zonen. Diese Zonierung zeigt sich deutlich in sublitoralen und eulitoralen Bereichen und wird in Richtung Supralitoral mit fallender Salinität geringer.

Mit der Integration der Supralitoralbereiche in die Analyse werden zehn Unterzonen im Brackwasserbereich identifiziert und anhand ihrer Fläche und benthischen Besiedlung verglichen. Alternativ zur früheren Klassifizierung der Gemeinschaften mittels dominanter und stetiger Arten wird eine Biotopcharakterisierung durch Brackwasserarten vorgeschlagen, die auch die Identifizierung kleinräumiger Strukturen erlaubt.

Die Analyse der benthischen Verteilung innerhalb der mesohalinen und polyhalinen Zonen in unterschiedlichen räumlichen Maßstäben zeigt grundsätzlich ähnliche Muster der Besiedlung. Diese Besiedlungsmuster sind eine Reaktion auf die hydrologischen Bedingungen in einem Ästuar, wie z.B. Salinitätsgradienten und Tideströmung. Die hydrologischen Parameter prägen die Morphologie des Gewässergrundes und die Sedimente, die wiederum eine bestimmte Fauna beherbergen. Der Salinitätsgradient quer zur Fließrichtung, mit entsprechend geringen Salinitäten im Supralitoral, wirkt vergleichbar auf die Faunenverteilung wie der Salzgradient in Längsrichtung.

Die dynamisch wechselnden Gradienten vom Land zum Wasser und vom Fluss zum Meer schaffen eine Vielzahl von speziellen Biotopen, die eine hohe Anpassungsfähigkeit von den benthischen Besiedlern erfordern. Eine niedrige Punktdiversität, die eine starke Selektion der Arten durch die extremen Umweltparameter widerspiegelt, kombiniert mit einer höheren Gebietsdiversität wird als typisch für Übergangs- und Grenzökosysteme, wie Ästuare es sind, bestätigt. Einige kleinräumige biogene Biotope, die von strukturgebenden Arten wie *Mytilus edulis*, *Lanice conchilega* oder *Obelia*- Arten bereitgestellt werden, sind die Basis für relativ komplexe und diverse Gemeinschaften assoziierter Arten.
Künstliche Substrate wie Buhnen und Salzwiesengräben können einerseits die natürlichen Prozesse im Ästuar beeinträchtigen, stellen andererseits jedoch exklusive Biotope für Brackwasserarten dar. Funktion und Wert solcher Strukturen als Ersatzhabitate in einem technisch ausgebauten Ästuar werden diskutiert.
Die Identifizierung und Charakterisierung ausgedehnter Brackwasserzonen und kleinräumiger Biotope ermöglicht eine raumbezogene Bewertung, welche durch eine GIS-gestützte kartografische Auswertung erfolgt. Der Anteil der polyhalinen Prielsysteme liegt bei 51,3% des Gesamtgebiets (91.850 ha), während die polyhalinen Salzwiesen nur 1,6% erreichen. Seegraswiesen und Muschelbänke als besondere Biotopbildner bedecken beispielsweise nur 0,4% der gesamten Wattfläche. Kombiniert mit Informationen zum Rückgang und zur Bedrohung dieser Biotope wird eine Rangliste der besonders wertvollen Biotope für eine benthische Ästuarbewertung erstellt. Die starke Begrenzung einiger Arten auf einzelne kleinräumige Strukturen, wie z.B. die trophische Bindung der Nacktschnecke *Alderia modesta* an eine bestimmte Gattung von Grünalgen (*Vaucheria* sp.), zeigt die Sensibilität der Beziehungen in diesem System.
Die Sensibilität gegenüber Eingriffen zeigt sich an bestimmten biologischen Kriterien auf der Ebene von Arten und Gemeinschaften. Im Gegensatz zu kurzlebigen und mobilen Arten, die eine hohe Toleranz oder sogar eine opportunistische Reaktion gegenüber Störungen des Sediments zeigen, sind sessile Epibionten oft sensible Anzeiger solcher Eingriffe. Neben der Mobilität ist die Anatomie und Ernährungsweise beider Gruppen oft ganz verschieden.
Indikatorarten und Gemeinschaften, die zu einer naturschutzfachlichen Bewertung des Ästuars sowie zu Monitoringfragen beitragen können, werden vorgeschlagen und diskutiert.
Darüber hinaus werden geeignete Methoden vorgestellt, um menschliche Eingriffe in Ästuaren unter Berücksichtigung der räumlichen Einheiten zu erfassen und zu bewerten.

Ein effektiver Schutz der ästuarinen Funktionen, wie aktuell von der EU gefordert sowie ein Naturschutzmanagement sollte die dargestellten Verhältnisse mit ihren kleinräumigen Strukturen und die spezielle Empfindlichkeit der benthischen Gemeinschaft gegenüber Eingriffen berücksichtigen, um ein Fortbestehen des Ästuars als Funktions- und Lebensraum zu gewährleisten. Eine räumliche Trennung in ökologische und ökonomische Vorranggebiete innerhalb eines solchen Managements, gestützt auf benthische flächenbezogene Daten, wird vorgeschlagen.

1 INTRODUCTION

The estuary as a mouth of a river influenced by the tides of the Sea is a unique and important part of the aquatic environment. It forms the transition zone between the inland world of fresh water and the ocean. As such, it retains some characteristics of both fresh-water and marine environments, but it also has unique properties of its own (KETCHUM 1983).

Estuaries are ecosystems with an extreme contrary picture to the public: On one hand the world's major cities are located alongside estuaries which are most likely to be affected by the highest inputs and concentration of contaminants (McLUSKY 2001). The estuarine biocoenosis, controlled by highly dynamic abiotic parameters, is often described as a little diverse assemblage of a few specialists and adaptive cosmopolitans that can withstand low or fluctuating salinities (BARNES 1994). Terms like “death zone” and “species minimum” conjure a negative mental image of these characteristics. This, combined with the high pollution in industrialised estuaries reinforces the impression of extremely low diversity or even low qualities.

On the other hand estuaries belong to the most productive natural habitats of the world with an intensive transfer from nutrients to biomass and utilisation of energy by succeeding trophic levels (McLUSKY 1989). Estuaries provide most important ecological functions such as the linkage of different ecosystems, the filter function for particulate and dissolved matter, the sediment supply of coastal waters and the habitat function for many specialised invertebrates and fishes (WOLFF 1973, DE JONGE 1999, McLUSKY 2001). The nursery and feeding areas for juvenile fish, the spawning grounds, acclimatisation zones for migrating fish and the resting and feeding areas for migrating birds are examples for estuarine functions far beyond the regional scale (KETCHUM 1983).
Benthic invertebrates have a central position within these functional relationships e.g. in the estuarine food web as food supply for fish and migrating birds, but also within the regeneration of water and sediment quality. The perturbation of sediments and incorporation and filtration of particular organic material by benthic invertebrates is the basis for the transfer from nutrients to biomass, the ventilation for microbiological processing and the decomposition of xenobiotica.

The increased loss of estuarine biotopes and the destruction of brackish water habitats by industrialisation have been documented by several authors (DITTMER 1981, KETCHUM 1983, McLUSKY 1989, SSYMANK & DANKERS 1996, DE JONGE 1999). The German “Red List” of threatened biotopes (SSYMANK & DANKERS 1996) classifies semi-natural and natural estuaries, brackish salt marshes, estuarine tidal flats, fresh water tidal flats of estuaries and coastal lakes as threatened by complete destruction (Status 1). Brackish reed marshes and mud flats are classified as heavily endangered (Status 2). Recently established European environmental directives may provide protection for estuarine areas in the future:

- The European Water Framework Directive (WFD)(2000/60/EG-of 23-10-2000) was installed in the EU in 2000 (ratification by the national law of Germany in 2001) to improve and control water quality of all European river systems. This includes the biological evaluation of all riverine, estuarine and coastal waters to define an actual quality status and a target status, which should be reached by improvements (target quality). A management plan is supposed to be implemented to reach these targets in an efficient manner. “Quality” in the understanding of the directive has to be linked with an historic, natural situation (SCHLUNGBAUM 1999, IRVINE 2004, http://www.wrrl.de, www.wasserblick.net).
- The European Habitat Directive (92/43/EEC of 21-05-1992) aims at the conservation of habitats including estuaries within a European network of protected sites (NATURA 2000). Similar to the Water Framework Directive the quality status of a protected estuarine area has to be evaluated and controlled by biological criteria on a regular basis (BALZER et al. 2002, http://forum.europa.eu.net).

These directives emphasize the importance of estuarine biotopes and the need for conservation management, but the practical implications are still uncertain (IRVINE 2004).

While most river systems and coastal areas have been well investigated by fresh water and marine research techniques, there is still a gap between these two research fields concerning basic biological information from estuaries (BARNES 1994, McLUSKY 1989). Being in a transitory zone between three large ecosystems, i.e. the fresh water, the land and the ocean, scientific work in estuaries needs to combine several different research techniques to get sufficient estuarine biological data.

The important ecological function of macrozoobenthos in marine ecosystems (ARNTZ et al. 1999) and its value for indication of environmental impacts (PEARSON & ROSENBERG 1978, ARNTZ 1981, UNDERWOOD 1991, HALL 1994, NEWELL et al. 1998) put it in focus for estuarine monitoring. Biological evaluation of marine, coastal and estuarine biotopes and methods to monitor and control biological quality is a major target of European nature conservation (e.g. DAVIES 2001, CEFAS 2002, CIS 2003, ICES 2003).

1.1 Objectives of this study

This study aims to characterise estuarine habitats of the Weser estuary by their benthic invertebrate communities. A first step towards an environmental quality control and management of the estuary is an inventory of benthic biological features and their quantification. The consideration of the sensitivity of benthic assemblages to human activities and actual threats and a comparison with the historical situation is the second step. An identification of species and habitats that indicate ecological quality to focus on during monitoring and the control of improvement efforts offers an additional perspective.

While most studies of estuarine communities have focused on “along-estuary” distribution aspects within the estuarine channel system which are controlled by salinity, recent publications emphasize the need for the integration of aquatic biotopes of salt marshes, such as ditches and tidal ponds (ARMITAGE et al. 2003). All different biotopes, such as natural and anthropogenic hard substrates, supratidal areas and biotopes along the shoreline need to be integrated. Such an approach of gathering data from different studies and different sampling techniques was used for the Weser estuary for the first time, thus providing basic information of estuarine invertebrate distribution.

An evaluation of an estuary based on benthic assemblages has to consider the spatial distribution of species and their sensitivity and threats. Therefore the specific objectives of this study are the following:

Spatial differentiation:

- Analysis of spatial distribution patterns of benthic invertebrates on different scales
- Inventory of benthic macrofauna and biotopes including all salinity and tidal zones

Sensitivity, threats and impacts:

- Analysis of negative human impacts on estuarine benthic communities
- Evaluation of benthic communities considering their sensitivity to these threats
- Suggestions of priorities for an environmental estuarine management.

1.2 Structure of the thesis

This study is separated into 5 sections. It begins with a description of the estuary, giving general abiotic and historic information. The second part is an inventory of the species and their habitats within the estuary and its different zones, compiling all available data from other studies. The third part is based on the author`s investigations and contains publications I to III, with a detailed analysis of species spatial distribution in the mesohaline zone (publication I) and in the polyhaline zone (publication II) of the Weser estuary. The impact assessment in publication III gives an example of threats to estuarine communities and shows ways to assess them properly.

In the discussion (section 4) the results of the distribution analysis, the inventory of biotopes and species and their sensitivity and threats will be discussed on the scale of the estuary. An evaluation of selected biotopes is suggested as a basis for an estuarine management further on.

In the last section, all references used for this thesis are given. The appendix lists the different species and additional data sources. Fig. 1 shows the major components of the thesis by their interaction with the contents.

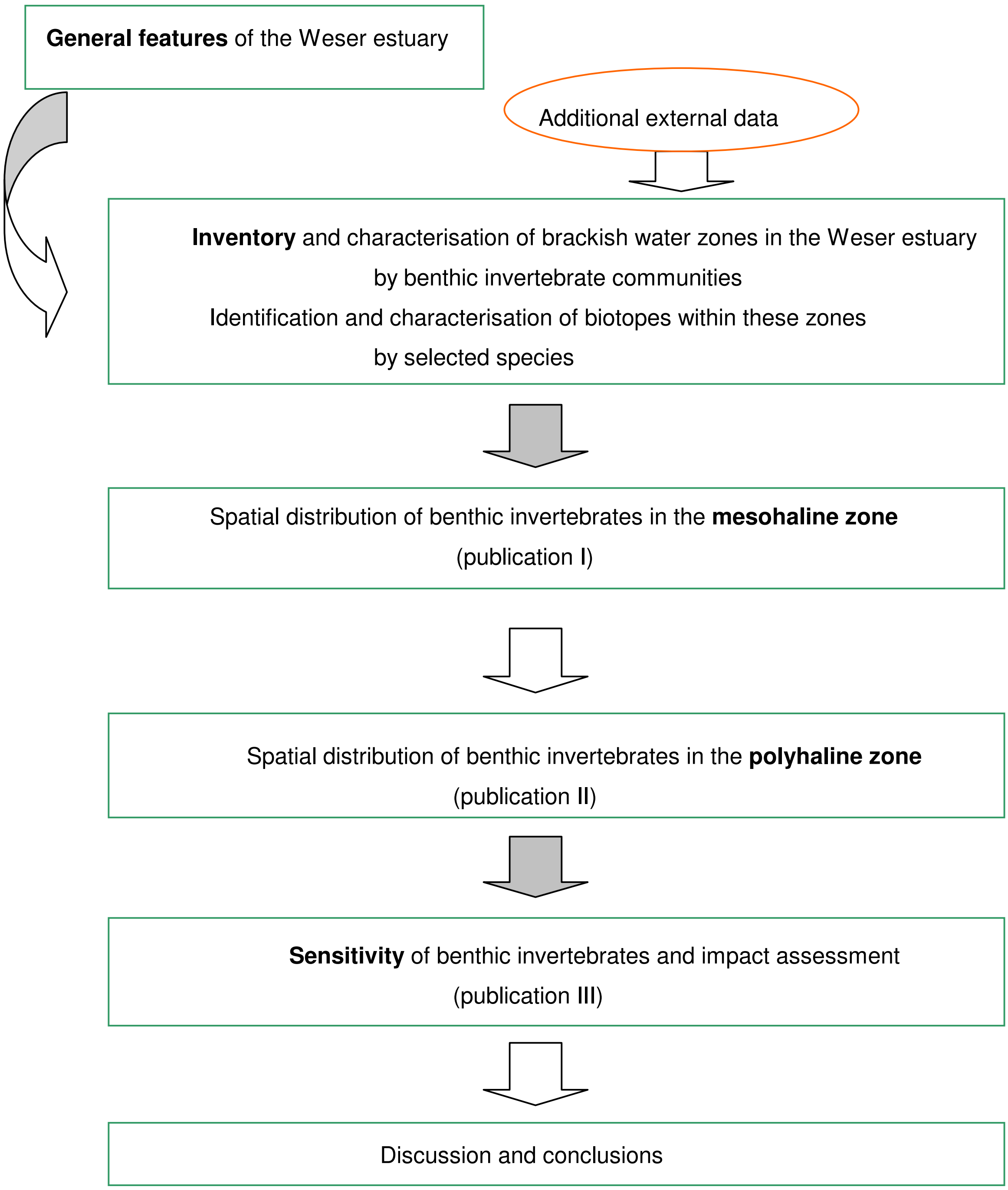


Fig. 1 Major components of the thesis and interaction with its contents.

1.3 Estuarine characteristics

As an ecosystem, the estuary performs several vital functions. Besides being a habitat for species, which live their entire life cycle within the estuary, it forms part of the migration routes of fish and invertebrates to their breeding grounds. Furthermore, it provides important nursery areas for juvenile fish and invertebrates and feeding grounds for migrating birds (KETCHUM 1983).

The complex interaction of abiotic parameters, such as tidal currents, turbidity, sediments and salinity in spatial and temporal variations in an estuary has attracted scientists from many disciplines. REMANE & SCHLIEPER (1971), DEN HARTOG (1961, 1964, 1971), WOLFF (1973), KETCHUM (1983), Mc LUSKY (1989) and BARNES (1994) provide a basic understanding of estuarine biology. The biology of German estuaries has been the subject of early studies by DAHL (1893), REMANE (1934, 1940, 1950, 1958,), DAHL (1956), KINNE (1966) and CASPERS (1948, 1958, 1959). The definitions of, and classifications for brackish waters have been the subject of many investigations and discussions.

PRITCHARD (1967) defines an estuary as “a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water from land drainage”. This type of definition leaves both the landward and the seaward boundaries of the estuary vague because of the salinity variation during tides and the strong influence of weather conditions. While the “Venice system” of brackish waters (VENICE SYSTEM 1959) defines boundaries by salinity only, other aspects have been discussed to define the estuarine reach. According to KETCHUM (1983) the tidal influence, which includes a sometimes-expanded river section of tidal fresh water, defines the inner boundary of an estuary. The outer boundary should be defined by a line between the land masses on each side of the entrance to the estuary, instead of the definition by a measure of reduced salinity. The change of salinity with distance is generally more gradual in the costal waters than it is within the estuary itself. The fresh water influence can be traced for many miles from the geographical mouth of the estuary (KETCHUM 1983).

Additional to the salinity gradient along the estuary the substrates reflect a certain change in hydrology and morphology within the estuarine zones as described by CARRIKER (1967), McLUSKY (1989) and WILSON (1994) (Table 1). DEN HARTOG (1964) and DITTMER (1981) emphasize animal distribution as a major parameter for the determination of an estuary and its zones. According to DEN HARTOG (1964), in most brackish waters the fauna of three salinity zones (oligohaline, mesohaline, polyhaline) is distinguishable irrespective of exactly the same salinity. Special adaptive mechanisms allow benthic invertebrates to withstand the extremely variable conditions in an estuary e.g. the tidal change of salinity.

Table 1 The physical, chemical and biological zones of an estuary (WILSON 1994).

Estuary division	*Substrate*	*Salinity range (PSU)*	*Zone*	*Organism type*
River	gravels	< 0.05	limnetic	freshwater
Head	becoming finer	0.5-5.0	oligohaline	oligohaline, freshwater migrants
Upper reaches	mud, currents minimal	5.0-18.0	mesohaline	true estuarine
Middle reaches	mud, some sand	18.0-25.0	polyhaline	estuarine, euryhaline
Lower reaches	sand /mud	25.0-30.0	polyhaline	estuarine, euryhaline, marine migrants
Mouth	clean sand	30.0-35.0	euhaline, marine	stenohaline marine

2 STUDY AREA

2.1 Location

The river Weser originated, as did most European rivers, during the final stages of the last glacial period and is formed by the confluence of the Werra and Fulda rivers. BEHRE (1978) and STREIF (1978, 1996) give a detailed picture of the dynamic morphologic development of the German North Sea coast since the ice age.

Geographically the river can be divided into 4 sections: the Upper, Middle, Lower and the Outer Weser. The estuary itself includes the Lower Weser with the tidal reach from Bremen (km 0) to Bremerhaven (km 65) and the Outer Weser, which reaches from Bremerhaven to the North Sea (km 120) (Fig. 2).

The estuary is further subdivided into brackish water zones with an oligohaline, mesohaline and polyhaline section. The study area covers the brackish water zone from river km 45 to km 112 as defined by the Venice System for the classification of brackish waters (DITTMER 1981, MICHAELIS 1981) (Fig. 2). The tidal reach of brackish water into the salt marshes at spring tide defines the survey area across the river. In contrast to other studies this includes littoral biotopes such as reedbeds, ditches and ponds. The tidal reach, as a definition of an estuarine system by the European Water Framework Directive (WFD), includes a large fresh water area in the Weser estuary, which is not referred to in this study.

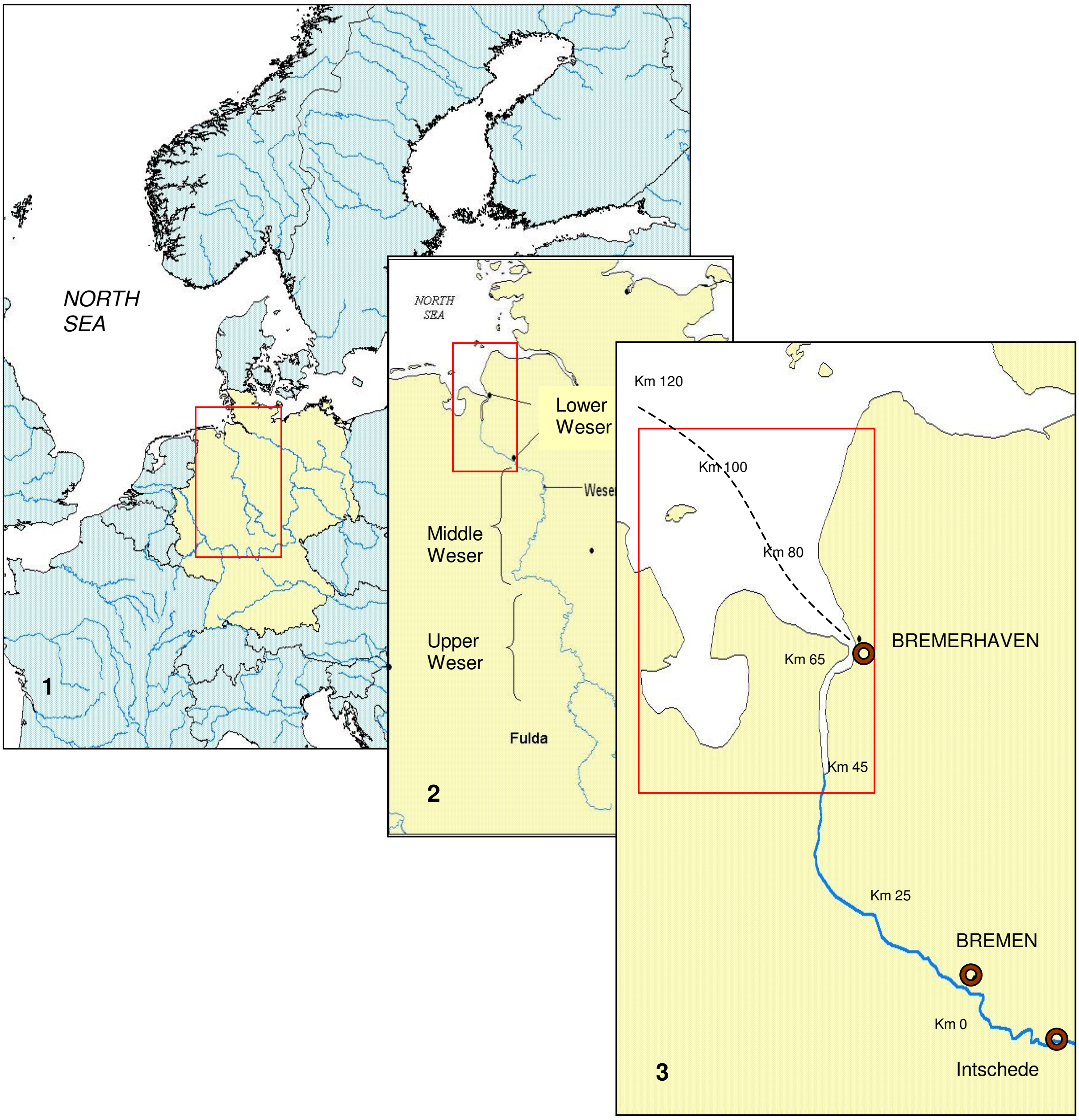


Fig. 2 The location of the Weser (1), its estuary (2) and the survey area (3) with major sections (broken line indicates shipping lane in the Outer Weser, numbers of km indicate distance from the weir at Bremen-Hemelingen, km 0).

2.2 Hydrology and salinity

The hydrology of the Weser has been described by several authors (LÜNEBURG 1954, LÜNEBURG et al. 1975, WELLERSHAUS 1981, ENGEL 1995). The Weser has a total length of 432 km and drains an area of 46 136 km². Main factors influencing the estuarine waters are wind, tides, seawater inflow and freshwater outflow, which correspond to the regional climate (LÜNEBURG et al. 1975). The river fresh water outflow, with a mean of 323 m³/s (registered at Intschede, southeast of Bremen, Fig. 2), shows its annual maximum flow during the period of snow melting in the low mountain range of Germany (January to March). The strong variation of fresh water outflow during a year (summer, winter) and between years (wet, dry years) basically controls the salinity regime of the estuary (Fig. 3). In Table 2 some main characteristics of the freshwater outflow of the Weser are given.

Table 2 Mean and maximum freshwater outflow of the Weser at Intschede between 1941 and 1990 (SCHIRMER 1996).

Mean low water outflow	127 m³/s
Mean outflow (all year)	323 m³/s
Mean high water outflow	1250 m³/s
Maximum outflow (1946)	3500 m³/s

In Fig. 3 the strong correlation of fresh water outflow (Intschede) and salinity (several sampling locations along the estuary from km 25 to km 120) is depicted. Besides the seasonal variation (low salinity in winter or spring, high salinity in late summer or autumn), the difference between years can be seen. The riverward border of seawater influence is generally found at about km 45, but shifts upstream in dry summers.

Under certain conditions (tides, wind, weather) a distinct salt wedge is separated from the surface layer by a discontinuity layer (salinity stratification). However, in most cases the salinity of the Weser increases steadily with depth up to 7 PSU (LÜNEBURG et al. 1975). MICHAELIS (1973) found salinity stratifications only at slack high and low water. Apart from vertical salinity gradients in cross sections, the salinity is 1 to 5 PSU higher at the western than at the eastern side of the estuary. This is a result of the Coriolis force (Kelvin wave), which is caused by the earth´s rotation directing the ebb current towards the eastern and the flood current towards the western banks (LÜNEBURG et al. 1975, KETCHUM 1983).

A peculiarity of the Weser estuary is its high content of salts in the former freshwater zone, caused by the discharge of waste material from potassium mining in the Upper Weser and its tributaries. Salt input has been reduced strongly after the closing of the potassium industries since 1990. Effects of salt pollution on the invertebrate fauna in the former fresh water zone are given in HAESLOOP (1990).

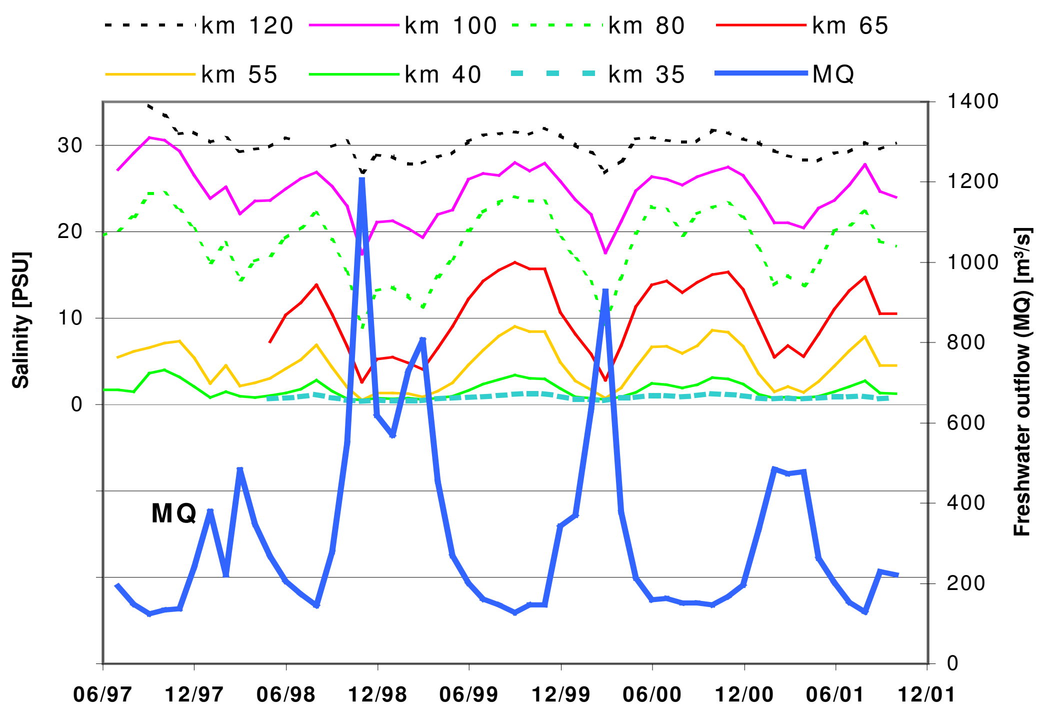


Fig. 3 Freshwater outflow (MQ) at Intschede (s. Fig. 2) and corresponding salinity (coloured curves) of the Weser at different sites along the estuary (distance of sites in km from Bremen down the river) from June 1997 to December 2001 (WSA unpublished data, modified).

The Venice System of brackish waters (VENICE SYSTEM 1959, CASPERS 1959) defines 4 zones within an estuary, which can be applied to certain river sections of the Weser during mean conditions of fresh water outflow, tides and wind (DITTMER 1981):

- (Former) fresh water zone (0-0.5 PSU) from km 0 to km 45 (not true fresh water because of anthropogenic salt pollution, s. text).
- Oligohaline zone (0.5-5. PSU) from km 45 to km 65
- Mesohaline zone (5.0-18.0 PSU) from km 65 to km 80
- Polyhaline zone (18.0-30.0 PSU) from km 80 to km 112

In Fig. 4 the salinity zones are presented in a map, which gives a rough relation to the different areas. Due to the funnel shaped coastline of the estuary the area of the oligohaline zone is much smaller than the mesohaline and the polyhaline area.

The high turbidity of the brackish water zone is characteristic of North Sea estuaries (LÜNEBURG et al. 1975). While the turbidity in the Weser estuary varies between 100 mg/l and 2000 mg/l suspended matter, the central turbidity zone is defined by a minimum of 250 mg suspended matter per litre (LÜNEBURG et al. 1975, WELLERSHAUS 1981). The position of the turbidity zone in the Weser depends on the amount of freshwater runoff.

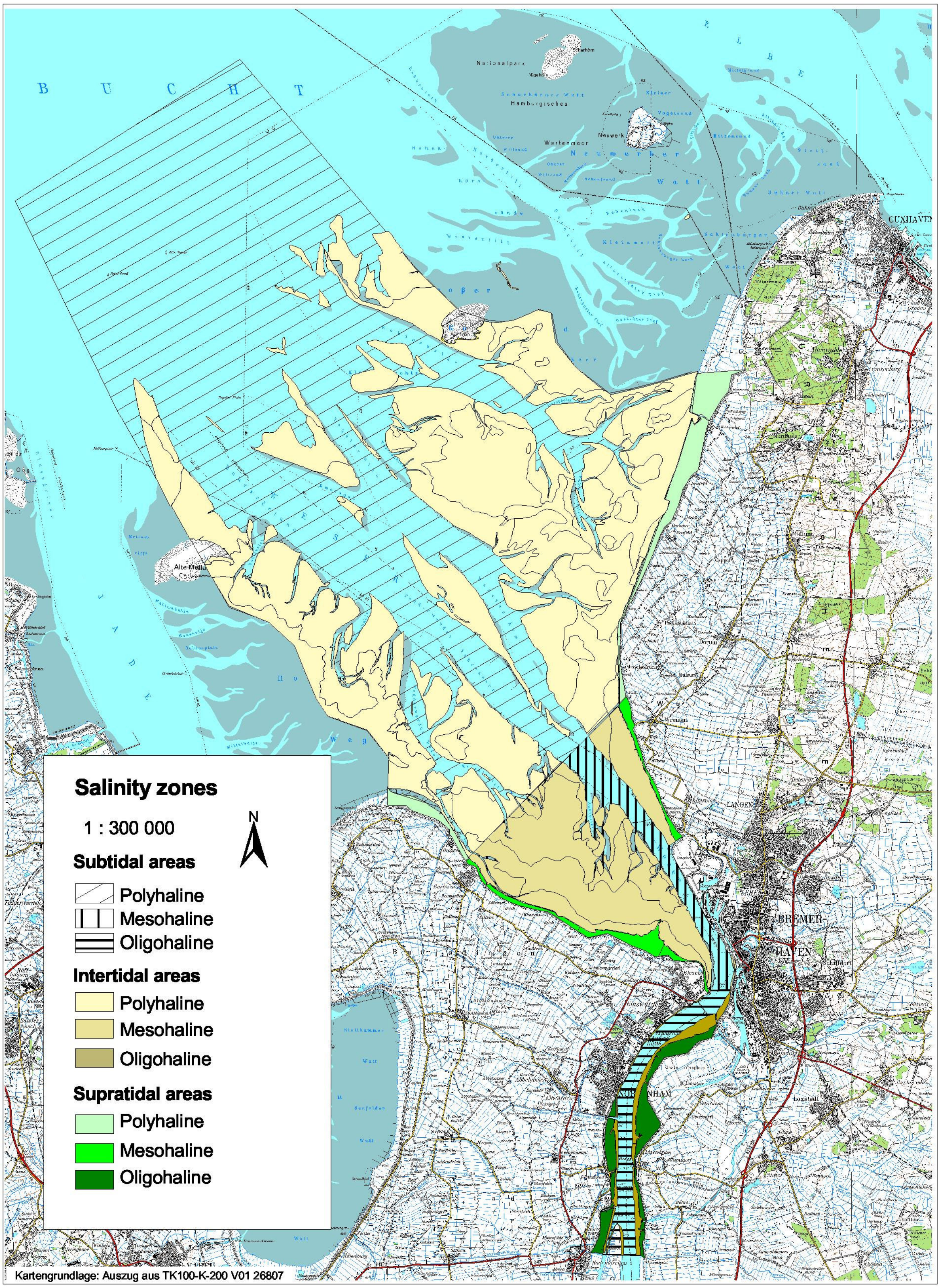


Fig. 4 Salinity zones of the Weser estuary with subtidal, intertidal and supratidal areas (zonation from subtidal salinity data, e.g. LÜNEBURG et al. 1975).

Its maximum is found between km 56 at slack high and at km 64 at slack low water (DITTMER 1981). MEYBIER & BÖMEKE (1970) showed that the maximum turbidity of the near bottom water did not occur in the centre of the riverbed but at the shore. In dry years it has been registered as far upwards as km 25 (ARGE WESER 2001). In wet years, with a high freshwater runoff, the turbidity zone moves down the river as far as km 80 (GRABEMANN & KRAUSE 2001).

2.3 Morphology and sediments

The Weser estuary is a funnel shaped estuary of a typical lowland river with a wide opening towards the North Sea (Fig.4). Similar to the neighbouring Elbe, Jade and Ems river systems it has a large tidal zone with a longitudinal gradient of increasing seawater influence. The dynamic hydrology has created a continuously changing riverbed which has split into many channels through intertidal flats and salt marshes.

While in the mountain regions of the Weser and its tributaries different geological rock strata form the riverbed, the estuary is situated on glacial sands and stones from the Pleistocene epoch, which are covered with different fluvial and marine deposits. STREIF (1996) describes the sequence of geological layers as a surface layer of silt and clay of 25 m and a Pleistocene sand layer that splits into coarse sand and pebbles in the upper layers and fine sands and silt deeper down.

Dynamic processes since the ice age, namely a sea level rise of about 45 m, periodical changes of sedimentation and erosion by tides and floods have continuously modelled the coastline of the Weser estuary (STREIF 1978, 1996). This can be seen by the scattered distribution of different types of marshes, clay and sandy soils in the former river valley and from an analysis of historical coastlines (STREIF 1996).

The former morphological dynamics along the coasts have been systematically reduced by man for land use and shipping purposes (WETZEL 1987, see next chapter). Most of the former river valley is now separated from the river by dykes. Semi-terrestrial biotopes influenced by tidal change are therefore restricted to small areas along the river (Fig. 4).

The actual morphology of the Weser estuary is depicted by the depth contours in Fig. 5 (WSD Aurich, unpubl. data). Depths of the riverbed vary from the intertidal flats to depths of up to -20 m SKN (below sea chart zero) in the channels of the Outer Weser. The contour lines indicate steep edges at some of the deep channels and shallow slopes towards the flats. There are no depth data available from the eastern intertidal flat area as seen in Fig. 5 (area without any depth lines).

The intertidal sediment distribution in the Weser estuary is given in Fig. 6 (RAGUTZKI & MEYER 1999). While most of the intertidal flats in the outer estuary consist of bright and dark sands, the muddy sands and mudflats are restricted to the inner estuary close to the shore. Taking low numbers of sites and the variability of sediments into account Fig. 6 gives a basic overview of the distribution of surface sediments.

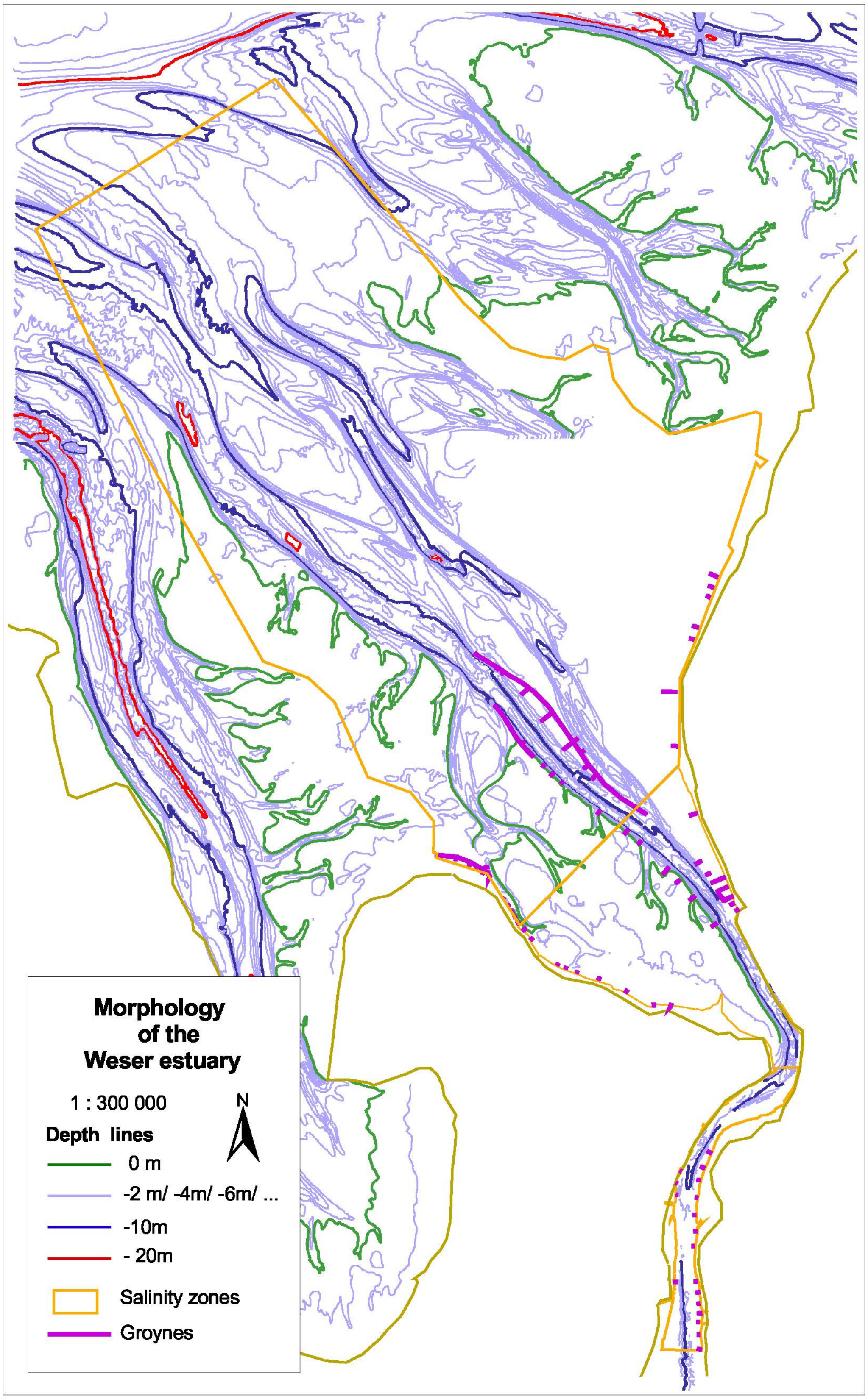


Fig. 5 Morphology of the Weser estuary by depth contours (WSD Aurich, unpubl. data).

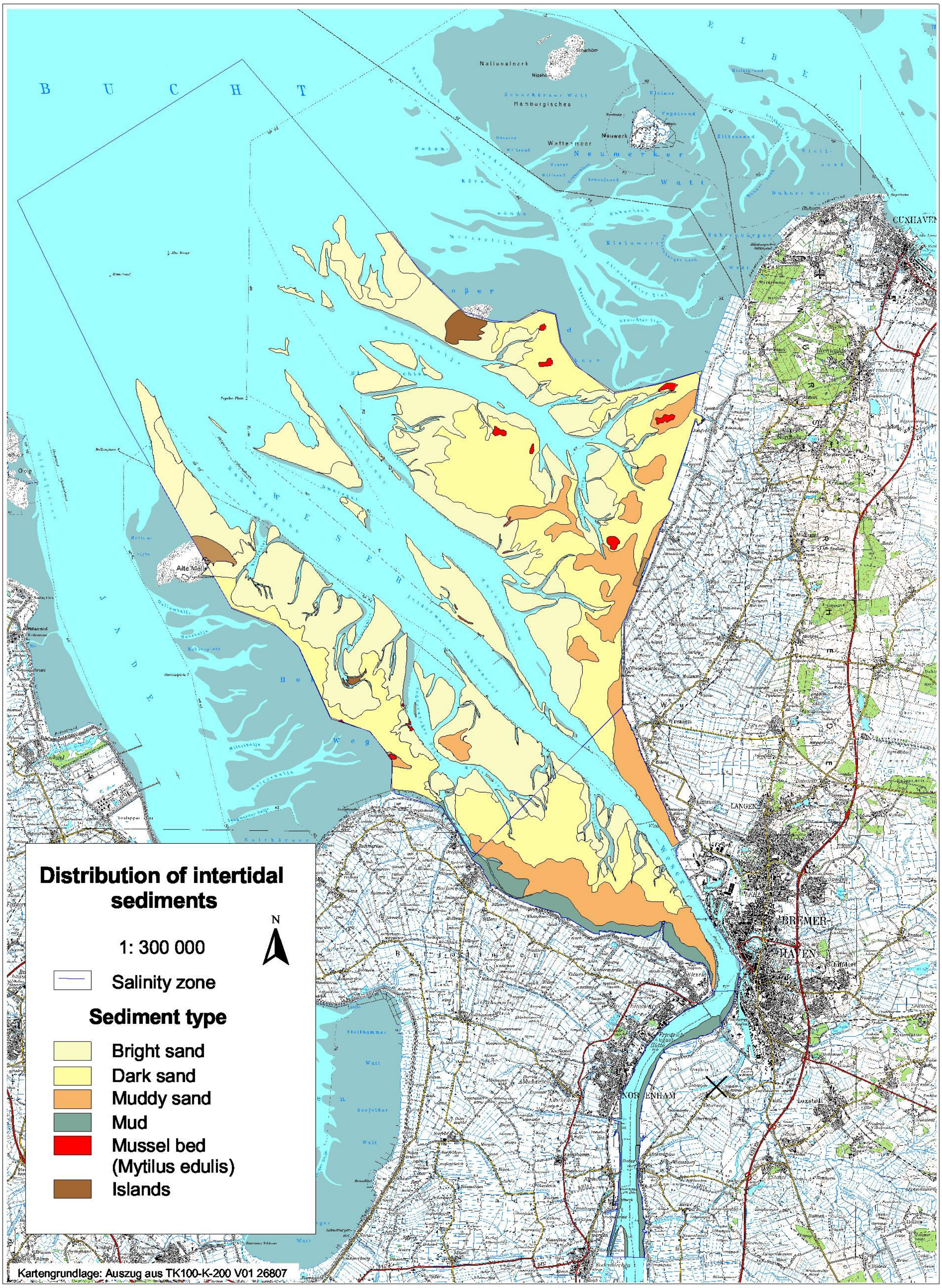


Fig. 6 Distribution of intertidal sediments in the Weser estuary (RAGUTZKI & MEYER 1999).

A more detailed investigation of intertidal flats at km 73 (KÜFOG, unpublished) showed a more differentiated distribution with high variation in the sediment composition during the seasons and also between years.

The subtidal sediments in the central riverbed are mostly fine sands, which are continuously moving with the currents. In the brackish water zone a strong sedimentation of fine material creates soft deposits at the upper slope of the channels. Stones and pebbles are quite rare in the riverbed and absent from the shores or the intertidal flats. At greater riverbed depths and at steep edges the currents prevent the stony surfaces being covered by sediments (GOSSELCK et al. 1993).

2.4 Historical changes

The historical changes in the postglacial hydro-system of the river Weser have endogenic and anthropogenic causes (RAMACHER 1974, WETZEL 1987, BUSCH et al. 1989, GRABEMANN et al. 1993). The first humans to settle along the river triggered clay sedimentation on the sand and gravel floodplains by deforesting and cultivating the valley slopes. The result was a drift in the vegetation and animal life, to species that preferred more fertile soil conditions (FITTKAU & REISS 1983, BEHRE 1985). From around the 5th century local fishermen and millers harnessed the potential energy of the river by building dams (LOEBE 1968). Dykes separated stepwise the floodplain from the river since the 12th century. The early usage of the main river and the tributaries as shipways had effects (e.g. tow path maintenance) on the riparian vegetation, but did not influence the hydro-system. Organized regulation started around 1800 and resulted in a new structure for the Weser (WETZEL 1987).

Due to erosion upstream and resulting sedimentation the depths in the Lower Weser decreased markedly during the Middle Ages. To ensure the economic competitiveness of the harbours of Bremen, the first substantial deepening was done from 1887 to 1895 (FRANZIUS 1888). Additional to deepening by dredging, river bifurcation was diminished and the tidal currents were concentrated to the navigable channel by embankments and groynes. Shallows and side arms were filled in with dredged material and the river became narrower and deeper in just a few decades (WETZEL 1987).

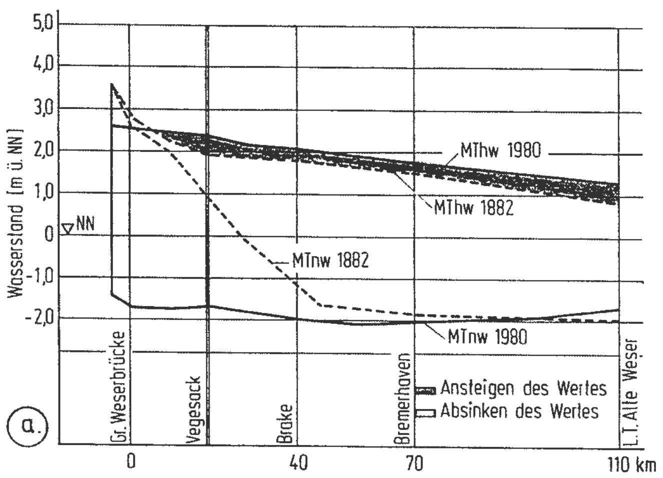


Fig. 7 Change in high and low water levels along the Weser estuary between 1882 and 1980 and change in tidal amplitude, MTnw– low water level, MThw– high water level (WETZEL 1987).

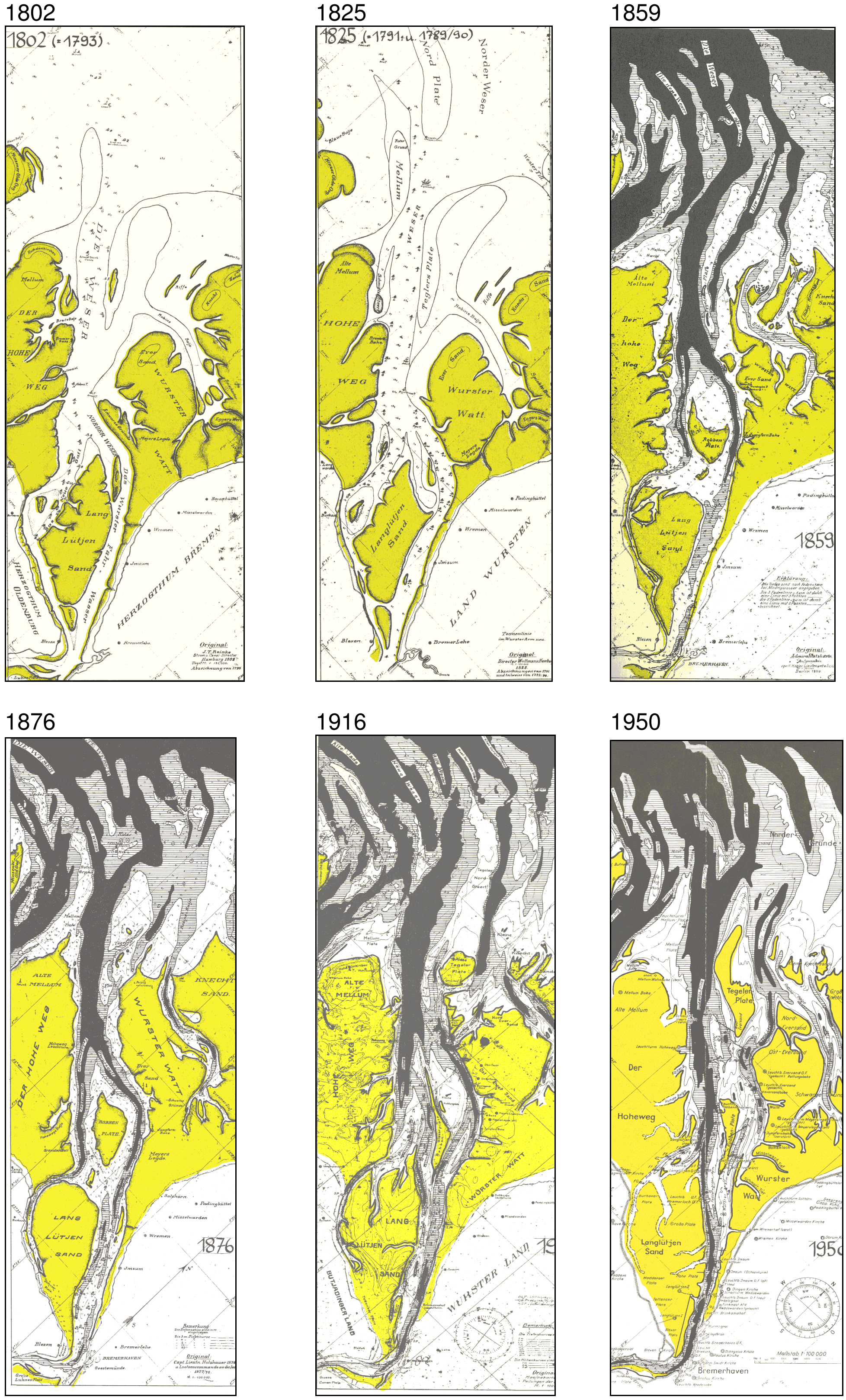


Fig. 8 Morphological changes of the Outer Weser estuary since 1802 (HOVERS 1973).

Further periods of channel constructions followed with the river being stepwise deepened to 7 m, 8 m, 8.7 m and finally to a depth of 10.5 m. This caused drastic changes to the morphological, hydrological and ecological conditions of the river (BUSCH et al. 1989).
The tidal range at Bremen increased from 0.3 m in 1880 to 4.0 m in 1990 by dropping low water levels and this altered littoral zones (Fig. 7). The river`s surface and the riparian area were reduced, reedbeds, mudflats and marshes were lost by the construction of dykes in the Outer Weser. The river`s profile was reduced to one channel; monotonous and deep with stronger currents.
Loss of backwaters, siltation in the intertidal areas and the rapid currents in the channels limited the development of submersed vegetation and phytoplankton production with negative consequences for the estuarine fauna (BUSCH et al 1989). The length of the former shoreline was reduced by approximately 120 km. Today only 40% of the remaining shoreline is free from artificial shoreline protection constructions (SCHUCHARDT et al. 1984).

The natural depth (up to 20 m) of the Outer Weser made deepening unnecessary until 1884. In Fig. 8 the more or less natural change of the morphology by continuously moving channels and sandbanks driven by tides and storms is shown by maps from the Outer Weser estuary from 1802 to 1950 (HOVERS 1973). The high fluctuation in water depths and channel positions made shipping difficult in former days. The deep water (black colour, -10 m depth) did not reach the inner part of the estuary until 1950. In 1884, when the shallows in the Bremerhaven area had to be dredged to keep a minimum depth of 7.3 m along the shipping lane, the first groynes were built in the Outer Weser to lead currents to the shipping lane (WETZEL 1987). In 1917 the shipping lane was moved into a deeper western channel system paying tribute to the strong natural changes of the system (Fig. 9).

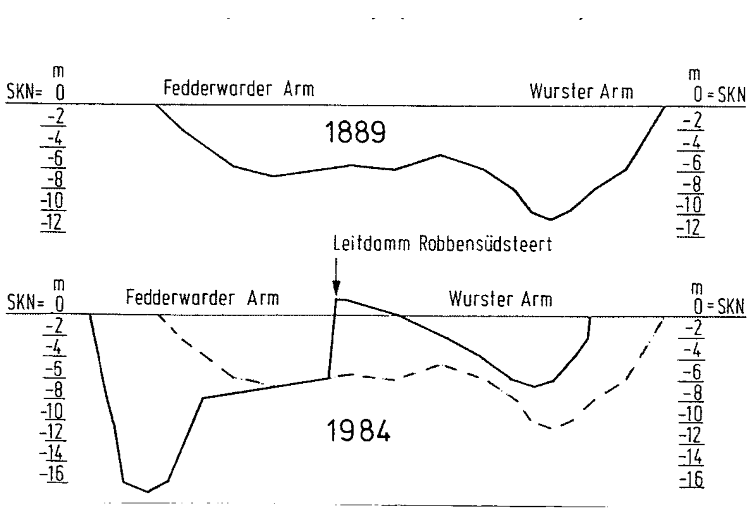


Fig. 9 Cross-section of the Outer Weser at km 81 in 1889 (before shifting the shipping lane to the western channel and before dredging works) and 1984 (after deepening and constructing a central groyne to lead currents to the shipping lane), depths in m SKN (sea chart zero).

The depth of the western channel (Fedderwarder Arm) was kept at –10 m since 1928 by dredging 40 million m³ sand and clay within several years (WETZEL 1987, Fig. 9). After that stepwise deepening followed. In Fig. 10 the change of the riverbed morphology over 100 years is indicated by lines along the shipping lane of the Outer Weser. The major dredging along the Outer Weser was done in the area of Bremerhaven (km 65-85), where the bottom currents periodically build up sandbars (Fig. 10).

In 1971 a depth of -12 m and in 1998 of -14.3 m (below sea chart zero) was created to allow larger container ships to use the harbour facilities in Bremerhaven. All deepening periods were accompanied by the installation of groynes and sidewalls to force the main currents into the shipping channel. Generally the Outer Weser was much less influenced by the alterations and deepening compared to the Lower Weser. Channel dynamics were reduced by the installations, but the hydrology of the Outer Weser was not completely changed (BUSCH et al. 1989).

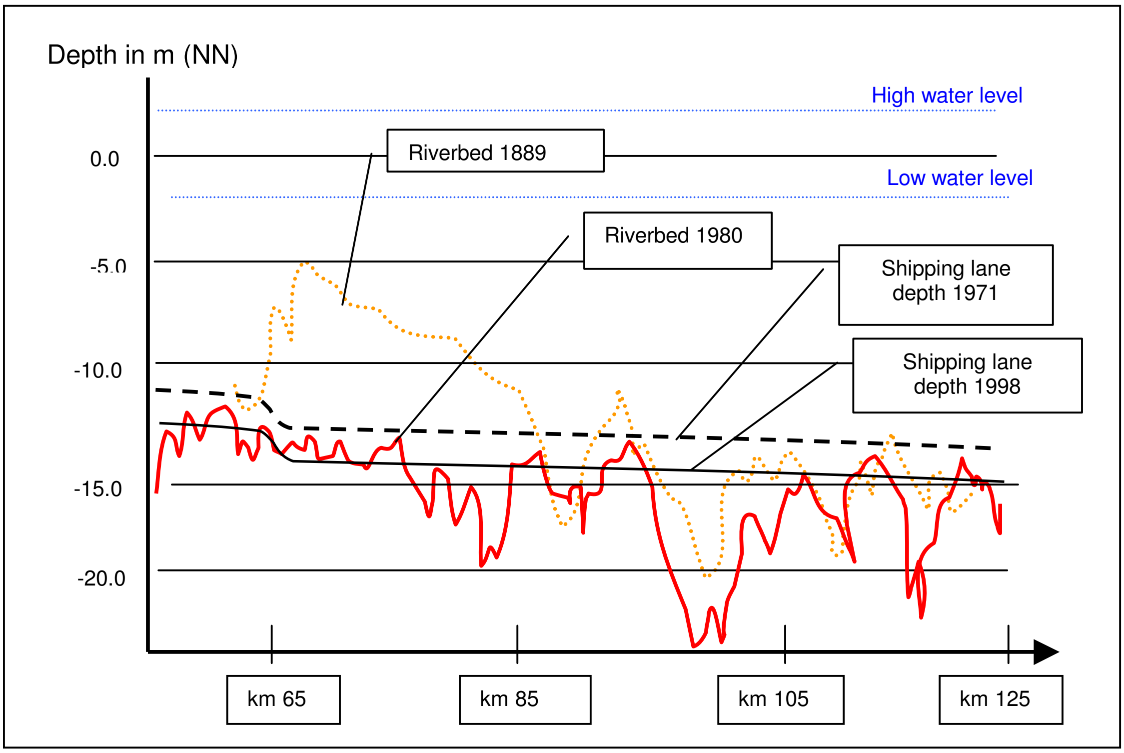


Fig. 10 Riverbed morphology (central depth) along the Weser estuary from km 60 to km 125 in 1889 and 1980 (redrawn after RAMACHER 1974).

3 INVENTORY AND CHARACTERISATION OF BENTHIC HABITATS IN THE WESER ESTUARY

In this chapter benthic data from baseline studies within the Weser estuary since 1980 are compiled and analysed. It is intended to transfer results of local analyses of distribution patterns (publication I and II) together with external data from other studies to a larger scale analysis of the estuary. In comparison to investigations before 1980 (e.g. DITTMER 1981) a more comprehensive database for an inventory is presented, which allows a better reflection of the actual benthic situation in the Weser estuary.

3.1 Methods

The methods used for the aggregation of data and analysis of large scale distribution will be described in the following section. Methods of data analysis and statistics have been similar applied to the data of publication I-III and detailed information on these methods can be found therein.

3.1.1 Aggregation of macrobenthic data

Benthic data from all available studies of the brackish water part of the Weser estuary since 1982 were compiled and processed to provide a comprehensive inventory of the actual benthic community and brackish habitats. The benthic fresh water community of the tidal Weser (km 0-45) was described by SÖFFKER (1982), HAESLOOP (1990), BÄTHE (1992), HAESLOOP & SCHUCHARDT (1995), SCHOLLE & SCHUCHARDT (1997) and MEYERDIERKS et al. (2003). Some of these studies provided data for the oligohaline zone which were added to this analysis in order to cover the biotopes of all brackish water zones (see Table 3).

The year 1982 was chosen for pragmatic reasons: seeking to represent all biotopes by actual benthic data. Most of the data were collected within the last 10 years (Table 3). All aggregated surveys with their numbers of sites, time of collection and sampling methods are listed in Table A-2 (Appendix). Most of the studies are unpublished baseline investigations of biological monitoring or impact assessments. Before the aggregation the differences in the methods of collecting, treatment and presentation of the benthic data were analysed. Minimum of accepted mesh size was 0.5 mm, most studies applied methods with 1 mm sheets. Taxonomic groups, especially Diptera, Oligochaeta and Ostracoda are identified at very different levels. For reasons of comparability certain taxa e.g. the larvae and adults of flying insects (Heteroptera, Coleoptera, Odonata), which sometimes occur even in mesohaline waters, were integrated into the data set on a higher taxon level only.

All data were pooled to a minimum common level of detail to allow a comparison of the different data sets. A semi-quantitative classification system was implemented as given in Table A-1 (Appendix).

The data represented the different salinity zones, which have been described in chapter 2. Furthermore, the data were separated into different biotopes, found to be important to different

3 INVENTORY AND CHARACTERISATION OF BENTHIC HABITATS IN THE WESER ESTUARY

In this chapter benthic data from baseline studies within the Weser estuary since 1980 are compiled and analysed. It is intended to transfer results of local analyses of distribution patterns (publication I and II) together with external data from other studies to a larger scale analysis of the estuary. In comparison to investigations before 1980 (e.g. DITTMER 1981) a more comprehensive database for an inventory is presented, which allows a better reflection of the actual benthic situation in the Weser estuary.

3.1 Methods

The methods used for the aggregation of data and analysis of large scale distribution will be described in the following section. Methods of data analysis and statistics have been similar applied to the data of publication I-III and detailed information on these methods can be found therein.

3.1.1 Aggregation of macrobenthic data

Benthic data from all available studies of the brackish water part of the Weser estuary since 1982 were compiled and processed to provide a comprehensive inventory of the actual benthic community and brackish habitats. The benthic fresh water community of the tidal Weser (km 0-45) was described by SÖFFKER (1982), HAESLOOP (1990), BÄTHE (1992), HAESLOOP & SCHUCHARDT (1995), SCHOLLE & SCHUCHARDT (1997) and MEYERDIERKS et al. (2003). Some of these studies provided data for the oligohaline zone which were added to this analysis in order to cover the biotopes of all brackish water zones (see Table 3).

The year 1982 was chosen for pragmatic reasons: seeking to represent all biotopes by actual benthic data. Most of the data were collected within the last 10 years (Table 3). All aggregated surveys with their numbers of sites, time of collection and sampling methods are listed in Table A-2 (Appendix). Most of the studies are unpublished baseline investigations of biological monitoring or impact assessments. Before the aggregation the differences in the methods of collecting, treatment and presentation of the benthic data were analysed. Minimum of accepted mesh size was 0.5 mm, most studies applied methods with 1 mm sheets. Taxonomic groups, especially Diptera, Oligochaeta and Ostracoda are identified at very different levels. For reasons of comparability certain taxa e.g. the larvae and adults of flying insects (Heteroptera, Coleoptera, Odonata), which sometimes occur even in mesohaline waters, were integrated into the data set on a higher taxon level only.

All data were pooled to a minimum common level of detail to allow a comparison of the different data sets. A semi-quantitative classification system was implemented as given in Table A-1 (Appendix).

The data represented the different salinity zones, which have been described in chapter 2. Furthermore, the data were separated into different biotopes, found to be important to different species in the estuary. Because of different sampling techniques, including non-quantitative sampling, the analysis was focused on presence/absence comparisons or restricted to quantitative data subsets. The following biotopes were represented by data from the different studies:

- Subtidal areas (including different sediments and substrates)
- Eulittoral intertidal flats (including different sediments)
- Supralitoral shores (including reedbeds, beaches and shoreline protection constructions in the reach of high or spring tide)
- Groynes (subtidal and intertidal hard bottom structures)
- Ditches and lagoons (small water bodies corresponding with the estuarine tides)

All benthic taxa are listed in Table A-1 (Appendix), presenting the maximum abundance within each habitat in abundance classes.

The locations of all included sampling sites are shown in Fig. 11. The number of symbols basically represents the number of sites, but different numbers of replicates and sampling repetitions, result in a differing sampling effort. Sites and datasets within each biotope are compiled in Table A-2 (Appendix). In Table 3 the origin of presented data is listed for each biotope and salinity zone.

Table 3 Origin of pooled data from all biotopes (salinity zone of sampling sites is indicated by: O-oligohaline, M-mesohaline, P-polyhaline, sampling effort and data sources are given in Table A-2, A-4, Appendix).

Study (Data source)	*Sublitoral*	*Eulittoral*	*Supralitoral*	*Groynes*	*Ditches*
BACKHAUSEN 2002	M	M	M		
BFG 1997, unpubl.				O, M, P	
FRÄMBS et al. 2002		P			P
HAESLOOP 1990	O	O			
HEIBER 1988	P	P			
KÜFOG 1994-2002, unpubl.	M, P	O, M	M, P	M	O, M
MEYERDIERKS et al. 2003		O			
NLÖ 2001		O, M	O, M		
SÖFFKER 1982		O	O		
DB Weser 1991-2002, unpubl.	O, M, P				

The most comprehensive sublitoral data set is named “DB Weser” (Table 3). It contents grab sample data from 1991 to 2002 collected by several institutes (listed in Table A-4, Appendix) on behalf of the Harbour Authority of Bremen (bremenports GmbH), the Federal Agency of Water and Shipping Administration (WSA Bremerhaven) and the Federal Institute of Hydrology (BFG, Koblenz).

3.1.2 Data collection and processing

The methods of data collection within the analysed studies (Table A-2) followed scientific standards. Standard methods were applied using a Van Veen sediment grab (0.1 m^2), sediment corers with 15 cm diameter and 20 cm depth, a frame-dredge with 1 m width (0.5 cm mesh size) and for small water bodies hand nets with 0.5 mm mesh size. Data from own investigations are presented in publications I-III. The methods of the collection and processing of the samples in the field and in the laboratory is described in detail in publications I-III.

3.1.3 Data analysis

The benthic data presented in Table A-1 (all data) were used to characterise the benthic fauna of the different salinity zones and biotopes. The taxonomic community composition of each biotope was analysed with regard to its preference of salinity, percentage of genuine brackish water species and threatened species. The similarity between the biotopes of the brackish water zones was analysed on a qualitative basis. The most extensive quantitative data set includes grab samples and dredge samples from subtidal areas of the main channel (DB Weser, Table A-2). As a first step the quantitative and comprehensive data set was used to analyse the distribution along the estuarine gradient. For a quantitative characterisation of the zones the presence, dominance, average and maximum abundance and average biomass (fresh weight in mg/m^2) of the most dominant species is presented (grab samples, DB Weser). Quantitative characterisation was focused on subtidal endobenthic data. Comparisons were furthermore based on ecological categories, such as salinity tolerance, feeding type, mobility or sediment preferences using information from the literature (e.g. LINCOLN 1979, BARNES 1994, HAYWARD & RYLAND 1990, HARTMANN-SCHRÖDER 1996). The following categories of salinity tolerance and types of brackish water organisms were basically drawn from REMANE & SCHLIEPER (1971):

1. Fresh water species confined to fresh water with low (or uncertain) tolerance to brackish water.
2. Euryhaline fresh water species penetrating from fresh water more or less extensively into brackish waters.
3. Brackish water species are genuine brackish water organisms confined to brackish water.
4. Euryhaline marine species that reach the brackish water from the sea.
5. Marine species confined to marine salinities with low (or uncertain) tolerance to brackish water.

Holeuryhaline species inhabit the whole salinity range from fresh to sea water, but are integrated here in the class of euryhaline marine species. The differentiation especially between the categories 1 an 2 or 4 and 5 depends on ecological knowledge, which is not available on the same level for all species. The different degrees (1-3) of euryhaline species in the classification of REMANE & SCHLIEPER (1971) are not separated here. The determination of tolerance limits and salinity range is generally difficult because of high regional variation and external factors (REMANE 1940, REMANE & SCHLIEPER 1971).

3.1.4 Statistics

The PRIMER 5.2 software package (Plymouth routines in multivariate ecological research, Plymouth Marine Laboratories) was used for statistical analyses of faunal data (CLARKE & WARWICK 1994, CLARKE & GORLEY 2001). Non-metric multi-dimensional scaling (MDS ordination, KRUSKAL & WISH 1978) and cluster analysis by dendrograms were used to identify patterns in the species distribution. The inter-sample similarity was calculated by the Bray-Curtis coefficient (BOESCH 1977). Fourth root transformation on quantitative data was applied to reduce the influence of dominant species. A presence/absence transformation of data was used to minimize the influence from differences in sampling methods.

The purpose of an MDS ordination is to represent the samples as points in two-dimensional space such that the relative distance between points is in the same rank order as the relative dissimilarities of the samples. Therefore, the ordination has no axis scales. Points that are close together represent samples that are very similar in species composition, points that are far apart correspond to very different communities (CLARKE & GORLEY 2001). The stress coefficient indicates how faithfully the high dimensional relationships among the samples are represented in the two-dimensional ordination plot. A good representation shows a stress less than 0.2 (CLARKE & WARWICK 1994).

The ANOSIM tool was used to analyse similarities and significance of differences in groups of samples. It allows a statistical test (one-way layout) of the null hypothesis that there are no assemblage differences between groups of samples specified *a priori* (CLARKE & GORLEY 2001). The routine uses a permutation/ randomisation test with a maximum of 999 permutations. If there are no differences between groups then between-group and within-group similarities will be equal and the resulting coefficient (Global-R) is close to zero. A value of R=0.5 or larger represents clear separation of groups, while R=1 represents a complete separation between groups. The p-statistic gives the error probability at which the null-hypothesis is rejected. For more detailed description of methods see publications.

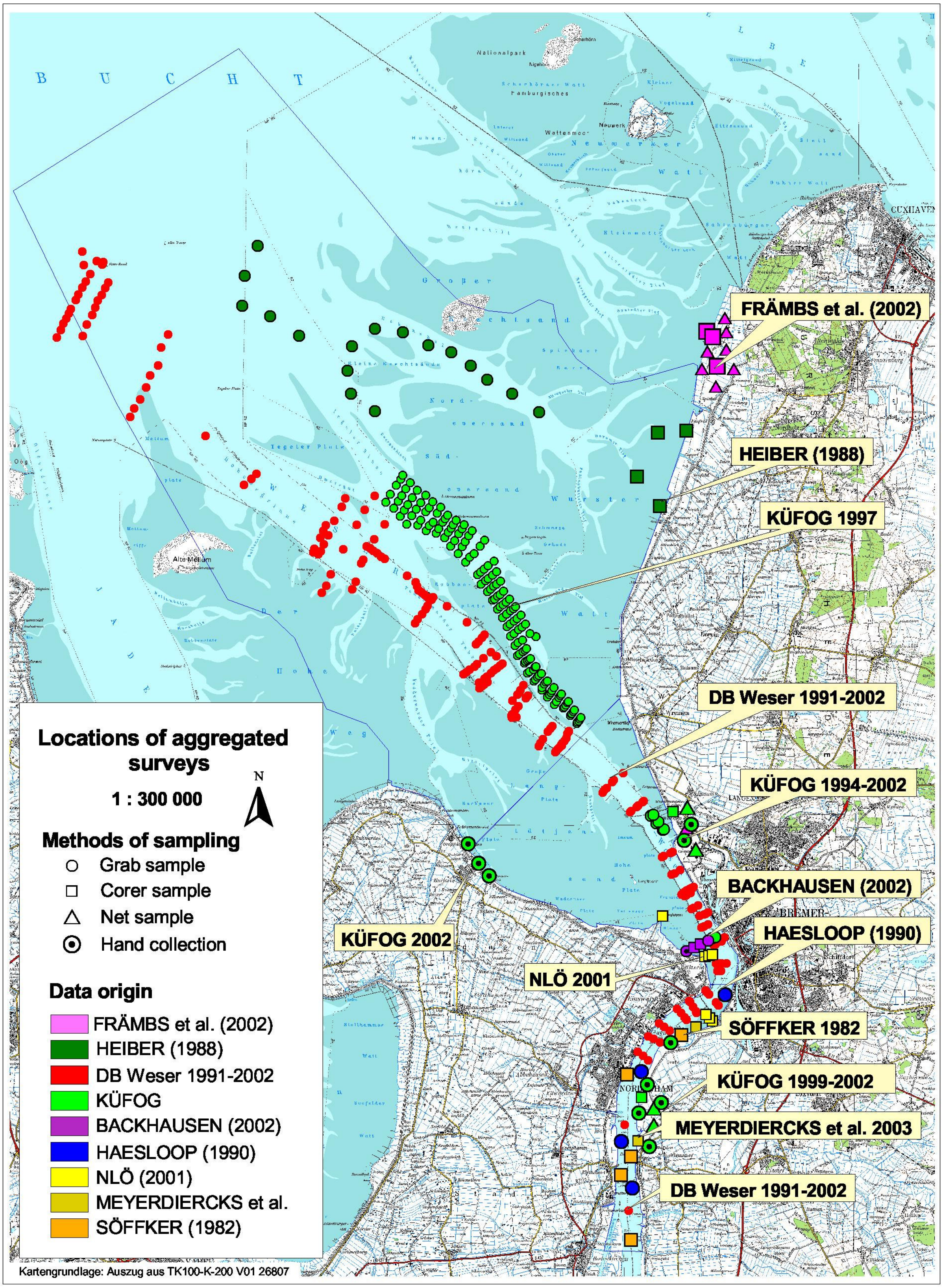


Fig. 11 Locations of sampling sites of the aggregated data (colours indicate origin of site groups as given by the text label, for more detailed information see Table 2 and Table A-2, Appendix).

3.2 Benthic community response to salinity

3.2.1 Along-estuary distribution

To analyse the compliance of benthic assemblages with the salinity zones of the Venice System cluster analysis and MDS plots of subtidal soft bottom macrofauna (grab samples) and epibenthic fauna (dredge samples) are applied.

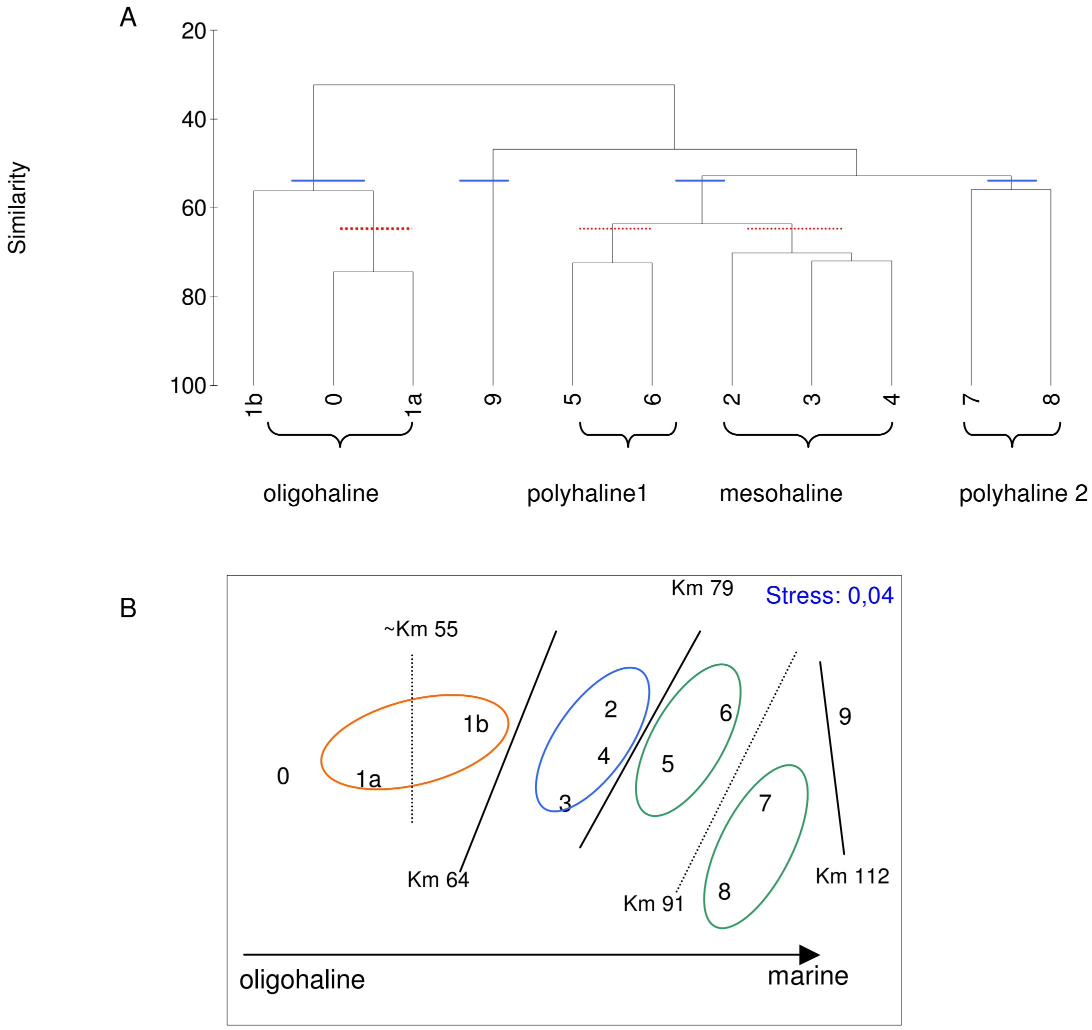


Fig. 12 Faunal similarity within an along-estuary gradient indicated by similarities of endobenthic macrofauna (grab sample data, presence/absence transformation) of ~5 km sections (0-9) from km 45 to 115. A- dendrogram with lines indicates groups at different similarity levels, B- MDS plot with ellipsoids indicates zones by salinity, lines indicate faunal breaks at certain km, broken lines indicate faunal breaks within salinity zones.

The actual benthic data (DB Weser) are used to analyse faunal discontinuities along the estuary and to determine positions of borderlines between salinity zones (see DITTMER 1981).

In Fig. 12 the dendrogram and MDS plot of subtidal grab samples is given from 11 data subsets drawn from sections along the river of about 5-8 km length each (km 45-115, DB Weser, Table

A-2). The salinity zones referred to the Venice System are marked by ellipsoids. Additional bars indicate borderlines between clusters from the similarity analysis.

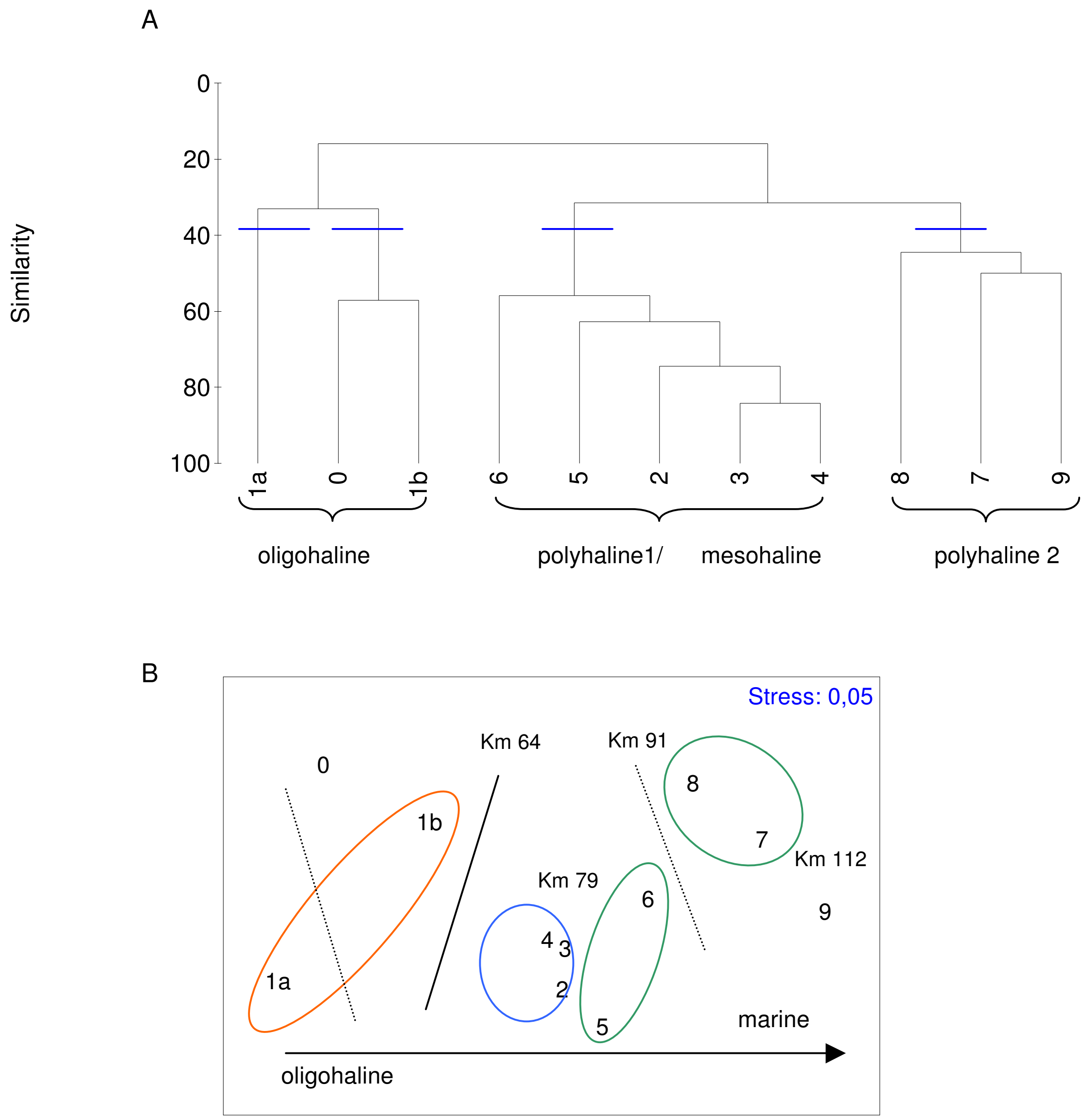


Fig. 13 Faunal similarity within an along estuary gradient indicated by similarities of epibenthic macrofauna (dredge trawl data, presence/absence transformation) of ~5 km sections (0-9) from km 45 to 115. A- dendrogram with lines indicates groups at a similarity level, B- MDS plot with ellipsoids indicates zones by salinity, lines indicate faunal breaks at certain km; broken lines indicate faunal breaks within salinity zones.

The along-estuary gradient is well reflected in the benthic soft bottom fauna (Fig. 12) and the epibenthic fauna (Fig. 13). Faunal discontinuities are determined in both plots and are clearly a response to the salinity zones. In general the endobenthic data (Fig. 12) give a more detailed picture of similarities, while the epibenthic data are basically separated into the 3 brackish salinity zones. The borderline between the mesohaline and polyhaline 1 zone is less clear within epibenthic data than in endobenthic data.

The section of tidal freshwater (0) is added to show similarity to oligohaline data (1a, b). However, ordinations of epibenthic species (Fig. 13) and endobenthic data (Fig. 12) give no clear indication of subdivisions. Section 9 (data beyond km 112) is similar to the polyhaline section in epibenthic data and clearly separated in endobenthic data. Both MDS ordinations show additionally to three major salinity zones a subdivision within the polyhaline zone at km 91 and within the oligohaline zone at about km 55.

The ANOSIM analysis confirms the separation into the salinity zones (Table 5). The subdivision of the polyhaline area into poly 1 and poly 2 shows no significant separation, although clusters are clearly separated in all plots.

Table 5 Analysis of similarities (ANOSIM) of salinity zones within endobenthic data (km 45-115 DB Weser grab samples, Table A-2, significant separation of groups indicated by * $p<0.1$, ** $p<0.05$).

Groups	*R-statistic*	*Significance level (p)*
all	0.72	0.10 *
Oligo/ meso	0.89	0.02 **
Oligo/ poly	0.43	0.05 **
Meso/ poly	0.43	0.05 **
Meso/ poly1	0.75	0.20
Poly1/ poly2	0.25	0.60

3.2.2 Across-estuary distribution

Due to less salinity in the shallow waters along the shores the response of other biotopes and assemblages to the salinity gradient is less obvious. In Fig. 14 all biotopes (data from Table A-1, Appendix) are presented by their similarity in species composition (MDS plot, presence-absence transformation). Most biotopes are clustered according to the salinity zones which are indicated by ellipsoids (Fig. 14). The data show higher similarities within the supratidal biotopes (and ditches) from different salinity zones than for subtidal or intertidal communities. Especially the polyhaline supratidal habitats show a high similarity to the biotopes of the mesohaline zone (Fig. 14). In the supratidal areas the salinity-induced faunal gradient therefore diminishes most probably due to stronger fresh water influence from land drainage into the water bodies at the shore. Therefore the supratidal fauna can not be separated into mesohaline and polyhaline sub-communities as given schematically in Fig. 4.

The intertidal flats show a similar salinity zonation according to MICHAELIS (1981). The positions differ from subtidal zones as given in Fig. 15. The combination of both gradients, the along-estuary gradient and the across-estuary gradient lead to distinct sub-zones within the benthic distribution. They basically reflect the major distribution factors of benthic invertebrates such as bottom morphology, salinity and sediment composition.

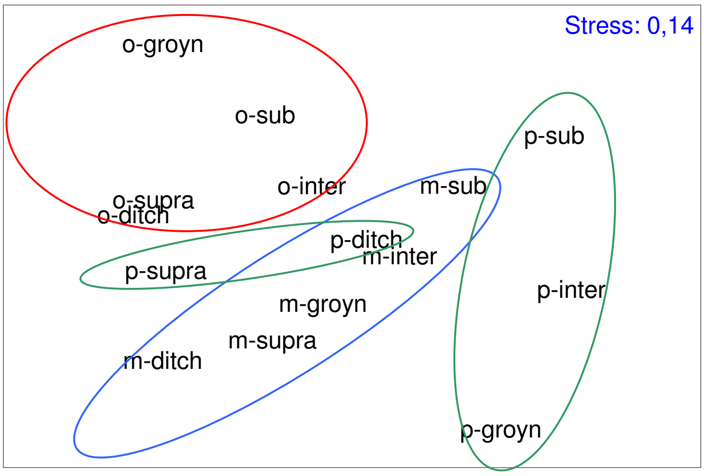


Fig. 14 Faunal similarity of all biotopes from the different salinity zones (MDS ordination, presence-absence transformation, Bray Curtis similarity, all data, Table A-1, Appendix, o-oligohaline, m-mesohaline, p-polyhaline, sub-subtidal, inter- intertidal, supra-supratidal).

As a result of the analysis, with a strong response to the salinity gradient in the subtidal area and additional influence of the tidal height, there are 10 major areas within the brackish part of the estuary which can be distinguished by faunal data (Fig. 15):

1. oligohaline subtidal (possibly subdivided)
2. oligohaline intertidal
3. oligohaline supratidal
4. mesohaline subtidal
5. mesohaline intertidal
6. mesohaline/ polyhaline supratidal
7. polyhaline 1 subtidal
8. polyhaline 2 subtidal
9. polyhaline 1 intertidal
10. polyhaline 2 intertidal

All these different zones have to be taken into account within an evaluation of estuarine biotopes based on benthic communities. Besides the salinity aspect the sediment borderlines are considered within the separation of polyhaline and mesohaline sub-zones (Fig. 15). This leads to a v-shaped borderline along the muddy sand area instead of a straight borderline across the estuary (Fig. 15). This seems to be a small-scale adjustment which reflects the natural borderlines within this environment more adequately. But it has to be realized that variation of sediment composition fluctuates strongly within an annual and inter-annual cycle, so that sharp lines between different zones are rather meant to explain principles than to occur in nature.

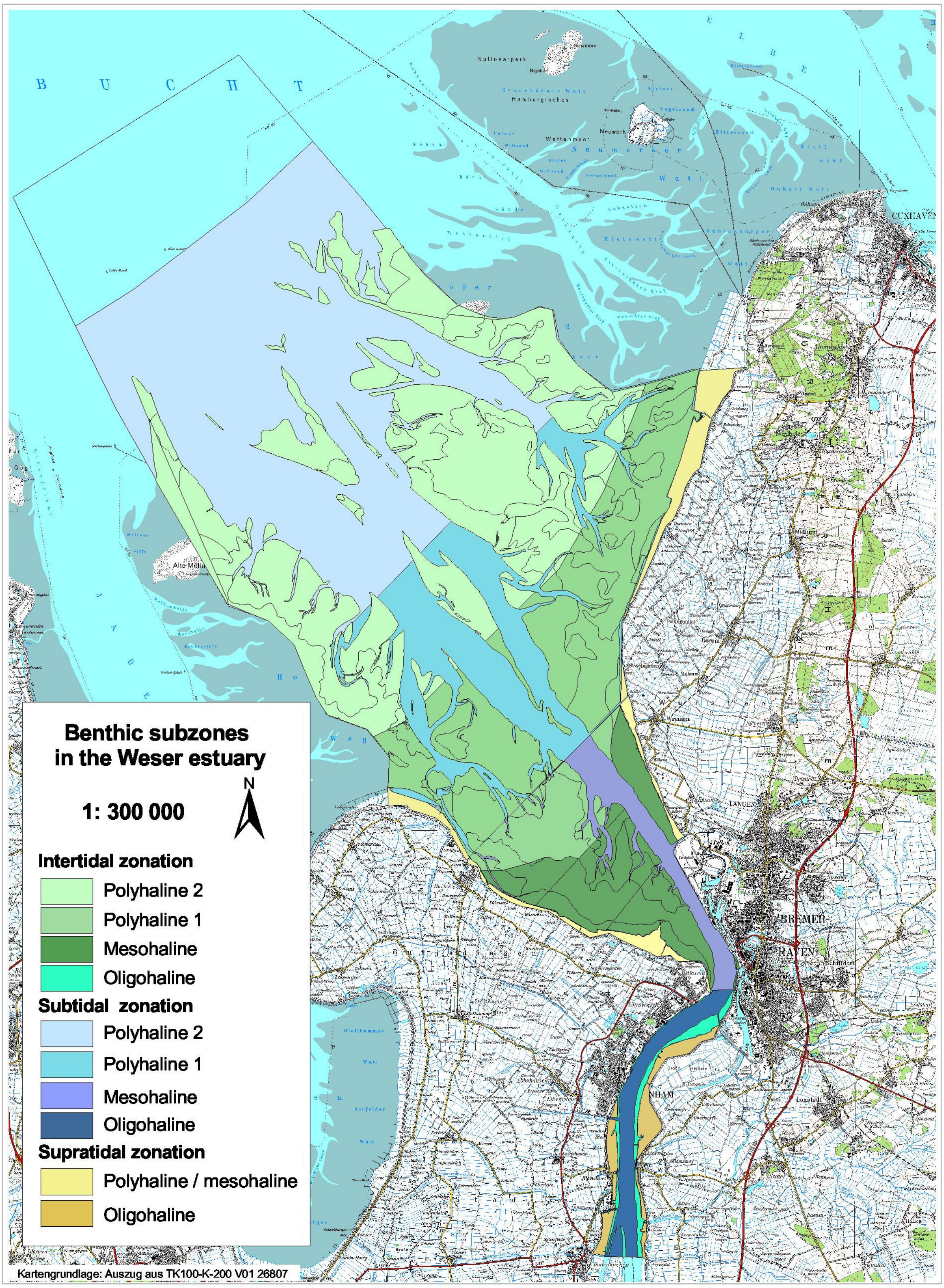


Fig. 15 Benthic subzones of the Weser estuary.

3.3 Abiotic characterisation of estuarine biotopes

Estuarine areas can be basically differentiated by hydrological or morphological features, which are partly reflected by the substrates in the different salinity zones. Most benthic species are related to certain substrates and structural features (DÖRJES 1978, GRAY 1981). In order to compare different biotopes by size the areas of the intertidal sediments (Fig. 6) within the salinity zones, as shown in Fig. 15, are analysed. In Table 4 the sizes of the most evident biotopes by areas and lengths from a GIS supported calculation are presented. Locations of small sized biotopes, such as mussel beds are presented in Fig. 16.

As shown in Table 4 the main part of the brackish water area is covered by sublittoral channels (58.4%) and intertidal flats (38.6%). A minor part (2.9%) is represented by supratidal marshes and reedbeds. The major sediment type by area is sand, which covers most of the intertidal flats (75%) and almost all polyhaline sediments (dark and bright sands, Table 4).

Table 4 Size of major biotopes in the different salinity zones of the Weser estuary. (GIS-based calculation of areas as presented in Fig. 6, with sediment classification from RAGUTZKI & MEYER (1999), quantification of sea grass meadows from ADOLPH et al. 2003, mussel beds (*Mytilus edulis*, intertidal), MILLAT & HERLYN (1999), Reedbed areas estimated from HEINRICH & MÜHLNER (1981), *Lanice* beds and *Sabellaria* reefs (BUHR 1979).

	Weser estuary salinity zones							
Biotopes/ structures	**all zones, brackish**	**%**	**oligo**	**%**	**meso**	**%**	**poly 1 / 2**	**%**
Total length (km along shipping lane)	67		20		14		33	
Total area (ha)	**91,850**	**100**	4,800	5.2	10,090	11.0	76,960	83.8
Supratidal marshes	2,870	2.9	790	0.9	590	0.6	1,490	1.6
Sublittoral channels	53,592	58.4	3,480	3.8	3,017	3.3	47,095	51.3
Intertidal Flats	35,388	38.6	530	0.5	6,483	7.1	28,375	30.1
Intertidal Flats	**35,388**	**100**						
Mudflats	1,429	4.0	530	1.5	855	2.4	44	0.1
Muddy sands	4,690	13.3	--	--	2,568	7.3	2,120	6.0
Bright sands	14,956	42.3	--	--	891	2.5	14,065	39.7
Dark sands	11,392	32.2	--	--	2,152	6.1	9240	2.6
Others (e.g. islands)	2,361	6.6	--	--	7	0.1	2354	6.7
Sea grass meadows	125	0.4	--	--	--	--	125	0.3
Mytilus mussel beds	148	0.4	--	--	--	--	148	0.4
Sabellaria reefs	248	--	--	--	--	--	248	--
Lanice beds	247	--	--	--	--	--	247	--
Reedbeds (~area in ha)	520	--	410	--	110	--	--	--
Shoreline (~km length)	91	--	35	--	33	--	23	--
Groynes (~km length)	40	--	3,5	--	2,5	--	34	--

The quantification in Table 4 is a basic calculation, which does not include all biotopes in detail, due to a lack of exact area data and strong variation during time. For example the areas of intertidal mussel beds are strongly variable between years as documented in MILLAT & HERLYN (1999). Other important structures such as subtidal stone substrates and subtidal mussel beds, which have been identified in several surveys mostly by accident, are not investigated by area for a precise cartography yet and therefore are indicated by symbols (Fig. 16). The supratidal water bodies such as ponds, ditches and tidal pools can not be quantified from the data at hand.

3.3.1 The oligohaline salinity zone

In the Weser estuary the oligohaline salinity zone includes an area of 4,010 ha and a length of 20 km from km 45 (Brake) to km 65 (Bremerhaven). Soft mudflats cover all intertidal sediments in the oligohaline areas from Bremerhaven to Sandstedt (530 ha) due to the high suspension load in the water column and resulting sedimentation rate. Few small sandy beaches in the area of Dedesdorf (km 55), Nordenham (km 58) and Strohhauser Plate (km 49) show a strong coverage of mud at the low water level. Most subtidal areas belong to the shipping lane with soft muddy sediments mixed with sand and pebbles. Natural hard substrates at the subtidal sediment surface seem to be apparent in small patches at most sites referring to the benthic data. Artificial hard substrates from harbour facilities and watershed constructions cover most of the shoreline (SCHUCHARDT et al. 1984). Reedbeds dominate the remaining natural shorelines and estuarine marshes within tidal reach. Due to the funnel-shape of the mouth of the Weser the oligohaline areas are small compared to the large polyhaline areas. The dykes separate most of the former floodplain from the river. Pools, tidal channels and ditches in the tidal areas are characterised by the high turbidity of the water and the high sedimentation rate of silt.

3.3.2 The mesohaline salinity zone

The mesohaline zone with a salinity range from 5.0 to 18.0 PSU covers an area of 9,500 ha from km 65 to km 80 in the central Weser estuary (Table 4). Compared to the oligohaline zone an opposite ratio between subtidal areas (3017 ha) and intertidal flats (6483 ha) is obvious. The sediment is characterised by sandy subtidal sediments with different amounts of silt, stone substrates and wide intertidal flats dominated by muddy fine sands. Mudflats cover the inner part and areas along the shore due to the sheltered location with less currents and wave energy. The typical sediment gradient with finer sediments towards the shore is obviously influenced by the large number of groynes reaching from the shore to the deep central areas of the shipping lane (publication I). Subtidal stone layers have been found at eastern steep slopes of the shipping lane and within deep wash outs in the central riverbed. Turbidity and sedimentation is reduced towards the lower reaches and salinity variation is higher than in the oligohaline zone. Reedbeds diminish in this section and turn into salt marshes with increasing salinity. Small patches of green algae (*Vaucheria* spp.) along the shoreline provide a special habitat for certain gastropods.

3.3.3 The polyhaline salinity zone

Wide intertidal flats dominate the polyhaline zone of the Weser estuary. The salinity ranges from 18.0 to 30.0 PSU at mean fresh water outflow referring to the Venice System (1959). Following DITTMER (1981) the polyhaline zone reaches from km 80 to 112 and includes an area of 76,960 ha. As presented in Fig. 4 the boundaries east and west of the central channel are defined by the watersheds to the neighbouring Jade and Elbe estuaries. The subtidal sediments range from peat, clay and stones in strong currents of the main channels to fine and muddy sands in sheltered areas. The intertidal flats cover 28,375 ha of sandy sediments with different grain size compositions due to the exposure to currents and wave energy. Mudflats are restricted to small areas along the shore. The biogenic hard substrates within the polyhaline zone are characterised within the chapter of small sized biotopes. The supratidal areas consist of estuarine salt marshes and most are used intensively as pastures. Some areas at the shores are covered with solid constructions of stones and concrete to protect the land from erosion.

3.3.4 Small scale biotopes

Additional to the large area biotopes that are based on a certain sediment type in the respective salinity zone there are small sized biotopes within the estuary with a variable or undetermined area. In Fig. 16 locations of all small sized biotopes from the compiled data and additional notices from the cited literature are shown. Sites of special substrates (e.g. stones) and sites with a certain density of species that provide biogenic hard structures (see legend) are represented by symbols.

Especially the polyhaline area provides certain biogenic substrates, such as intertidal mussel beds of *Mytilus edulis* (in 1999 about 148 ha) and shell deposits in subtidal and intertidal areas. Intertidal mussel beds are subject to regular monitoring (MILLAT & HERLYN 1999). The sea grass beds (*Zostera noltii*) are restricted to small patches in the upper polyhaline intertidal with an actual area size of about 125 ha as drawn from ADOLPH et al. (2003). Specific subtidal structures such as *Sabellaria* reefs and *Lanice* beds as mentioned in BUHR (1979) were not recorded within the actual data and are therefore added from the literature.

Most characteristic estuarine biotopes in the Weser estuary such as brackish reedbeds are situated in the mesohaline and oligohaline zones. Together with special habitats for benthic macrofauna, such as mats of certain green algae (*Vaucheria* spp.), they will be characterised by their benthic fauna from the respective literature and personal investigations (publication I). Despite expectations subtidal mussel beds of *Mytilus edulis* were found within the inner estuary in the mesohaline zone (KÜFOG, unpubl.) and thus the structural importance of these assemblages for associated estuarine benthic species is documented (publication I).

The groynes that have been built to stabilise the position and depth of the shipping lane and to protect the shores against erosion provide artificial hard substrates for benthic species. In

Table 4 a rough estimation of the total length is given, showing the main part (34 km) within the polyhaline zone. With an average width of 5 m a total area of 20 ha of artificial hard substrates from groynes can be estimated for the Weser estuary. A precise calculation of the area is not possible because of an unpredictable coverage of groynes by sediment. A coverage by algae (*Fucus vesiculosus*) gives a special structure to most intertidal groynes (publication I). The knowledge of supratidal small water bodies such as lagoons, ditches and semi-aquatic habitats at the shoreline is sparse and relevance for benthic communities is drawn from examples. A more detailed picture of the distribution of sediments, substrates and related macrofauna is given in publication I and II.

The presentation of these biotopes (Fig. 16) gives indication of certain structures but does not reflect a complete picture of the distribution of small scale biotopes within the estuary on a whole. Especially side channels and polyhaline intertidal flats suffer from lack of sufficient data to provide a comprehensive picture.

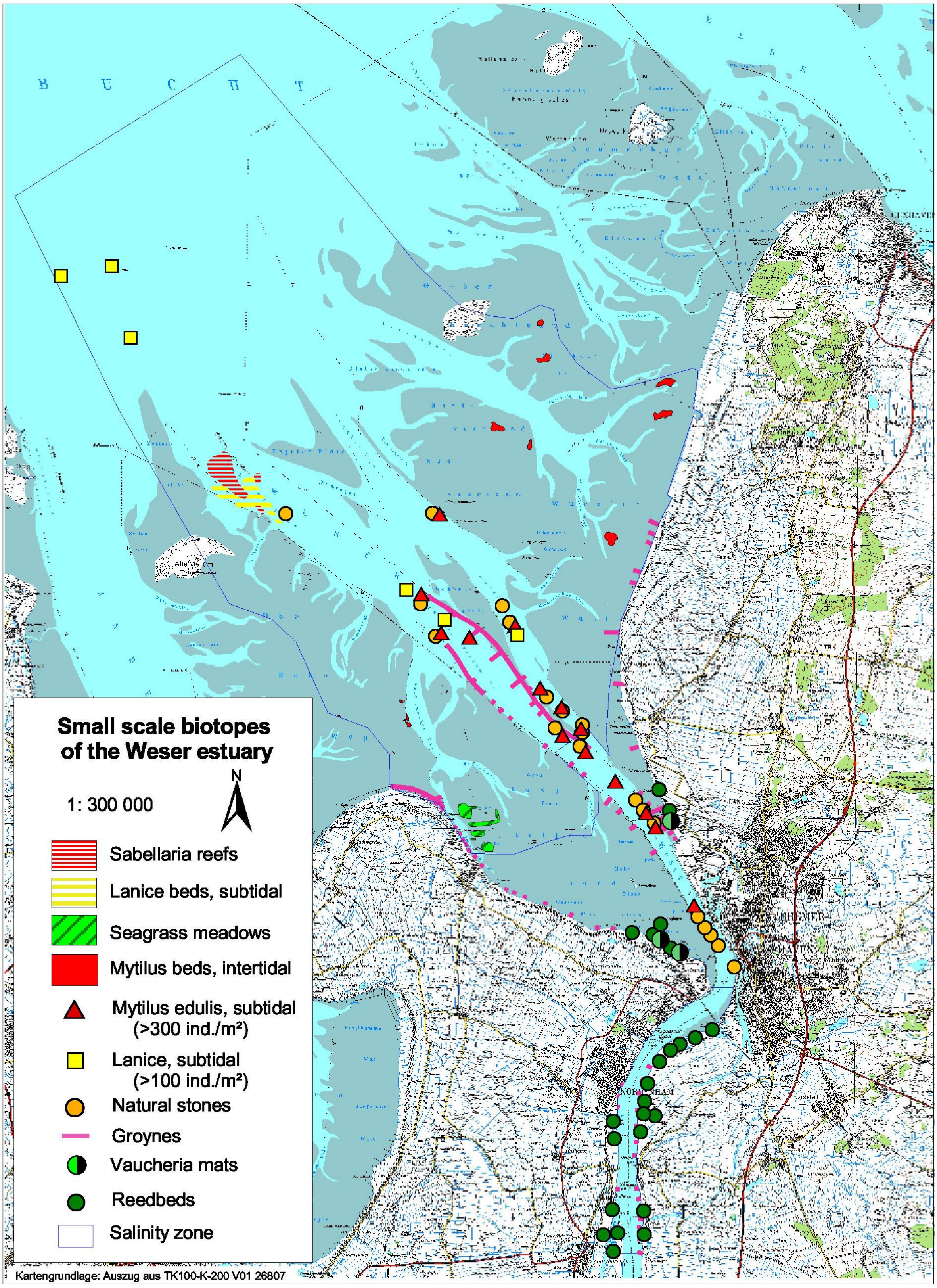


Fig. 16 Small scale biotopes of the Weser estuary.

3.4 Benthic characterisation of salinity zones

The pooled data, listed in Table A-1 (Appendix) present a total of 223 taxa. Several taxa were determined to the family level (e.g. Diptera) or even higher taxon level only (e.g. Nemertini). A total of 31 species are listed on the “Red List” of benthic species of Germany (PETERSEN et al. 1996, RACHOR 1998) and 40 genuine brackish water species were found. Of the latter 15 species belong to the category of “Red List species” mentioned above. The major taxonomic group, the Crustacea, yielded 70 species (31%), the Polychaeta 61 species (27%) and the Mollusca 30 species (13%). All other groups hold less taxa, for example Hydrozoa 17, Oligochaeta 14 and Insecta 9 taxa.

The numbers of taxa vary strongly between salinity zones and biotopes (Fig. 17). This is partly due to differences in sampling effort, but also typical of along-estuary patterns (e.g. decreasing species occurrence with decreasing salinity). The subtidal biotopes generally show more taxa than the other biotopes of the respective salinity zone.

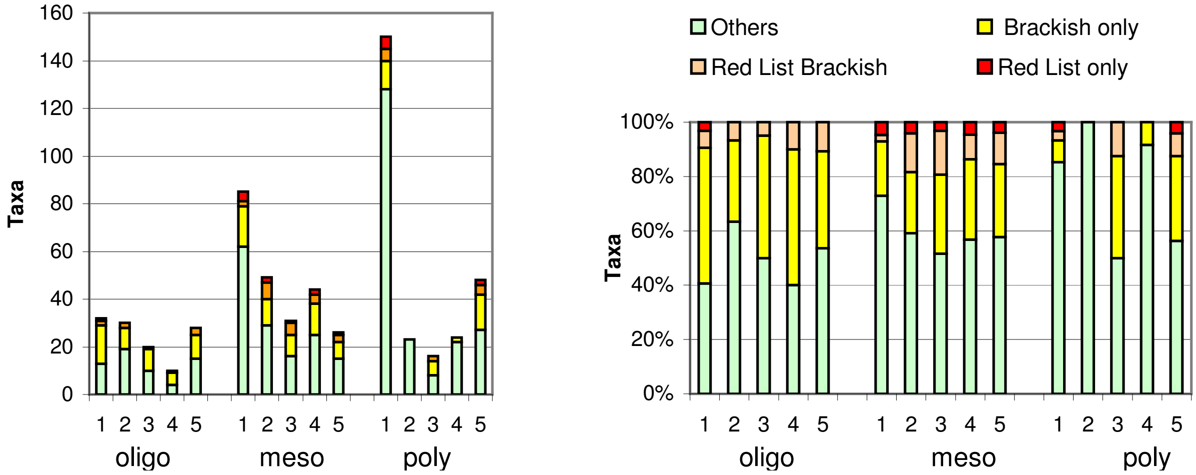


Fig. 17 Total number of taxa, number of threatened and brackish water species in different salinity zones and biotopes (left: absolute numbers, right: percentage, 1- subtidal, 2- intertidal, 3- supratidal, 4- groynes, 5- lagoons, ditches).

The polyhaline subtidal area yields with 150 taxa more species than all other biotopes. Except for the polyhaline intertidal zone all biotopes in all zones are inhabited by threatened and /or brackish water species. In most biotopes the percentage of brackish water species is high in the oligohaline zone and decreases towards the sea (higher salinity), except the supratidal (3) and the lagoons (5) with equal percentages in all salinity zones. In the following chapter the salinity zones will be characterised by benthic data listed in Table A-1. The quantitative aspect of most dominant benthic species will be given from grab sample data from the DB Weser data set (see Table A-2). Additional quantitative aspects will be drawn from Table A-1 (Appendix).

3.4.1 The oligohaline salinity zone

The benthic fauna is represented by 60 taxa (Table A-1) and consists mainly of brackish and freshwater species and only few marine taxa. A total of 25 brackish water species and 8 threatened species are listed. The percentages of the salinity categories within the different biotopes are given in Fig. 18. Brackish water species have high percentages between 40 and 60 % in all biotopes (Fig. 18).

Fresh water species increase towards the shore and occur with 8 benthic taxa in the ditches and pools. Marine species were not found at the supratidal shorelines nor in the ditches and pools.

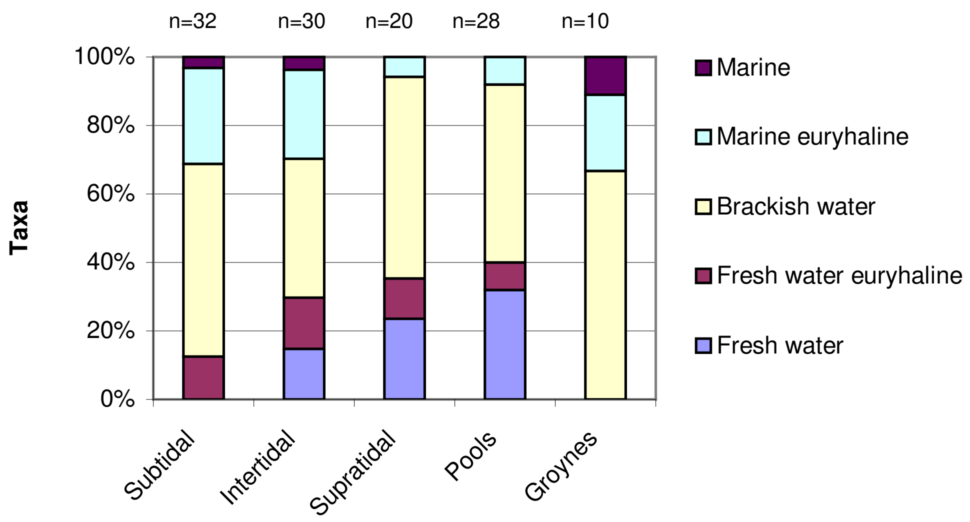


Fig. 18 Salinity preferences of species at different biotopes in the oligohaline zone (n= number of taxa on species level in Table A 1, 60 taxa in total).

A total of 14 taxa such as the molluscs *Corbicula fluminea, Galba truncatula* and the oligochaete *Limnodrilus claparedeanus* occur in the oligohaline zone only (Table A-1). Some of these species are of fresh water origin and occur regularly in the fresh water section of the estuary (HAESLOOP 1990, MEYERDIERKS et al. 2003). In Table 5 the most dominant species from grab samples are presented by quantitative parameters. 7 brackish water species belong to the most dominant species in the oligohaline zone (Table 5). The polychaete *Marenzelleria c.f. viridis* dominates most subtidal sediments in the oligohaline zone of the Weser estuary since its invasion of North Sea estuaries in 1987 (ESSINK & KLEEF 1988). High abundances of *Balanus improvisus* indicate a common presence of hard substrates at the surface layers of subtidal sediments in this zone. *Cordylophora caspia* (Hydrozoa) is found at hard-bottom substrates frequently, although not listed within the dominant species in Table 5.

Table 5 Dominant taxa in the oligohaline zone of the Weser estuary (grab sample data DB Weser, 29 sites, 48 data sets from 1992-2000, km 45-65; dominance of individuals in %; presence at sampling sites in %; mean- mean abundance in ind./m²; max- maximum abundance per site in ind./m²; biomass- mean wet weight in mg/m²).

Taxa	***Dominance*** %	***Presence*** %	***Mean*** Ind./m²	***Max*** Ind./m²	***Biomass*** mg/m²
Marenzelleria c.f. *viridis*	58.5	95.8	1,226	13,273	1111.5
Balanus improvisus	27.4	22.9	575	14,053	--
Corophium volutator	4.0	41.7	83	2,202	627.2
Corophium lacustre	1.6	27.1	34	827	20.0
Mesopodopsis slabberi	1.3	37.5	27	269	54.2
Heteromastus filiformis	1.1	43.8	24	182	743.8
Tubificidae.	0.9	29.2	19	337	12.6
Polydora sp.	0.7	4.2	15	697	606.0
Electra crustulenta	0.5	10.4	10	496	--
Marenzelleria c.f. *wireni*	0.4	2.1	9	452	--
Boccardiella ligerica	0.4	20.8	9	160	--
Bathyporeia pilosa	0.4	16.7	8	230	17.4
Neomysis integer	0.4	39.6	7	73	--
Oligochaeta	0.3	4.2	6	260	1111.5

The intertidal mudflats are dominated by oligochaetes such as *Tubificoides heterochaetus*, *T. costatus* and *Paranais litoralis* in the lower oligohaline zone accompanied by *Corophium volutator* and few polychaetes such as *Marenzelleria viridis* and *Nereis diversicolor*. The upper reach is dominated by oligochaetes only, most of them originated from fresh water such as *Limnodrilus hoffmeisteri*, *L. claparedeianus* and *L. udekemianus* (KOLBE & MICHAELIS 2001, MEYERDIERKS et al. 2003). A maximum abundance of *T. costatus* in oligohaline mudflats with over 50,000 ind./m² is recorded by KOLBE & MICHAELIS (2001).

The high content of organic matter and water creates a special consistence of very soft mudflats in the lower oligohaline zone at Nordenham (km 60). These “fluid muds” show less dense and diverse macrofauna most probably due to a lack of sediment stability for burrowing species (compare MEYERDIERKS et al. 2003).

The supratidal areas in the oligohaline zone are represented by 20 benthic species (Table A-1). Most abundant is the mollusc *Assiminea grayana* and the crustacean *Orchestia cavimana*, which were found at most natural shores between reeds and debris. The oligochaete family of Enchytraeidae is apparent on most shores too, but taxonomic level of identification is low.

The benthic assemblages on subtidal groynes in the oligohaline zone show 10 species, drawn from investigations of two groynes (No. 54 and 59, BFG, unpubl. collected in 1998, Table A-1). The most dominant taxa in these low diversity habitats are the balanid *Balanus improvisus* (max 33,733 ind./m²) and brackish water species such as *Corophium lacustre* (max 399 ind./m²) and

Bocardiella ligerica (max 333 ind./m²). Natural hard bottom substrates have not been investigated yet with similar methods for comparison.

The pools and ditches in the oligohaline floodplains are inhabited by 28 species (Table A-1). Due to the exchange of tidal water and rain water drainage the salinity regime within these small water bodies is individually different. The benthic fauna reflects these circumstances with high variability within the percentage of fresh water species. The crustaceans *Palaemonetes varians* and *Neomysis integer* and insect larvae of Chironomidae spp. and Ceratopogonidae spp. sometimes reach high densities within these habitats (KÜFOG, unpublished, MEYERDIERKS et al. 2003). Many insect species and their larvae that occur in these habitats are included on a higher taxonomic level (see chapter 3.1).

3.4.2 The mesohaline salinity zone

A total of 119 taxa are registered from the mesohaline zone (Table A-1). 34 brackish water species are found and 16 taxa are listed on the Red List of threatened species. The most severely threatened species of this zone are the opisthobranch gastropods *Limapontia depressa* and *Alderia modesta*, which are restricted to the mats of certain green algae (*Vaucheria* spp.) at two small sites at present (Fig. 16).

The benthic community is more influenced by the sea; fresh water taxa are less frequent and are replaced by euryhaline marine and marine taxa. Brackish water species are present in all mesohaline habitats. The vertical salinity gradient from the subtidal areas towards the supratidal biotopes with decreasing numbers of marine species and increasing numbers of fresh water species is obvious (Fig. 19). In Table 6 the most dominant species of subtidal sediments are presented by their dominance, presence and average abundance during the surveys. Similar to the oligohaline zone the strong dominance of *Marenzelleria viridis* is obvious, providing 72 % of all individuals with almost 70% presence and a major contribution to average biomass. The percentage of *Marenzelleria wireni* in "*Marenzelleria* sp." is uncertain because of taxonomic uncertainties of young individuals. Only 5 brackish water species are listed within the dominant species; most abundant species have to be considered as marine euryhaline. *Heteromastus filiformis,* a marine species shows a high presence in the subtidal areas (62.2 % presence, Table 6). Besides *Marenzelleria* spp. the bivalves *Mytilus edulis* and *Macoma balthica* are contributing major amounts to the biomass when present in the samples.

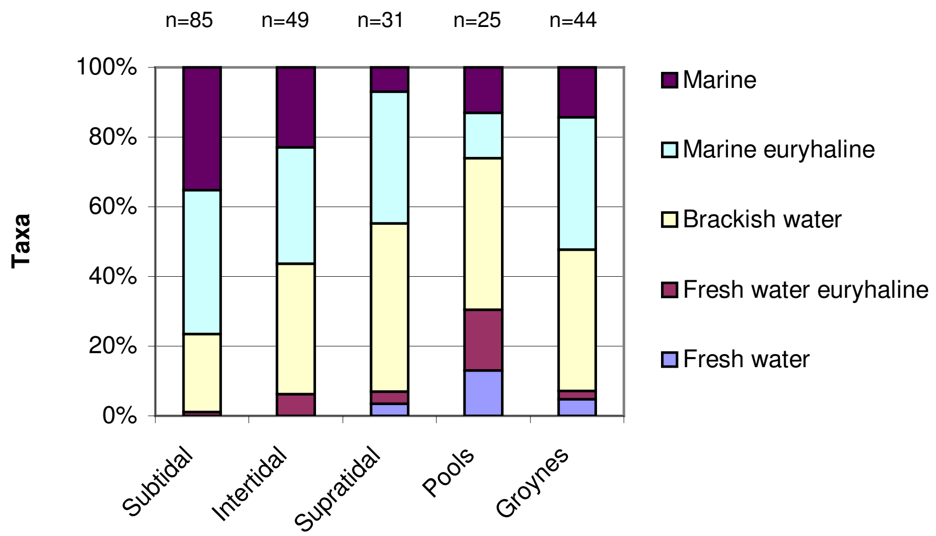


Fig. 19 Salinity preferences of species at different biotopes in the mesohaline zone (all taxa at species level in Table A 1, 119 taxa in total).

Table 6 Dominant taxa in the mesohaline zone of the Weser estuary (139 sites, 278 samples from km 65-80 DB Weser data from 1992-2001; dominance of individuals in %; presence at sampling sites in %; Mean- mean abundance in ind./m²; Max- maximum abundance in ind./m²; Biomass- mean wet weight in mg/m²).

Taxa	***Dominance*** %	***Presence*** %	***Mean*** Ind./m²	***Max*** Ind./m²	***Biomass*** mg/m²
Marenzelleria c.f. *viridis*	75.2	69.8	1890.5	78125	11945.5
Marenzelleria sp.	7.6	18.0	191.3	9080	27319.3
Heteromastus filiformis	6.3	62.2	158.1	6172	2941.6
Corophium volutator	3.5	34.5	87.8	8317	1024.7
Bathyporeia pilosa	1.3	32.4	32.1	2179	200.9
Mytilus edulis	1.1	23.0	28.0	4505	83784.1
Gammarus salinus	1.0	25.9	26.4	3710	1087.3
Bathyporeia pelagica	0.5	22.7	11.7	1229	139.4
Polydora ligni	0.4	9.7	10.4	1640	55.1
Eteone longa	0.4	32.0	9.2	401	93.1
Neanthes succinea	0.3	22.3	7.9	440	493.7
Tubificoides benedeni	0.2	10.1	5.9	310	68.2
Pygospio elegans	0.2	8.3	5.4	587	69.3
Macoma balthica	0.2	29.1	4.4	175	2488.3
Neomysis integer	0.2	27.3	3.8	101	102.0

The intertidal flats are characterised by a similar community with a high dominance of *Corophium volutator*, *Marenzelleria* spp., *Macoma balthica* and *Heteromastus filiformis*. Due to the grain size and the contents of silt within the sediments the composition of benthic invertebrate faunas shifts on small scales.

Brackish water species such as *Streblospio benedicti* and *Manayunkia aestuarina* are characteristic but not dominant in this zone. Similar to the oligohaline area the anthropogenic influence on this estuarine zone is obvious. In publication I the different biotopes within this zone are analysed in detail. The artificial substrates and structures such as groynes are compared to natural biotopes in accordance with their habitat function for benthic invertebrates.

3.4.3 The polyhaline salinity zone

In the polyhaline area 168 taxa are registered in total. 30 brackish water species are found and 23 taxa are listed on the Red List of threatened species. Marine and euryhaline marine taxa dominate the community while brackish species occur in low densities (Fig. 20). Fresh water species are absent from the channels and intertidal flats but occur in the salt marsh ditches and supratidal biotopes with low salinity.

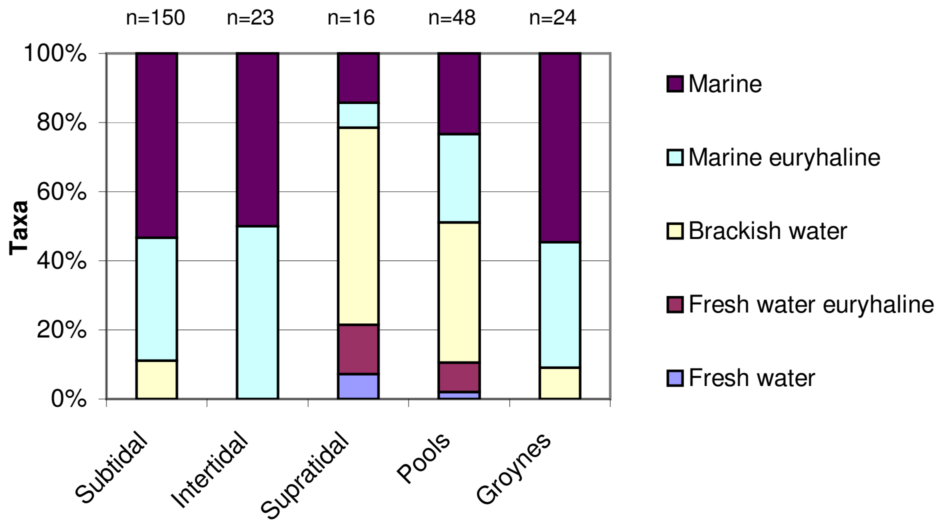


Fig. 20 Salinity preferences of species at different biotopes in the polyhaline zone (all species from Table A 1, 168 taxa in total).

As demonstrated in Fig. 15 the polyhaline zone is subdivided into a southern part (polyhaline 1, km 80-91) and northern part (polyhaline 2, km 91-112). The quantitative characterisation is split similarly (Table 7 and 8).

The most dominant species in the southern polyhaline area (polyhaline 1, Table 7) is *Hydrobia ulvae* with extreme abundances in shallow muddy sand areas. *Marenzelleria viridis* is still dominant especially in the polyhaline 1 zone with low salinities (publication II). Euryhaline marine taxa and only three brackish water taxa belong to the most dominant species. The molluscs *Hydrobia ulvae* and *Mytilus edulis* contribute mainly to high biomass values (Table 7).

Table 7 Dominant species in the southern polyhaline zone of the Weser estuary (polyhaline 1) (99 sites, 225 samples, DB Weser grab sample data from km 80 to 90,9 in 1991-1998; numerical dominance of individuals in %; presence at sampling sites in %; Mean- mean abundance in ind./m²; Max- maximum abundance in ind./m²; Biomass- mean wet weight in mg/m²).

Taxa	***Dominance*** %	***Presence*** %	***Mean*** Ind./m²	***Max*** Ind./m²	***Biomass*** mg/m²
Hydrobia ulvae	89.3	56.9	9096.5	106150	54015.2
Marenzelleria c.f. *viridis*	5.2	54.2	526.2	21892	4136.5
Mytilus edulis	2.0	21.3	206.5	25212	35467.2
Heteromastus filiformis	1.2	73.3	124.3	4910	2127.3
Tharyx marioni	0.4	21.3	41.5	2859	400.8
Bathyporeia pilosa	0.3	37.8	31.5	1128	191.4
Polydora ligni	0.2	5.8	22.0	4343	612.5
Gammarus salinus	0.2	12.4	21.6	2550	1394.5
Pygospio elegans	0.2	29.3	21.2	2470	87.3
Macoma balthica	0.1	53.3	13.4	610	3006.7
Bathyporeia pelagica	0.1	30.2	12.7	333	86.3
Capitella capitata	0.1	31.1	8.8	485	43.0
Tubificoides benedeni	0.1	30.7	6.1	216	27.9
Nephtys hombergii	0.0	28.0	4.6	61	674.6
Eteone longa	0.0	28.0	2.7	44	41.6

The dominance structure in the northern polyhaline area (polyhaline 2, Table 8) is completely different from the southern polyhaline area (polyhaline 1, Table 7). *Magelona mirabilis*, *Bathyporeia pelagica* and *Ophelia limacina*, all species that prefer sandy sediments, are the most dominant species in the polyhaline zone 2. *Hydrobia ulvae*, *Marenzelleria viridis* and *Heteromastus filiformis* are more abundant in the polyhaline zone 1. Only marine taxa and no brackish water species belong to the most dominant species. The bivalve *Ensis directus* and the polychaete *Lanice conchilega* contribute mainly to high biomass values (Table 8). A more detailed analysis of subtidal biotopes is given in publication II (polyhaline zone).

The intertidal flats are dominated by marine taxa such as *Heteromastus filiformis*, *Corophium volutator*, *Arenicola marina*, *Macoma balthica*, *Hediste diversicolor* and *Hydrobia ulvae*. Special intertidal habitats are provided by sea grass meadows (*Zostera noltii, Z. marina*) in the western part of the estuary and blue mussel beds in the east (Fig. 16). Position and area of shell deposits as mentioned in MICHAELIS (1981) have not been recorded since then.

Table 8 Most dominant species in the northern polyhaline zone of the Weser estuary (polyhaline 2) (99 sites, 111 samples; DB Weser grab sample data from km 91 to 112 in 1991-2001, numerical dominance of individuals in %; presence at sampling sites in %; Mean- mean abundance in ind./m²; Max- maximum abundance per site in ind./m²; Biomass- mean wet weight in mg/m²).

Taxa	***Dominance*** %	***Presence*** %	***Mean*** Ind./m²	***Max*** Ind./m²	***Biomass*** mg/m²
Magelona mirabilis	23.4	18.9	54.5	4909	791.6
Bathyporeia pelagica	11.0	51.4	25.7	350	101.2
Lanice conchilega	5.5	9.0	12.9	919	6134.0
Ophelia limacina	5.4	26.1	12.5	320	1473.7
Gastrosaccus spinifer	4.9	31.5	11.4	485	583.8
Eumida sanguinea	4.0	3.6	9.2	848	699.5
Goniadella bobretskii	3.4	13.5	7.8	320	60.2
Nephtys longosetosa	2.8	45.0	6.4	75	2416.0
Nephtys cirrosa	2.8	22.5	6.4	131	986.0
Phyllodoce mucosa	2.5	9.0	5.7	475	510.6
Ensis directus	2.4	9.9	5.7	430	29390.8
Scoloplos armiger	2.3	46.8	5.3	58	266.4
Bathyporeia elegans	2.3	6.3	5.3	321	22.3
Microphthalmus similis	2.0	14.4	4.7	172	7.2
Mytilus edulis	1.6	10.8	3.7	102	50.1

The groynes within the polyhaline area are inhabited by a more diverse benthic assemblage compared to the inner estuary (Table A-1). The balanids *Balanus crenatus*, *B. improvisus* and the bivalve *Mytilus edulis* are most dominant and create thick coverages on suitable locations. The actiniarians (most frequent is *Metridium senile*) occur with high numbers on subtidal groynes (not identified to species level within data of BFG). Additional amphipods such as G*ammarus salinus* and polychaetes such as *Polydora* spp. and *Nereis virens* are frequent on the rocky substrate of the groynes.

The supratidal areas in the polyhaline zone have been investigated by FRÄMBS et al. (2002). The salt marsh ditches and tidal ponds show a similar benthic community to the mesohaline area. The composition varied due to tidal height and fresh water influence from rain water drainage. In addition to the species from the upper estuarine reaches, marine taxa intrude into the ditches and creeks from the polyhaline intertidal flats, which reflects an estuarine gradient on a small scale.

This characterisation of major biotopes within the estuary is intended to give an overview and will be completed and analysed more differentially within publication I and II.

3.3 Publications

Publication I J. Witt, R. Knust, W.E. Arntz: Spatial distribution of benthic invertebrates in anthropogenically influenced, mesohaline habitats of the Weser estuary (submitted to Aquatic Conservation: Marine and Freshwater Ecosystems)

Publication II J. Witt, A. Schroeder, R. Knust, W.E. Arntz: The macrobenthic community in a polyhaline channel system of the Weser estuary: Scales of spatial distribution and diversity
(submitted to Senckenbergiana Maritima)

Publication III J. Witt, A. Schroeder, R. Knust, W.E. Arntz: The impact of harbour sludge disposal on benthic macrofauna communities in the Weser estuary
(published in Helgoland Marine Research, online first)

Spatial distribution of benthic invertebrates in anthropogenically influenced, mesohaline habitats of the Weser estuary

Jan Witt[1, 2], Rainer Knust[2] & Wolf E. Arntz[2]

[1] Küstenökologische Forschungsgesellschaft mbH (KÜFOG), Alte Deichstr. 39, D-27612 Loxstedt-Ueterlande, Germany, Tel.: ++49 (0) 4740/ 1071, e-mail: info@kuefog.de

[2] Alfred Wegener Institute of Polare and Marine Research, Benthic Ecosystems, Columbusstraße, D-27515 Bremerhaven, Germany.

Abstract

The macrobenthic communities within the mesohaline zone of the Weser estuary (Germany) were investigated from 1993 to 2002 by a variety of sampling methods. Macrobenthic samples from intertidal flats, subtidal areas, artificial hard substrates of groynes and shoreline protection constructions were surveyed. Additional supratidal data from salt marsh ditches and brackish lagoons were analysed in order to detect spatial distribution patterns of species from all habitats in the tidal reach. The species showed preferences for certain habitats and were thus differentiated into sub-communities. Besides the substrate and the sediment composition, water depth was a main factor for species distribution. The importance of subtidal natural hard bottom substrates as a habitat for benthic species in a soft bottom dominated estuary is discussed. The widespread artificial hard bottom structures in an industrialised estuary, such as groynes, showed limitations in functioning adequately as a habitat substitute, presenting a less diverse benthic community than natural stony substrates.

Keywords: Weser estuary, macrobenthos, estuarine invertebrates, artificial hard substrates, supratidal habitats, brackish lagoon, groynes, spatial distribution

Introduction

European estuaries are unique natural areas which provide important feeding grounds for birds and fish, as well as supplying valuable habitats for many benthic invertebrate species (McLUSKY 1989, BARNES 1994). This is contrasted by the rapid loss of pristine estuarine areas to the ever-expanding needs of cities, their harbours and industries (McLUSKY 1989). Coastal engineering works of shoreline protection may affect natural estuarine biotopes on a large and long-term scale (SMAAL et al. 1991, MEIRE et al. 1994). The brackish communities with several endangered benthic species face the loss of brackish habitats as a result of this ongoing development (MICHAELIS 1981, MICHAELIS et al. 1992).

In the Weser estuary, new structures such as groynes and dams have been constructed to improve commercial shipping since 1890. These works have caused obvious changes to the original shoreline biotopes (SCHUCHARDT et al. 1984, BUSCH et al. 1989, SCHIRMER 1995).

The value of natural estuarine hard bottom or mixed bottom substrates for benthic diversity is demonstrated by WARWICK & DAVIES (1977). Artificial hard bottom structures may provide new habitats for benthic species and colonisation can be fast (ANGER 1978), however the function of artificial substrates such as groynes as substitutes for natural biotopes and their ecological value for benthic communities is still undetermined.

For the management of estuaries and coastal waters within the European nature conservation legislation (Water Framework Directive, Habitat Directive) an evaluation of benthic habitats is required (DAVIES et al. 2000). An inventory of benthic species and their habitats in today's estuaries, including all different structures, is intended to provide a database for such an evaluation.

In this investigation the benthic community of an estuarine area within the mesohaline zone of the Weser estuary is described, including subtidal, intertidal and supratidal habitats. The spatial distribution of the species is examined and factors for settlement are discussed. The integration of artificial structures and biotopes of the supratidal areas within an inventory is a new approach for evaluating estuarine communities.

Material and methods

Survey area

The investigation area is located north of the harbour facilities of Bremerhaven. The investigation of this area is one of the planning requirements for the various stages of planned harbour expansions. The survey was commissioned by the Bremen Harbour Administration (bremenports GmbH). Benthic data for the evaluation of the expected loss of habitats, such as intertidal flats or brackish lagoons, were surveyed in order to quantify such loss, and thus calculate adequate compensation measures. The data were collected during several surveys in intertidal, subtidal and supratidal biotopes from 1993 to 2002 (KÜFOG, unpublished data).

The survey area is dominated by muddy intertidal flats and belongs to the mesohaline zone of the Weser estuary (Fig. 1). A system of groynes and shoreline protection facilities has been installed to prevent the erosion of the shoreline, salt marshes and dykes. A former military base (fort) with a massive concrete foundation provides artificial, rocky shores and hard substrates for supratidal, intertidal and subtidal colonisation. The destruction of old groynes and stonewalls by the tidal currents and heavy storms has created new habitats, such as small lagoons and stony niches. The salt marshes have been used as pastures and for recreational purposes. Brackish reedbeds separate the mudflats from the salt marshes.

The salinity of the survey area varies between 3 and 20 PSU with an average of about 12 PSU (WSA Bremerhaven, unpublished data from 1999), depending on seasonal variation in the fresh water outflow, tides and wind strength and direction. The maximum velocity of tidal currents was 1.35 m/s about 1.5 hours after slack water with a tidal amplitude of 3.6 m. The turbidity of the Weser in the survey area is extremely high and varies between 100 and 1200 mg/l of suspended matter (WELLERSHAUS 1981). The position and length of the turbidity zone in the Weser varies, due to the amount of freshwater runoff. For most of the year, the maximum turbidity is located a few km upstream from Bremerhaven south of the survey area (GRABEMANN & KRAUSE 2001).

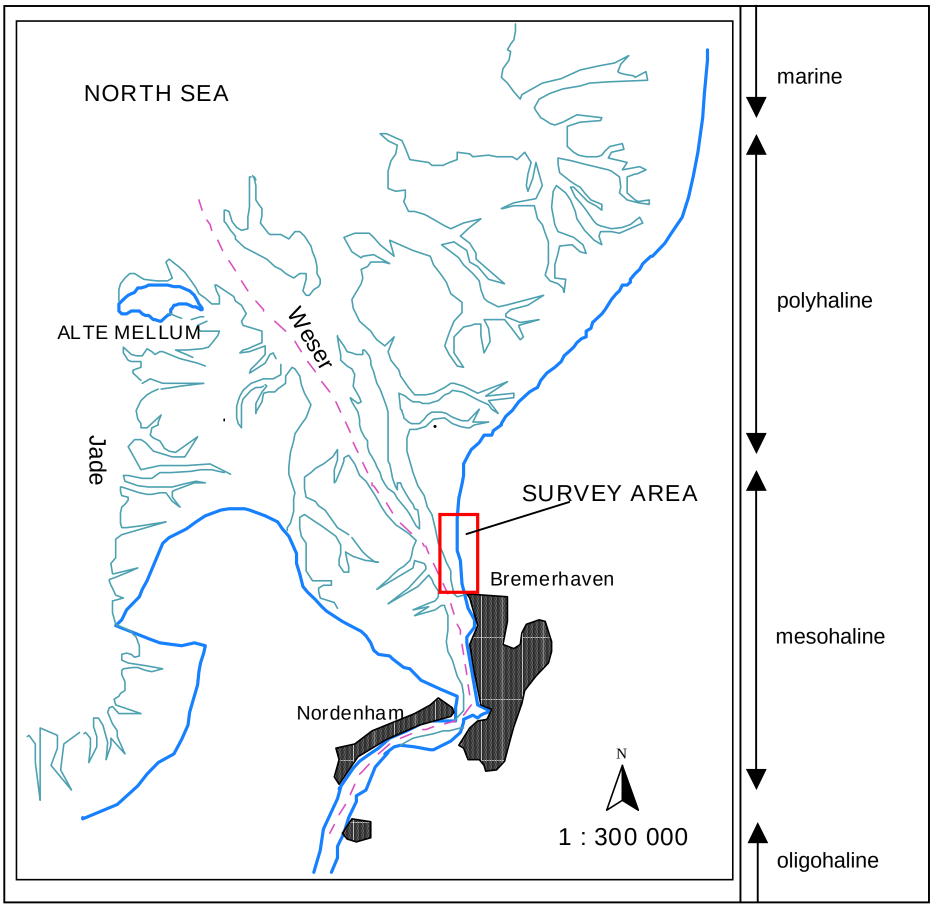


Fig.1 Survey area and salinity zones of the Weser estuary.

Field and laboratory methods

The surveys at 47 sites were carried out from 1993 to 2002. In Fig. 2 the locations of the sites are given. The biological data set, included quantitative benthic data from soft sediments (grab and corer samples), semi-quantitative data from hard substrates (hand collection) and data from ditches (net samples). The data have been compiled from different years and from different locations. The frequency of data collection varied from one to four times a year depending on the survey`s target (Table 1).

Intertidal sediments

The major quantitative data set was collected from intertidal mudflats on three transects with three sites each from the shore to the low water mark (Fig. 2). These sites were sampled with a sediment corer (15 cm diameter, 20 cm depth) four times a year (May to October) in 1994, 1995, 1997 and 1998 (measurements were validated by 3 replicates per site). Additional sites in the south of the survey area were sampled four times in 1997 (Table 1). After sieving through a cascade of 0.5 and 1.0 mm mesh size, the samples were transported to the lab and stored for identification processing in alcohol (70%). The further analysis will be summarized at the end of this chapter.

Subtidal sediments

The subtidal areas were surveyed by Van Veen-grab samples (0.1 m²) and a frame dredge (1 m width, 0.5 cm mesh size). Two to three replicates per site were taken with the grab and one haul per site was taken with the dredge (100 m trawl distance). The sieving and processing was similar to the process used for the intertidal sampling. A sieve of 1mm mesh size was used during the survey of subtidal sediments.

Artificial hard bottom substrates (groynes, fort)

The sites at the hard bottom areas (sub-, inter-, supratidal) were sampled by hand collection. A 15-minute collection with pincers of all structures (stones, debris, reeds) within 10 m² by an experienced person provided a representative sample. The number of detected individuals was estimated by using abundance classes. Species were preserved in alcohol (70%) and transferred to the laboratory for classification.

Small supralitoral water bodies (ditches, lagoons)

The salt marsh ditches were sampled at two sites, each being 5 m in length. A small net (25 cm diameter, mesh size of 0.5 mm) was pulled through all relevant structures in the ditch, such as water column, vegetation and surface sediments. The sites were sampled four times a year from May to October in 1993 and 1996, with three replicates per site for validation.
The lagoon in the south of the survey area was surveyed by a combination of methods. The sediments were sampled at 3 sites with the sediment corer as described above. Three sites at the shoreline of the lagoon were sampled by hand collection. An additional three sites were sampled using the same net as for the ditches. All sites were investigated four times from May to October 1999. The same process of sieving and preserving was used as mentioned above.

In the laboratory the samples were sorted with illuminated stereomicroscopes, species were removed from the sediments, counted and identified. Except Oligochaeta, Diptera and Ostracoda all taxa were classified to the species level, where possible.

Abiotic data

Sediment characteristics, such as major grain size components, silt, shells, stones and organic content were described from all quantitative sampling sites for interpretation of faunal data. Grain size analysis at each site was done once a year during stable summer periods (August). Process of fractionised sieving and analysis of total organic matter by loss of weight on ignition followed the method of BUCHANAN (1984).

Only basic physical measurements of water parameters such as temperature, salinity and pH were surveyed to characterise water quality during sampling. Extensive studies of salinity including tidal and seasonal changes were carried out by the local waterway authorities (WSA Bremerhaven). These results have been used to characterise the salinity of the survey area.

Table 1 Sampling methods, number of sites and time of collection (a, b, c, d - sampling of all sites, a-April/May, b-June, c-August, d-October, location of sites are given in Fig. 2).

Biotope	**Structure**	**Sites**	**Method of Sampling**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**
Subtidal	Sediment	6 (G1-6) 3 (G7-9)	Van Veen grab, dredge					 -b-d				-bcd	a---
Intertidal	Sediment	9 (W1-3) 4 (W4-7)	Sediment corer		abcd	abcd		abcd abcd	abcd				
Supratidal	Reedbeds Beach	1 (S4) 4 (S1-3)	Hand collection					abcd				 -bcd	 a---
Groynes	Stones-intertidal	2 (Bu4-5) 1 (Bu 6)	Hand collection					 abcd				-bcd	a---
	Stones-subtidal	2 (Bu1, 2) 1 (Bu3)	Coll. of stones net sampling									--- d -bcd -bcd	 a--- a---
	Stones-supratidal	1 (Bu7)	Hand collection									-bcd	a---
Lagoon	Sediment	3 (L1-3)	Sediment corer					abcd			abcd		
	Shoreline	3 (L4-6)	Hand collection					abcd			abcd		
	Water	3 (L7-9)	Net sampling					abcd			abcd		
Fort	Stones	2 (F1, 2)	Hand collection					abcd					
Salt marsh	Ditches	2 (N1, 2)	Net sampling	abcd			abcd						

Data analysis

All benthic data, which were collected by different methods in different surveys, as presented in Table 1, were pooled into abundance classes to aggregate the information of each biotope or structure, respectively. Each row of Table 1 represents the data source of pooled data for a species list with a semi quantitative data set (Appendix Table A-1).

For classification, maximum individual numbers per site were transferred into 6 classes:
0 - no find, 1 - single find, x - 2-10 individuals, xx - 11-100 individuals, xxx - 101-1000 individuals and xxxx > 1000 individuals per site and time of collection.
For quantitative analysis procedures, grab-sample data and corer samples were used. To achieve a similar data basis, data from 1mm and 0.5 mm sieving were used separately. Dredge-sample data were used on a semi-quantitative basis for analysing the epibenthic community. Pelagic species were excluded from the analysis.
The Mann-Whitney test was applied for testing significance of differences. Non-metric multi-dimensional scaling (MDS) and cluster analysis were used to identify patterns in the species distribution (CLARKE & WARWICK 1994). The inter-sample similarity was calculated by the Bray-Curtis coefficient (BOESCH 1977). Fourth root transformation on quantitative data was applied to reduce the influence of dominant species. The presence/absence transformation on qualitative data was used to consider differences in sampling methods. The statistical analyses were done with the software package PRIMER (v5.2) (CLARKE & WARWICK 1994, CLARKE & GORLEY 2001).

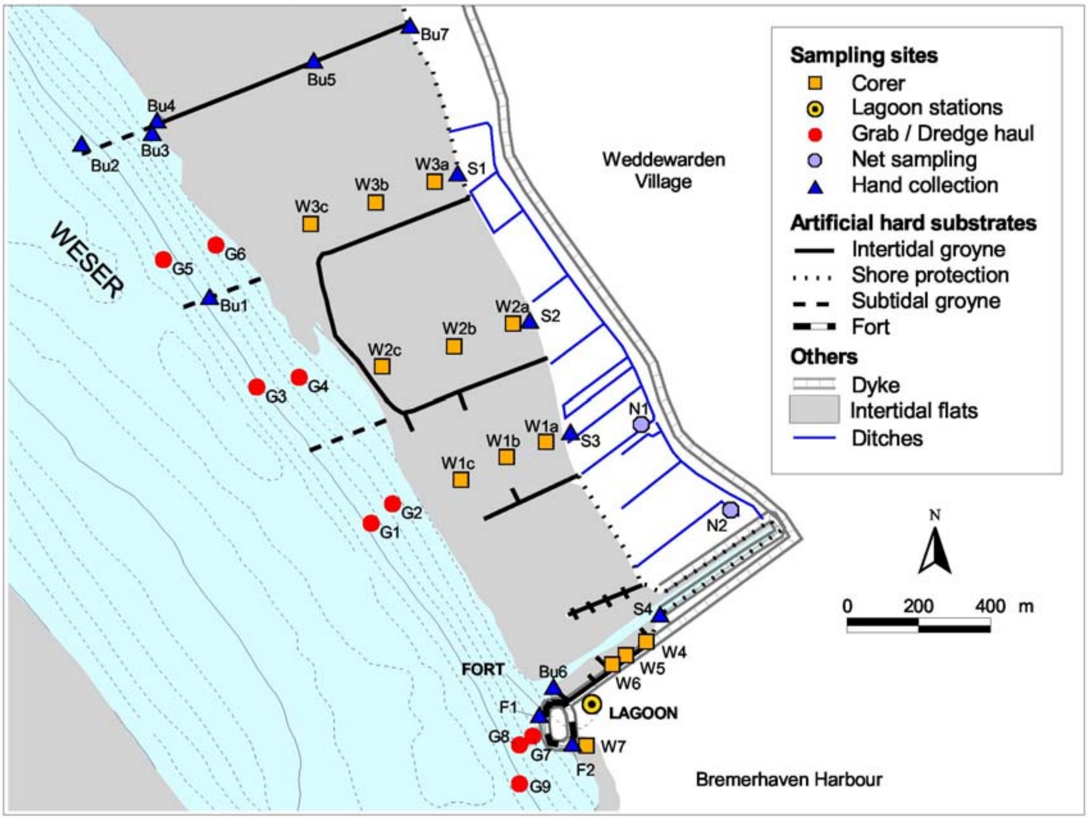


Fig. 2 Survey area with the positions of the sampling sites labelled.

Results

Morphology and sediments

The survey area shows the typical sequence of estuarine biotopes of a drowned river valley estuary type (McLUSKY 1989). Dykes keep the tidal influence away from most of the farmland and prevent settlements in the former river valley from being flooded. The salt marshes beyond the dykes get flooded in heavy storms during winter and spring. They are flat clay or sand areas only a few dm above mean high water level, used as grazing pastures or meadows.

The intertidal flats from 1.8 m down to -1.8 m are stabilized by groynes, which provide protection from erosive waves and currents. There is a strong sedimentation of soft mud along the groynes and the low tide mark. The subtidal upper slope down to the -5m depth line is a silt sand mixture of soft and enriched sediments. The strong tidal currents at the deeper slope area wash fine sediments away so that stony surfaces provide stable substrates for epibenthic fauna. This was confirmed by studying drilling samples from engineering surveys. These showed a widespread stony layer of glacial origin at between 8 to 10 m depth (Fig. 3).

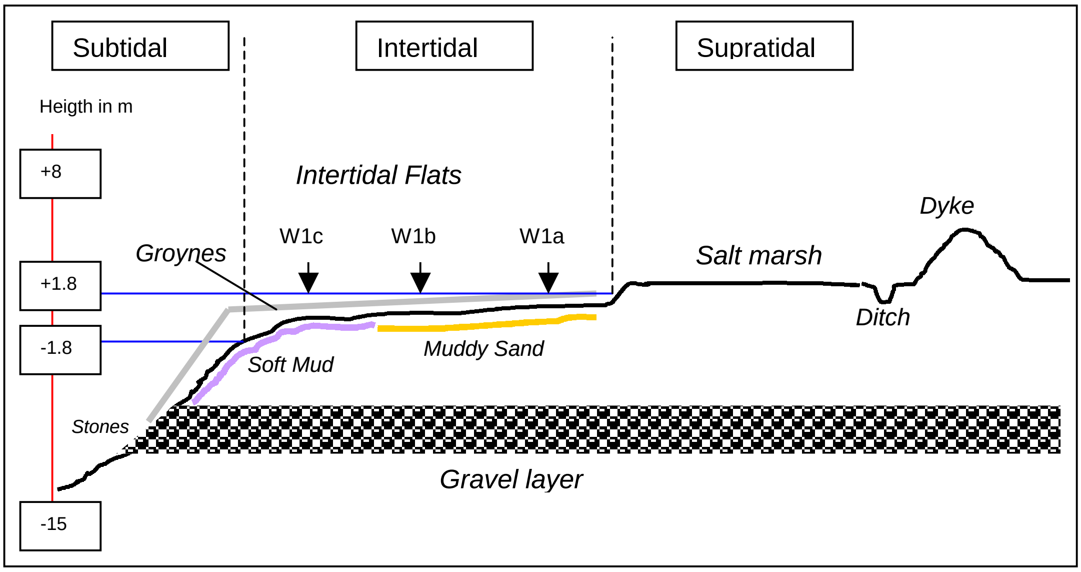


Fig. 3 Schematic cross section of the survey area at transect 1 (arrows mark positions of intertidal sites W1a, W1b, W1c, compare Fig. 2).

Most of the area had sediments of fine sand with differing percentages of silt. The areas next to the groynes and within reach of the low water level are muddy, soft sediments. Areas between the groynes and close to the shores have more sandy sediments due to waves and currents during high tide. In Table 2 selected results of the sediment analysis (percentage of silt and total organic matter-TOM) are presented.

Table 2 Results of the sediment analysis of 9 intertidal sites from 1994 to 1998 (TOM-total organic matter, for position of sites see Fig. 2).

	1994		*1995*		*1997*		*1998*	
Site	**TOM** in %	**Silt** in %	**TOM** in %	**Silt** in %	**TOM** in %	**Silt** in %	**TOM** in %	**Silt** in %
W1a	1.5	7.5	5.9	6.2	2.3	16.8	2.0	12.9
W1b	1.8	8.6	2.3	13.3	3.0	18.4	2.0	12.1
W1c	1.0	26.4	6.9	40.9	6.5	52.6	5.0	46.5
W2a	1.6	4.1	1.1	7.5	3.5	11.3	3.7	25.7
W2b	1.7	6.8	1.3	25.5	1.7	9.7	1.5	6.2
W2c	2.0	11.5	3.5	13.5	2.8	25.2	5.7	16.8
W3a	1.8	13.2	2.2	8.7	1.9	11.6	2.3	13.7
W3b	1.7	14.0	1.7	11.9	2.7	16.1	2.3	17.2
W3c	2.4	21.0	6.2	9.5	7.8	55.1	3.4	28.2

The sites close to the shore (W1a, 2a, 3a) and the central stations (W1b, 2b, 3b) show low silt and TOM percentage in most of the years. The highest amount of silt and TOM is found in soft muds at the low water level (W1c, 2c, 3c). A strong correlation of silt percentage and TOM is apparent (Table 2).

The benthic community in the mesohaline zone of the Weser

A total of 114 species were collected during the surveys, including 98 species of benthic macrofauna, 13 fish species and 3 pelagic species (Appendix Tab. A-1). Crustacea yielded 33, Polychaeta 18, Hydrozoa 9 and Mollusca 16 species. Insects were represented by 9 taxa, oligochaetes by 5 taxa; Plathyhelminthes, Nemertini, Bryozoa together contributed 8 taxa. A total of 34 genuine brackish water species was determined. A total of 6 species are listed in the “Red List of endangered species” (RACHOR 1998).

Spatial distribution of species

The analysis of the community composition by a qualitative comparison of the different biotopes (Appendix Table A-1) showed three main groups at the 50% similarity level (Fig. 4).

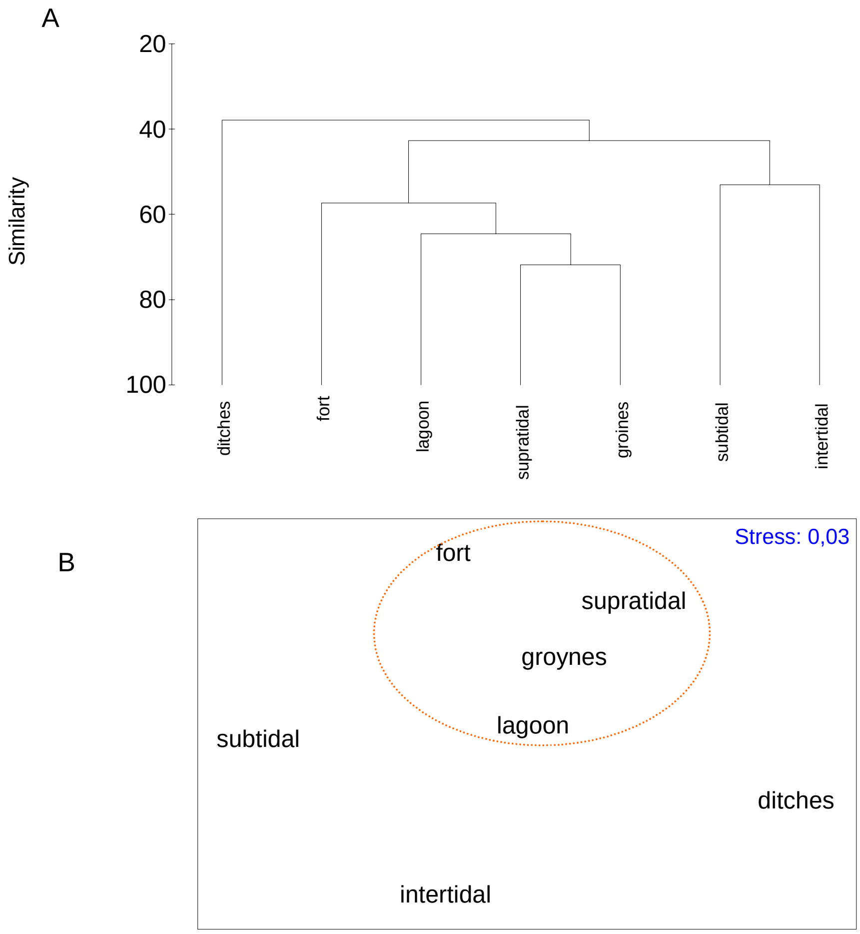


Fig. 4 Similarity of benthic data of the surveyed biotopes (Bray Curtis Similarity, presence-absence data transformation, A-dendrogramm, B- MDS plot, based on species data of the biotopes in Table A-1, Appendix).

Low similarity to all other biotopes was recognized in the salt marsh ditches. The intertidal and subtidal biotopes were similar to each other (55%) and a third group was formed by the groynes, fort, lagoon and supratidal biotopes. Within this group a high similarity (76%) between the groynes and the supratidal biotopes was registered.

The species number of the different biotopes in the survey area is shown in Fig. 5. The intensity of investigation, given as number of sites and number of available data sets, varies and will be discussed later on (compare Table 1). All biotopes contained genuine brackish water species and threatened species. The highest total species number (48 species) was found in the subtidal areas, most of the threatened species (5 species) appeared in the lagoons. The fort and the salt marsh ditches were inhabited by 26 and 23 species, respectively. The percentage of genuine brackish water species varied from 27% in the intertidal flats to 44% in the lagoons. A decreasing number of species from the subtidal to the supratidal areas was found (Fig. 5).

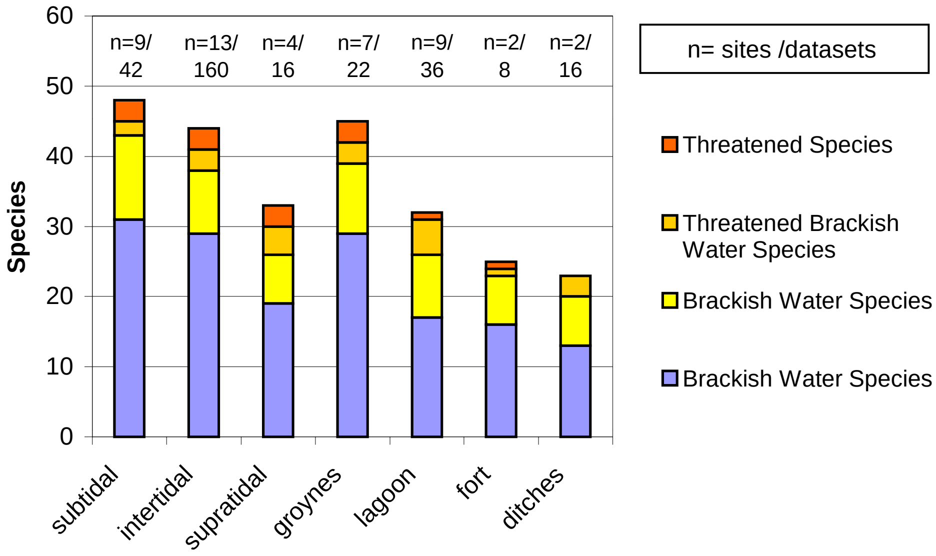


Fig. 5 Species number of different biotopes in the survey area (see also Table A-1).

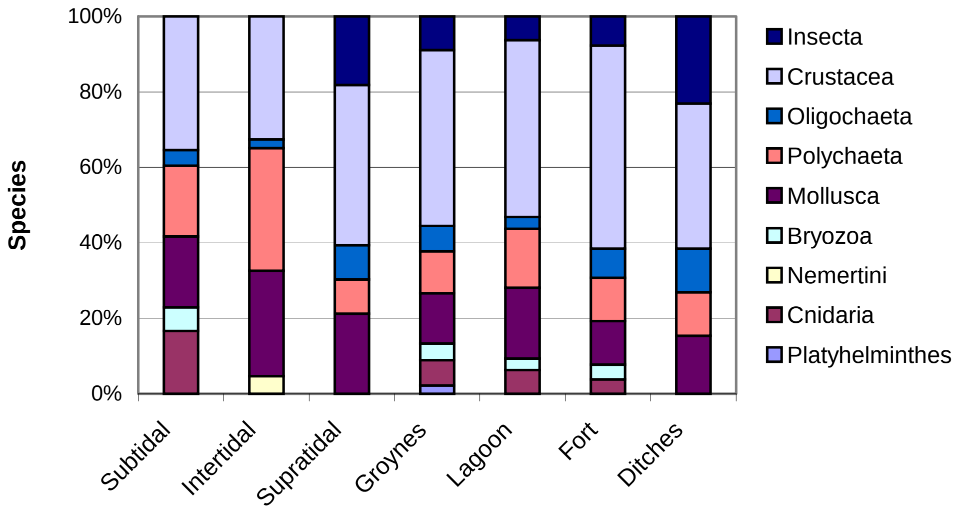


Fig. 6 Taxonomic groups at different biotopes in the survey area.

In Fig. 6 the taxonomic groups of the investigated biotopes are presented. The most speciose group in all biotopes were the crustaceans, which dominate hard- (groynes, fort) and soft-bottom habitats (ditches). From 32 identified species of crustaceans, 21 were found at the groynes and 10 appeared in the ditches. The second diverse group were the polychaetes, closely followed by the molluscs. The suspension feeding cnidarians and bryozoans were related to biotopes with hard substrates with permanent water coverage such as are found in lagoons and subtidal areas. These groups were not apparent in ditches or the intertidal flats. The insects did not occur in subtidal and intertidal biotopes, but yielded higher percentages in supratidal areas and ditches.

In Fig. 7 the feeding guilds of the invertebrates of the different biotopes are presented. The suspension feeders achieved the highest species number in the subtidal area. In all other biotopes, especially in the intertidal and supratidal zone, the deposit feeders dominated the species composition. The carnivorous / omnivorous species had a low percentage in all biotopes.

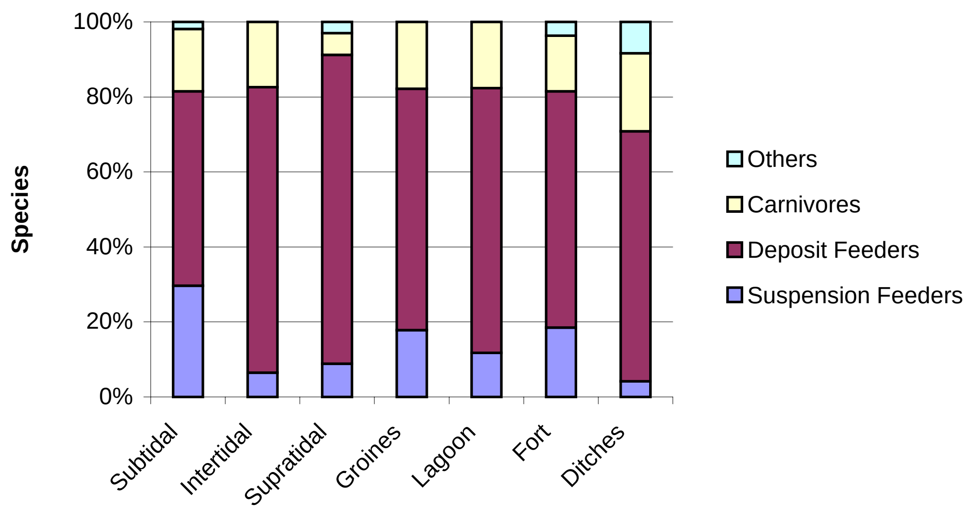


Fig. 7 Feeding guilds in different biotopes of the survey area.

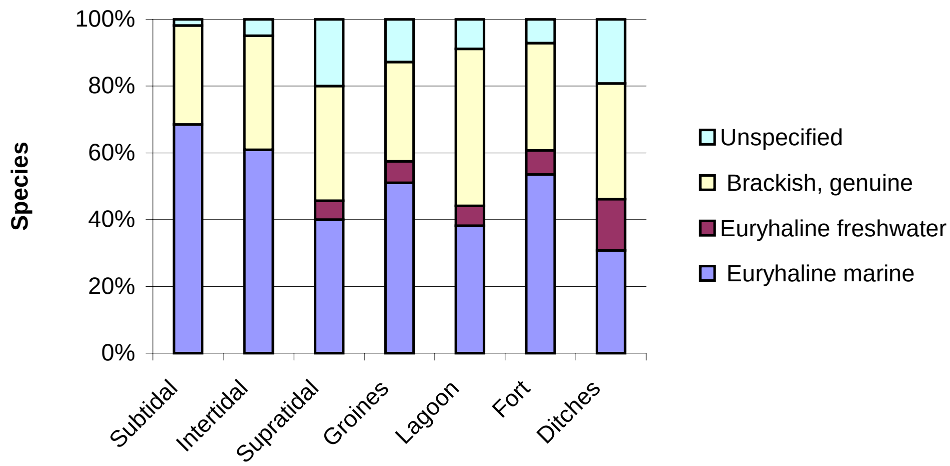


Fig. 8 Salinity groups of different biotopes in the survey area.

The comparison of all biotopes with the species relationship to salinity (Fig. 8) shows a slight gradient from the deep-water areas (subtidal) to the supratidal biotopes. The percentage of marine species decreased towards the supratidal, whereas the percentage of brackish water species increased. The freshwater species were rare in all biotopes and yielded most species in the ditches.

In Table 3 the most dominant species from the different biotopes are listed (biotopes with quantitative data only). The subtidal sediments were differentiated in deep and shallow areas because the dominance structure differed. Only few species were dominant in more than one biotope, which shows the individuality of the different biotopes.

Table 3 Most dominant taxa of investigated biotopes (numerical dominance of individuals in %, 4 most dominant taxa only). Data based on total individuals from grab samples (subtidal), corer samples (intertidal, lagoons) or net samples (ditches).

Taxa	*Subtidal deep*	*Subtidal shallow*	*Intertidal*	*Lagoons*	*Ditches*
Balanus improvisus	71	4			
Electra crustulenta	7				
Corophium volutator		5	52	26	
Oligochaeta spp.			13	51	
Macoma balthica			11		
Mytilus edulis juv.	7				
Heteromastus filiformis		43		2	
Marenzelleria c.f. *viridis*	2	43			
Hediste diversicolor			8	14	
Coleoptera spp.					12
Neomysis integer					41
Palaemonetes varians					3
Gammarus tigrinus					4

Subtidal sediments

The areas at -10 m depth (SKN- sea chart zero) with coarse sand and stable stone layers are inhabited by a special community, which is adapted to living in strong currents. The most dominant species, which are mentioned in Table 3, are sessile, epibenthic suspension feeders covering most of the stony surfaces. According to the dredge data from these sites the hydrozoan *Hartlaubella gelatinosa* occurred in this biotope in large numbers. The hydroids, because of their dense numbers, provided important structures for amphipods, polychaetes, juvenile *Mytilus edulis* and juvenile threatened fish (*Liparis liparis*, 25 ind./site). In addition to these species, *Palaemon longirostris* appeared to favour the stony structures, although it was less abundant. Other species feed on the hydroids, such as the mollusc *Tergipes* cf. *tergipes*. *Pholis gunnellus*, a characteristic fish species of stony areas, was found only in that biotope.

The soft muddy sediments at the upper slopes were similar to the intertidal areas at the low water mark. The most dominant species (43% dominance, both) were *Marenzelleria* c.f. *viridis* and *Heteromastus filiformis* (occurrence 100% and 92%, respectively). Both species occur in high abundances in most mesohaline, subtidal sediments in the Weser estuary.

Maximum density of *Marenzelleria* c.f. *viridis* reached 1983 ind./m² and *Heteromastus filiformis* achieved 2513 ind./m². *Corophium volutator* was less abundant than in intertidal areas, with a maximum density of 580 ind./m². *Crangon crangon* represented an abundant epifaunal species with a maximum number of 1001 ind./site. A maximum of 409 ind./site was found in the deep subtidal areas. Another characteristic species of this area was the polychaete *Neanthes succinea*, which occurred in this biotope frequently (83%) with a maximum of 223 ind./m².

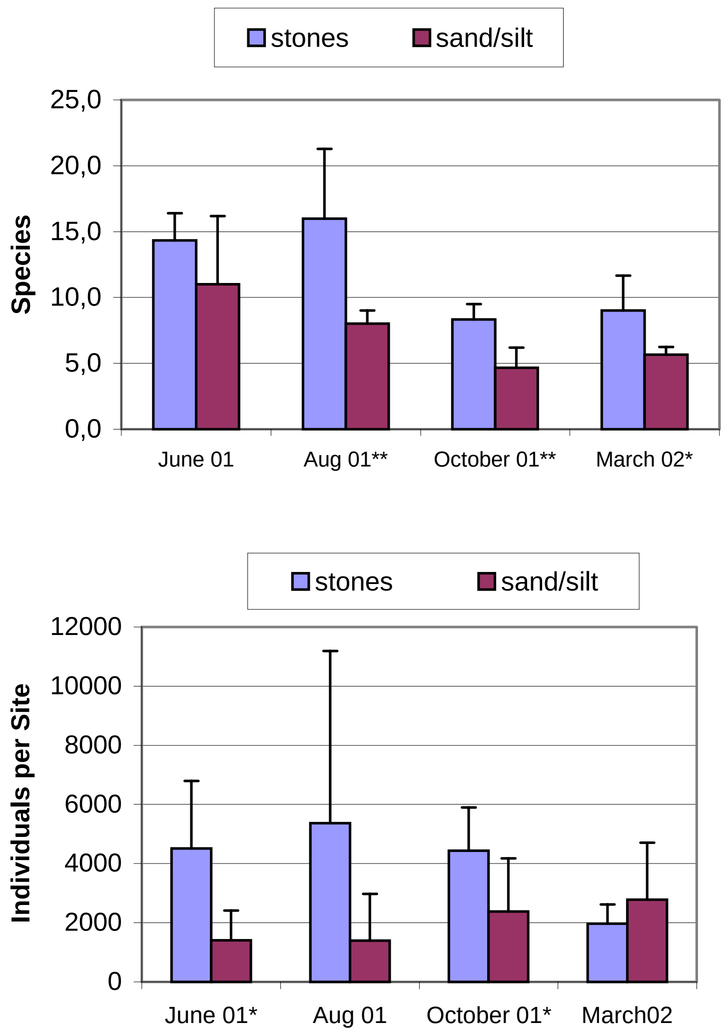


Fig. 10 Species number and density of deep and shallow subtidal sediments during the sampling of 2001 to 2002 (Mean indicated by columns (+SD), grab samples, n =3 sites, * p< 0.1; ** p< 0.5, Mann Whitney).

The differences between the deep subtidal areas and the shallow subtidal sites are obvious. In Fig. 10 a comparison of the different sampling periods in 2001 is presented. The deep areas with stony substrates had higher numbers of species at all times of the year. Significant differences were found in August and October 2001 and March 2002 (Fig. 10). The individuals showed significantly higher numbers in June and October 2001.

In Fig. 11 all sites of soft sediments (grab, corer samples, individuals per m², June 1997, 1998, 2002) were analysed for their similarity. The cluster show a clear separation between intertidal and subtidal sites (dotted line). A further differentiation by depth gives a gradient from upper intertidal to deep subtidal (marked by an arrow).

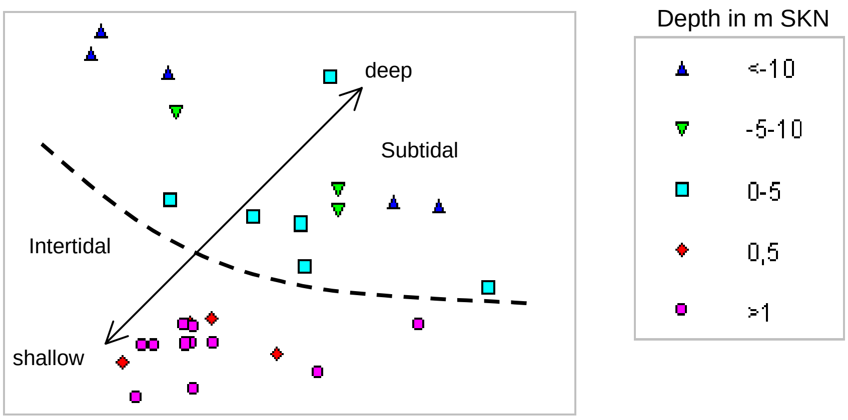


Fig. 11 MDS Plot based on Bray Curtis similarity of quantitative samples (grab samples, corer samples, data from June 1997, 1998, 2001, 4th root transformation), position of site (depth in m SKN).

Intertidal flats

The intertidal mudflats of the Weddewarden area are dominated by the amphipod *Corophium volutator* (52% dominance of individuals, Table 3). This species had a maximum abundance of 14603 ind./m² at W1b in 1998 and was present at every site during sampling. The species is often accompanied by endobenthic *Macoma balthica* (12019 ind./m² maximum), *Heteromastus filiformis (*2435 ind./m² maximum)*, Hediste diversicolor* (1431 ind./m²) and oligochaetes (8269 ind./m²). All these species are deposit or sediment feeders. This is in contrast to the suspension feeder dominated subtidal area.

The intertidal flats can be subdivided into different assemblages, which are related to the sediment types. In the more sandy areas away from the groynes, the species *Arenicola marina* and *Pygospio elegans* occur. The muddy areas along the low water mark and next to the groynes are dominated by *Heteromastus filiformis* and several species of oligochaetes. It was obvious that *Corophium volutator* had a preference for mud with a certain percentage of sand, most probably to gain more stability when burrowing. The soft mud had reduced abundances of this species. Small patches of coarse sand washed onto the shore showed few macrobenthic species. Also, very few *Bathyporeia* spp. were found in these dynamic, unstable sediments.

The distribution within the intertidal flats linked with sediments and distance from the shore is represented in the MDS plot of Fig. 12 . The soft mud in the lower intertidal (W1c, 2c, 3c) is well separated from the central sites (W1b, 2b, 3b) and the sites close to the high water mark (W1a, 2a, 3a). The site W2a shows a high similarity to W2c which separates it from the a-sites group.

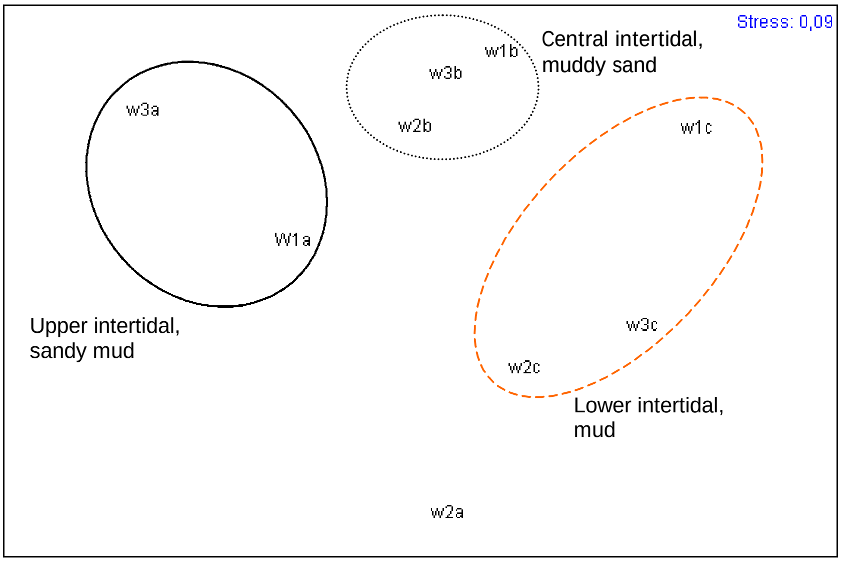


Fig. 12 Similarity of the benthic community at 9 intertidal sites (sediment corer data from July 1998, all sites, Bray Curtis similarity, 4th root transformation).

Although the survey covered only a few kilometers of the estuary, there were some obvious differences in the abundance of some species along the estuary. There was a reduction in abundance of *Littorina* sp., *Macoma balthica,* and *Scrobicularia plana* at the southern sites. Others, such as *Petrobius brevistylus and Manayunkia aestuarina* were found only in the south of the survey area.

Supratidal

As mentioned above, the supratidal areas were found to contain natural reedbeds (*Phragmites australis, Bolboschoenus maritimus),* which are gradually mixed with salt marsh vegetation and sandy beaches towards the upper supratidal. Next to these natural gradients some harsh borderlines of stony protection walls between intertidal flats and salt marshes have been installed. A major habitat is the mass of debris washed upon the shore, producing mats of different decaying stages. The amphipod *Orchestia gammarellus* is the most dominant species in the debris at all stages and on all sediments. *Platorchestia platensis* is less abundant but common at most of the sites. Arthropods such as Coleoptera, Heteroptera, Arachnida and Collembola are less abundant taxa. The terrestrial influence from the salt marshes is obvious as shown by the high number of insect taxa.

A special habitat in between the reedbeds close to mean high water level is provided by algae mats of the green alga *Vaucheria* spp., which is used as a feeding resource by molluscs such as *Alderia modesta* and *Limapontia depressa*, both specialized, endangered brackish species. Maximum densities of these species were 80 ind./m² and 15 ind./m² respectively.

In Fig. 13 the different sub communities are added to the cross section from the dykes to the deep subtidal. The species shown in the figure have been selected by major dominance and occurrence, when present in several sub-communities.

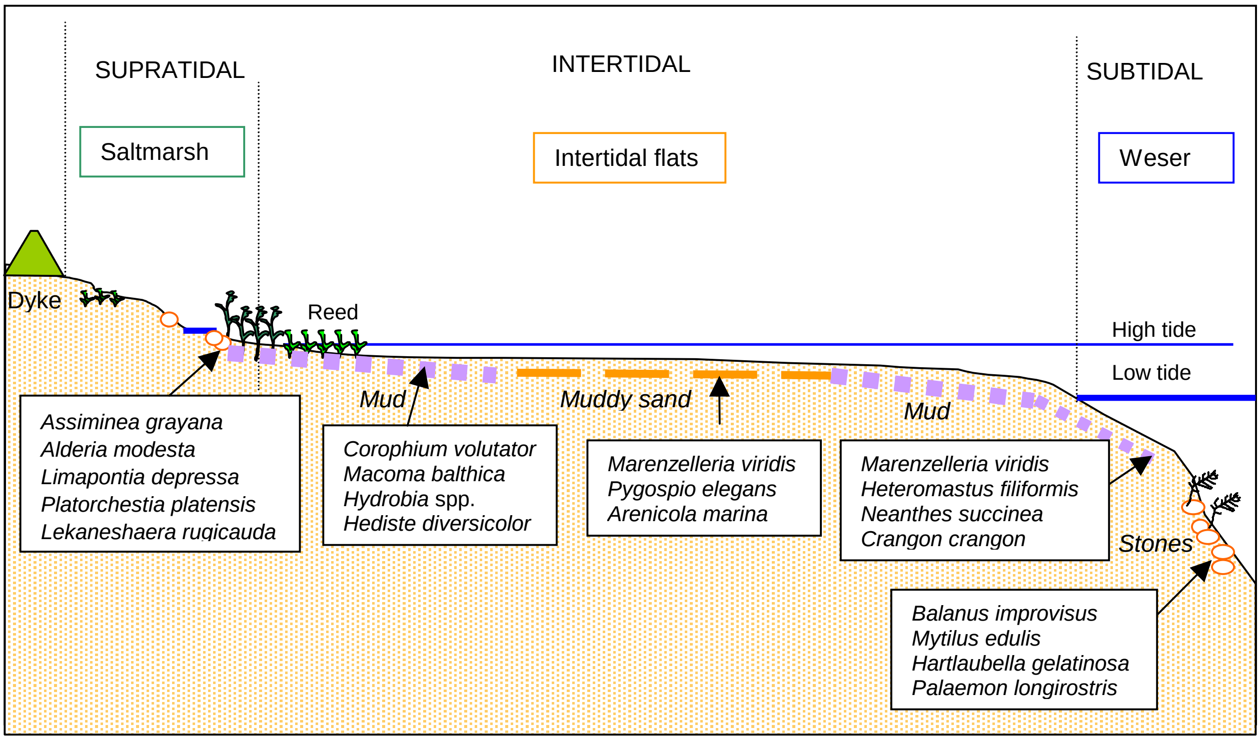


Fig. 13 Benthic assemblages along a cross section of the mesohaline zone of the Weser estuary (habitat of selected species is indicated by its maximal abundance).

Groynes

The groynes divide the flats into sections of about 500 m and provide artificial hard substrate for the species. They can be separated into a supratidal, intertidal and subtidal part. In Fig. 14 the separation of the sub-communities is presented. The overlap of species relates to the gradient of tidal range.

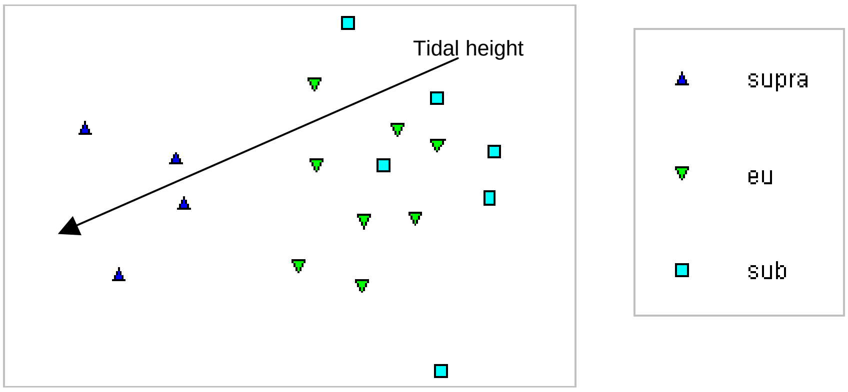


Fig. 14 Sampling sites on the groynes separated into subtital, intertidal and supratidal benthic assemblages (hand collection data, Bray Curtis similarity, presence-absence transformation).

At the low water mark the groynes show different degrees of age and destruction with repaired sequences apparent. The intertidal part was obviously the oldest and its destruction produced pools and lagoons between the stones. The subtidal species (hydrozoans) were registered in these sections. The description of the differences in the colonisation of certain parts of the groynes is schematically highlighted in Fig. 15 with the main habitats of a groyne in the mesohaline zone.

The supratidal part is similar to supratidal shore areas covered by stony constructions of shoreline protection. The basalt stones are not colonised except for some leeches or algae. The cracks between the stones are filled with debris and mud or covered by salt marsh plants and are inhabited mainly by arthropods and some gastropods. The species mentioned in Fig. 15 colonise all supratidal areas with a mixture of artificial hard substrates, mud, vegetation and debris. The intertidal part from 50 cm below high tide to almost low tide is covered with *Fucus vesiculosus*. The algae provide structures and feeding resources for crustaceans and gastropods. *Gammarus marinus*, *Melita palmata* and other amphipods feed on the thalli. The decapods *Carcinus maenas* and *Eriocheir sinensis* use the structures to hide, especially during low tide.

The areas at the low water line are strongly influenced by currents and therefore *Fucus vesiculosus* is absent. *Littorina* sp. was present on the stones with an abundance up to 25 ind./m². *Mytilus edulis* and *Balanus improvisus* cover most of the hard substrates, preferring the cracks and sheltered holes. Abundance is estimated at up to 120 ind./m² (*Mytilus edulis*) and 5500 ind./m² (*Balanus improvisus).* In the deeper parts of the groyne general abundance declined rapidly.

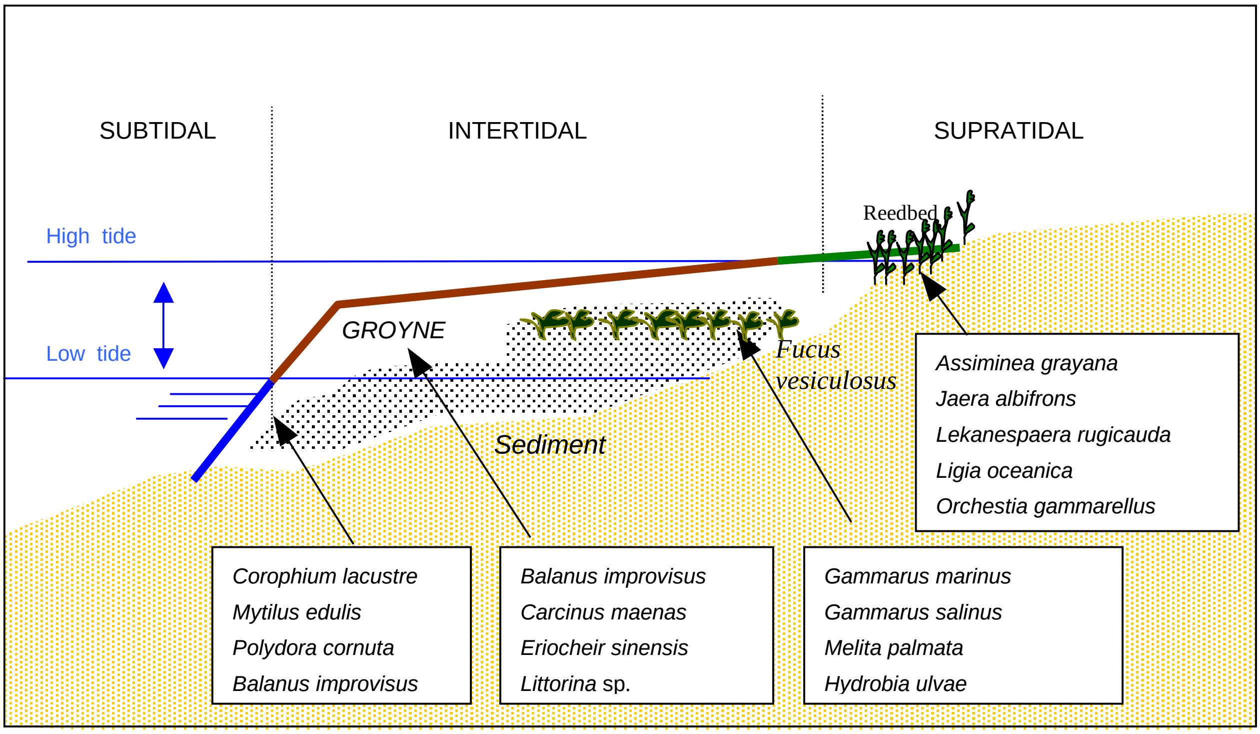


Fig. 15 Spatial distribution of benthic assemblages on a groyne in the mesohaline zone of the Weser estuary (maximal abundance indicates habitat of selected species).

Lagoons

The lagoons combined a variety of different biotopes in a small area. Subtidal sediments with stones, intertidal sediments with stones and supratidal reedbeds, algal mats and mud in a close mixture provided habitats for many species in a small area. The spatial differentiation followed basically the same rules as described for the whole study area. The vertical distribution in the lagoon was similar to the sediments and to the rocky shores on a small scale. There was a higher abundance of *Manayunkia aestuarina* in the lagoon sediments than in any other biotope (962 ind./m²). *Nereis virens* was recorded only under the stones of the lagoons. Besides those, most other species found in the lagoon were also apparent in the surrounding areas.

Salt marsh ditches

The ditches are long, straight lines of tidal water bodies with steep edges. The slopes are most of their length covered by reedbeds (*Phragmites australis*). During low water only a few dm of water remain in the ditches. The main function of the ditches is to drain water away from the foundation of the dykes and low areas. The colonisation by benthic invertebrates was poor compared to similar water bodies beyond the dykes, which, being off the tidal reach, contain fresh water. Brackish water crustaceans such as *Neomysis integer*, *Gammarus salinus* and *Gammarus tigrinus* were abundant. *Palaemonetes varians* occurred mainly in these biotopes. The insect taxa Coleoptera and Heteroptera were frequently found in these diluted, brackish habitats. Chironomids and oligochaetes were abundant in the muddy sediments of the ditches. Natural creeks in the same salinity zone are absent due to a long tradition of farming and coastal protection in that area.

Fort

The Fort was a military base from 1871 and was destroyed after the first World War. The concrete basement and massive stone cubes are covered by hydroids in the subtidal reach, by a thick *Fucus vesiculosus* layer in the intertidal and with green algae (*Enteromorpha* spp.*)* and leeches in the upper supratidal area. In Fig. 16 the vertical distribution is presented schematically.

The strong influence of waves hitting the stones made differences between sheltered and exposed habitats obvious. Exposed habitats were colonised by *Elminius modestus* and *Semibalanus balanoides*, with the sheltered areas being preferred by *Balanus improvisus*. The zonation will be compared to natural rocky coastlines in chapter 5.

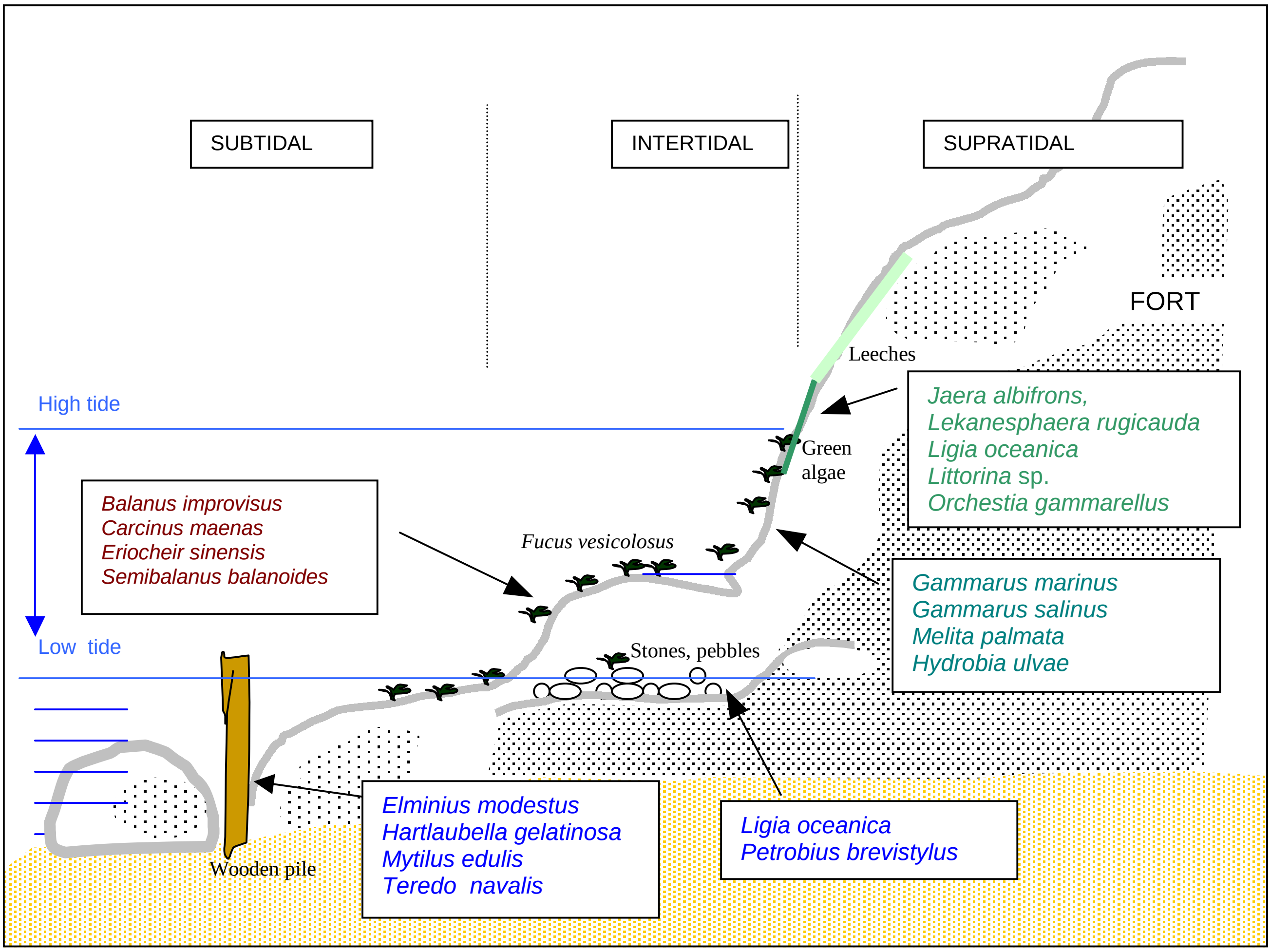


Fig. 16 Vertical distribution of invertebrates on artificial hard-bottom substrate (fort ruins) in the mesohaline zone of the Weser estuary (maximal abundance indicates habitat of selected species)

Discussion

The spatial distribution of benthic invertebrates in estuarine regions was investigated extensively by several authors, such as HOLME (1949), DÖRJES & HOWARD (1975), RISTICH et al. (1977). Most of the investigations emphasised the salinity gradient from fresh water to marine conditions. They found strong correlations to the benthic assemblages in an along-estuary gradient (BOYDEN & LITTLE 1973, DÖRJES 1978, JONES et al. 1986). The ecology of mudflats in estuaries has been subject to the early surveys of REMANE (1940), REES (1940), SPOONER & MOORE (1940) and BEANLAND (1940). More recent research on benthic distribution in mudflats was presented by REISE (1991, 1985) and TALLEY et al. (2000). Besides salinity, the sediment, water depth and distance from the shore were found to be most relevant for spatial distribution (COLEMAN et al. 1978, JONES et al. 1986, GARRABOU et al. 2002). The estuarine community on rocky shores is additionally controlled by current velocity and turbidity (BOYDEN & LITTLE 1973). Biological interactions within the biotopes and the influence and control by predators contribute additional aspects to benthic distribution over time (REISE 1985, SARDA et al. 1998).

Several authors have investigated the benthic invertebrates of the Weser estuary with a focus on intertidal mudflats (MICHAELIS 1973, HAUSER & MICHAELIS 1975, DÖRJES 1978, KOLBE & MICHAELIS 2001). The community of the tidal channel system was partly described by SCHRÄDER (1941), DITTMER (1981), HEIBER (1988) and GOSSELCK et al. (1993).

In this survey the mesohaline benthic community of the Weser estuary was presented to include the different biotopes of subtidal, intertidal and supratidal areas. This approach aims to integrate habitats in the upper tidal reach and habitats of anthropogenic structures to get a more comprehensive picture of the mesohaline area.

Vertical distribution

The communities of the different biotopes showed clear differences along a vertical gradient, and with varying substrates, distances from the shore and exposure to the currents. Additional to the main sections of subtidal, intertidal and supratidal areas, there were aspects of more detailed gradients.

Water depth is closely correlated to the distance from the shore, when looking at the cross sections of the shore and the groynes. Hydrology (tidal currents, waves) controls sedimentation and grain size composition. Usually the water energy decreases from the deep areas to the more sheltered, shallow areas and accordingly sediments become finer (DÖRJES 1978, GRAY 1981). The typical sequence was found to be reversed in this area, most probably due to the influence of the groynes.

The groynes create new currents and sheltered areas, which create new patterns of sedimentation. A major consequence of this is the soft mud deposited at the low tide line, which is untypical of natural flats and demonstrates the influence of these structures on the benthic environment (compare DÖRJES 1978, McLUSKY 1989).

As shown in chapter 3, there was a higher percentage of sessile, epibenthic filter feeders represented by taxonomic groups such as bryozoans and hydrozoans in the deep subtidal areas compared to the shallower areas. This is due to their sensitivity to high sedimentation and sediment coverage. The deposit feeders, however, had a higher percentage in the intertidal and shallow areas, because they benefit from organic input by sedimentation (MAURER et al. 1979, JONES et al.1986, DEGRAER et al. 1999).

Further differences between the deep and shallow areas show up at the species level, but with the same background. *Mytilus edulis* (epibenthic, sessile, filter feeding) represents a subtidal, bivalve species, whereas *Macoma balthica* (endobenthic, motile, deposit feeding) represents a bivalve from the upper intertidal area in this investigation.

Most of the sessile suspension feeders need hard substrates to attach to, which are generally absent in the intertidal areas (except some shells, small stones) and less frequent in the shallow subtidal area. Better conditions for settlement are given at the lower slope with strong currents and stony surfaces. The less diverse and abundant settlement on the groynes at that depth might be due to the strong exposure of these structures to the tidal currents. With the groynes, anthropogenic hard substrate is available from the subtidal region up to the supratidal. However, *Mytilus edulis* is restricted to a depth close to the low water line. For sessile epibionts, the spatial distribution is often correlated to the time of water coverage in the tidal cycle and current velocity. Quality of protection mechanisms against drying or predation controls their distribution in the intertidal zone, and currents or turbidity restrict the spread in the subtidal areas (LUTHER 1987, REISE 1985, RAFFAELI & HAWKINS 1996).

The restriction of *Neanthes succinea* to the subtidal areas and the main occurrence of *Hediste diversicolor* in the intertidal areas were obvious, but the reasons for their distribution are unclear (compare REES 1940, DÖRJES 1978). Feeding habits of both species are similar and perhaps by separating their range the species avoid competition.

Abiotic factor combinations, such as water depth, water energy, sediments and inundation time, control the distribution patterns. BEANLAND (1940) describes this combination with decreasing shelter towards the river and distance from the high tide mark. This is similar to what was found by HOLME (1949), BOYDEN & LTTLE (1973) and REISE (1987).

Sediments

In addition to the vertical gradient, there are also geographical patterns that are relevant to the benthic community. The sediment characteristics are presented in Table 4 and the relating community patterns from the intertidal flats are described before. The sediment analyses gives 3 main sediment types which can be linked to certain sub-communities. KOLBE & MICHAELIS (2001) separated the mudflats further upstream into 6 sub-communities adding the reedbeds and oligohaline mudflats to their survey. As found in this survey a vertical zonation from the shore to the river was a main distribution factor for benthic assemblages.

The mudflat community in this survey revealed a similar species composition to other estuaries in the North Sea area (BEANLAND 1940, HOLME 1949, BOYDEN & LITTLE 1973, DÖRJES 1978). In Table 4 the dominant and main characteristic species of the analysed sediments are listed and compared to the Severn estuary. The fluid mud at the low water line is unstable and therefore even the abundance of mud-preferring species was reduced (*Corophium volutator, Macoma balthica*). A specific colonisation of this mud by *Diastylis rathkei* as found by BOYDEN & LITTLE (1973) was not detected.

Table 4 Characteristic species of the mesohaline sediments of the Weser estuary (this survey) and the Severn estuary (BOYDEN & LITTLE 1973).

	Subtidal		*Intertidal*		
Weser	**Stony, coarse**	**Muddy sand**	**Sand**	**Muddy sand**	**Mud**
Dominant species	*Balanus improvisus* *Mytilus edulis* *Hartlaubella gelatinosa* *Electra crustulenta*	*Crangon crangon* *Heteromastus filiformis* *Marenzelleria viridis*	---	*Marenzelleria viridis* *Pygospio elegans* *Arenicola marina* *Macoma balthica*	*Oligochaeta* spp. *Heteromastus filifor.* *Corophium volutator* *Hediste diversicolor*
Typical, rare or local species	*Palaemon longirostris* associated species to hydroids and *Mytilus edulis*		*Bathyporeia pilosa*	*Scrobicularia plana*	
Severn	---	----	*Bathyporeia pilosa* *Haustorius* sp. *Nephtys cirrosa*	*Corophium arenarium* *Arenicola marina* *Nephtys hombergi* *Macoma balthica*	*Corophium volutator* *Hediste diversicolor* *Hydrobia ulvae* *Cyathura carinata* *Retusa obtusa*

The comparison between the two estuaries shows a major similarity between the species found and their preferred sediments. The reason for the absence of species like *Retusa obtusa* and *Haustorius* sp*.* from the Weser data is unclear. *Corophium arenarium* was found in deeper water further downstream with polyhaline salinities. The patchiness of occurrence for species such as *Scrobicularia plana* is similarly described by BOYDEN & LITTLE (1973).

Salinity

Although the salinity is the major factor for estuarine benthic distribution (REMANE 1940, RISTICH et al. 1977, McLUSKY 1989), it was not a target of this survey. The upstream penetration of estuarine species is extremely variable during the seasons and over the years. Therefore, detailed abiotic information and salinity data for several annual cycles are needed (BOYDEN & LITTLE 1973). For the Weser estuary the distribution of species along the salinity gradient was described by DITTMER (1981) and GOSSELCK et al. (1993). KOLBE & MICHAELIS (2001) found an upstream shift of benthic assemblages in a long-term survey of intertidal flats. BOYDEN & LITTLE (1973) emphasised strong variations in the along-estuary ranges of estuarine species in British estuaries.

A salinity gradient across the estuary, from deep waters to the shallow intertidal, is mentioned for stratified estuaries by McLUSKY (1989). The salinity data showed lower values in the ditches than in the river itself, due to dilution by surface water (MÜLLER 1994, MORGENTHAL 1995).

Therefore, species with high tolerance to fresh water influence, such as *Palaemonetes varians, Gammarus tigrinus and Gammarus duebeni* were caught mainly in the saltmarsh ditches. The high percentage of insects in this biotope indicates the transitory status of the ditches between estuarine and freshwater habitats. The identification of all insects (Diptera larvae) and oligochaetes to the species level would possibly help to clarify this aspect.

Artificial structures as benthic habitats

The importance of stable, hard substrates such as stones and boulders for species diversity, especially in soft bottom dominated communities, was demonstrated by KÜHNE & RACHOR (1996). The role of hard substrates in estuarine soft bottom dominated areas is sparsely described and probably strongly underestimated, because of the difficulties in quantitative sampling (WARWICK & DAVIES 1977, DAHL & DAHL 2002).

Natural hard substrates in estuaries are very sparsely documented. They probably cover only small areas in German estuaries and their importance for estuarine benthic species is completely ignored. Besides the lack of precise information about position and area of natural hard bottoms, such as mussel beds, glacial stone layers, shell layers, peat and clay substrates, there is no certain knowledge of their stability over time. In the Weser estuary, diverse and abundant colonised hard substrates have been found in the polyhaline and mesohaline areas (KÜFOG, unpublished data). Recent research emphasises their function as substitutes for benthic habitats and presents new aspects of evaluation in a restoration context (REILLY & SPAGNOLD 1999, LERBERG et al. 2000, ZAJAC & WHITLACH 2001).

The habitat function of artificial structures in estuarine biotopes is demonstrated in this survey by the number of species, which are related to hard bottom structures in the intertidal and the supratidal zone. Brackish water species and endangered species emphasise the value of such biotopes in industrialized estuaries. The change to less favourable conditions for estuarine benthic invertebrates in the industrializing process has been subject to many surveys, with the main focus on the pollution effects on soft bottom communities (PEARSON & ROSENBERG 1978, MICHAELIS 1981, 1994, McLUSKY 1989). However, the effects of pollution or dredging on small-scale hard bottom communities and its consequence for estuarine diversity are sparsely investigated.

In Table 5 evaluation criteria of benthic habitats are given for the different biotopes and grouped into natural (left) and artificial biotopes (right). The supralitoral shores were split into artificial stony slopes and natural reedbeds and beaches. Together the natural habitats were inhabited by a mean of 38.8 species whereas the artificial biotopes yielded 29.8 species. The number of brackish water species, endangered species and exclusive species is higher in the natural biotopes. Some species found in the artificial biotopes indicated certain abiotic parameters, such as freshwater influence. A comparison to a natural equivalent is not possible, because natural creeks are absent from the investigation site.

Table 5 The importance of different biotopes as a habitat for estuarine benthic species.

	Natural habitats				**Artificial habitats**				
Criteria	**Subtidal deep**	**Subtidal shallow**	**Intertidal**	**Supra-tidal (reedbed)**	**Groynes**	**Lagoons**	**Fort**	**Ditches**	**Supratidal Stone walls**
Species total	42	44	44	25	45	32	26	24	21
Brackish water species	14	12	14	7	14	16	9	9	4
Species endangered	6	2	6	5	6	6	2	3	2
Species exclusive	*Balanus crenatus* *Tergipes tergipes* *Electra pilosa* *Petricola pholadiformis*	*Farella repens* *Gastro-saccus spinifer*	*Bathyporeia sarsi* *Scoloplos armiger* *Tetra-stemma melano-cephalum*	*Alderia modesta* *Limapontia depressa*	*Praunus flexuosus*	*Mana-yunkia aestuarina*	*Elminius modestus*	*Sigara. lateralis* *Gam-marus duebeni*	*Ligia oceanica*
Importance function for non benthic species	Fish nursery, shelter within hydroids	Feeding areas, nursery for fish	Fish nursery, Feeding areas for birds	Breeding area for birds	Resting areas for birds	Fish habitat, Spawning area	---	Fish habitats	---
Variation within biotope maximum value status	Dense hydroids-, Mytilus-coverage.	----	Stable muddy sands	*Vaucheria* mats	High age, degree of destruction *Fucus* coverage	Variety of habitats	Variety of habitats	Low mainten-ance intensity	High age, degree of destruction, Variety of habitats

A substitute implies that there has been a natural equivalent of this biotope in former days or other regions. If so, the substitute took over the original function by providing similar habitats for the community. But, if the artificial structure puts a new structure or substrate into an area, then new species, not native to the area, may be introduced to the system, thus influencing others by predation or competition (WOLFF 1999, REISE et al. 1999).

Lagoons and tidal pools used to be wide spread in a drowned river valley type estuary such as the Weser (BUSCH et al. 1989). These biotopes have disappeared from the industrialised estuaries and artificial water bodies (McLUSKY 1989, BACHELET et al. 2000). The groynes or shoreline protection facilities added new structures to the estuary and created tidal lagoons as substitutes for original habitats.

The fort, however, with its massive hard substrates, similar to a rocky coast, is an entirely artificial structure, as no habitat of this type occurred naturally in the estuary.

Subtidal groynes and natural stony slopes from the same depth may reflect differences between natural and artificial hard substrates. However, comparisons are weak because of the differences in sampling methods used. A higher species number and abundance were registered on the natural stony sediments (42 taxa on the natural stones, 10 taxa on the subtidal groynes). The structurally important species such as *Hartlaubella gelatinosa* and *Mytilus edulis* did not provide the important structures on the groynes as they did in the natural stone areas.

Soft sediments dominate the intertidal flats. Most of them do not have natural hard bottom substrates, except some stony beaches, open shell layers and the eroded walls of creeks and channels. The effect of new structures in monotonous areas such as mudflats usually creates a higher diversity, which is not automatically of a high value. The effect, for example, of more hiding places for predators in the groynes, might change the natural balance of the food chain or even harm keystone species. These details cannot be analysed with this survey and need further investigation.

An evaluation of the estuarine condition based on biological parameters such as benthic macrofauna is an international target of European nature conservation (Water Framework Directive, Habitat Directive). The first step towards an assessment based on invertebrate communities and species is the inventory of present day, estuarine communities. The spatial distribution splits into a vertical distribution controlled by water depth, sediments, tidal influence, and a geographical distribution controlled by sediments (substrates) and salinity. Artificial substrates are wide spread in the Weser estuary as in most industrialised estuaries of today. They were found to provide benthic habitats as substitutes for rare natural structures and therefore they were included in this inventory. To improve the ecological situation of estuarine habitats protection or restoration plans for the small areas of natural hard bottom habitats that remain need to be designed and implemented.

Acknowledgements

We would like to thank the harbour authority of Bremen (bremenports GmbH) namely Mr. U. von Bargen for supporting this paper and for the data release. Many thanks also to the crew of the bremenports-vessel “Hol Deep” and to the KÜFOG team for being such a great help during the surveys, in the field and in the laboratory.

Appendix

Table A1 Species list of all biotopes (abundance classes per site and quantitative data per m²: 1- single, x- 2-10, xx- 11-100, xxx- 101-1000, xxxx- > 1000 individuals per site). B- genuine brackish water species (REMANE 1940), RL- Red List Status: 3- threatened, Vu- vulnerable, Su- suspectable, P- potentially threatened, G- geographical restricted (RACHOR 1998).

Taxa	B	RL	subtidal	intertidal	supratidal	groynes	lagoon	fort	ditches
Plathyhelminthes									
Plathyhelminthes sp.									x
Cnidaria									
Cordylophora caspia	B	G	1				x		
Eudendrium sp.			1						
Hartlaubella gelatinosa			xx			xx	x	x	
Laomedea flexuosa			x						
Obelia dichotoma			x						
Obelia longissima			xx			xx			
Obelia geniculata									
Podocoryne c.f. *borealis*			x						
Sertularia cupressina		3	x			1			
Nemertini									
Nemertini sp.				x					
Tetrastemma melanocephalum				x					
Bryozoa									
Electra crustulenta	B		xxx			xxx	x	xx	
Electra pilosa	B		1						
Farella repens			x						
Walkeria sp.			xx			xx			
Mollusca									
Alderia modesta	B	3		x	x		x		
Assiminea grayana	B	3		x	xx	x	xx		x
Hydrobia ulvae			x	xxx	x	xx	xx		x
Hydrobia ventrosa	B	Vu		x	1	xx	x		
Limapontia depressa	B	Vu		x	xx		x		
Litorina saxatilis		3	1		x	xx		x	
Macoma baltica			x	xxxx	x	x	x		
Mya arenaria			x	x					
Mytilus edulis			xx	xxxx		xxx		xx	
Petricola pholadiformis		G	x						
Potamopyrgus antipodarum	B		xx	x					x
Scrobicularia plana		3	x	x					
Teredo navalis			x					xx	
Tergipes c.f. *tergipes*			x						
Polychaeta									
Arenicola marina			x	xx					
Eteone longa			x	x					
Heteromastus filiformis			xxx	xxx	xx	x	x		
Manayunkia aestuarina	B			x					
Marenzelleria c.f. *viridis*	B		xxx	xxxx	x	x	x		x
Neanthes succinea			xxx	x					
Nephtys hombergi				x					
Hediste diversicolor			x	xxx	x	x	x	x	x
Nereis succinea			xx			xx			
Nereis virens				1			x	x	
Phyllodoce mucosa			x						
Polydora ciliata			xx						
Polydora cornuta			xx	xxx		x			
Polydora ligerica	B		x						

Table A-1 (continued)									
Taxa (Polychaeta continued)	**B**	**RL**	**subtidal**	**intertidal**	**supratidal**	**groynes**	**lagoon**	**fort**	**ditches**
Polydora pulchra				x					
Pygospio elegans			1	x			x	1	x
Scoloplos armiger				x					
Oligochaeta									
Chaetogaster sp.									x
Enchytraeidae					xx	x			
Naididae sp.									x
Oligochaeta sp.	(B)		x	xxxx	x	x	x	x	x
Paranais litoralis	B		x					1	
Tubifex costatus	B								x
Tubificoides benedeni			x		x	x			x
Crustacea									
Balanus crenatus			x						
Balanus improvisus	B		xxxx	xxxx	xx	xxxx	x	xxxx	
Bathyporeia pelagica			1		x				
Bathyporeia pilosa	B		x	x			x		
Bathyporeia sarsi				x					
Carcinus maenas			x	xx		xx	xx	xx	x
Chaetogammarus marinus				x	xx	xx	xx	xxx	
Corophium lacustre	B	3	x	xx					
Corophium volutator			xx	xxxx		x	xx	x	xx
Crangon crangon			xxx	xx		xx	xx		x
Elminius modestus					x	x		x	x
Eriocheir sinensis	B		x	xx	xx	x	xx	xx	x
Gammarus tigrinus	B								xx
Gammarus locusta					x	x	x	1	
Gammarus salinus	B		xx	xx	x	xx	xx	xx	
Gammarus zaddachi	B		x			xx			
Gammarus duebeni	B	Vu							x
Gastrosaccus spinifer			x						
Jaera albifrons			x	x	x	xx	xx	x	
Leptocheirus pilosus	B		1	x					
Ligia oceanica	B	P			x	xx	x	xx	
Liocarcinus holsatus			x						
Melita palmata	B					xx	x		
Neomysis integer	B		x	x		xx	x	x	xx
Orchestia cavimana					xx	x			
Orchestia gammarellus	B				xxx	x		1	
Orchestia platensis					xx	xx		x	
Palaemon longirostris	B	Vu	xx						
Palaemonetes varians	B	Su				1	x		xx
Praunus flexosus						x			
Semibalanus balanoides					xx	x		xxxx	
Sphaeroma rugicauda	B				x	x	x		x
Insecta									
Carabidae					xxx	1			
Coleoptera					xx	1			xx
Collembola					xx	xx	x	xx	xx
Diptera L.	(B)				x	1	x		xx
Heteroptera									xx
Petrobius brevistylus	B				xx			xx	
Sigara lateralis									x
Staphylinidae					x				

The following species were documented from the area by BFG (1997), Rode et al. 1992 and IFAÖ (unpublished data) and should be mentioned to complete above species list: *Dugesia tigrina* (Plathyhelminthes), *Nucula* sp. (Mollusca), *Scalibregma inflatum* (Polychaeta), *Pristina foreli* (Oligochaeta), *Proasellus coxalis* (Crustacea).

The macrobenthic community in a polyhaline channel system of the Weser estuary: Scales of spatial distribution and diversity

Jan Witt[1, 2], Alexander Schroeder[2], Rainer Knust[2] & Wolf E. Arntz[2]

[1] Küstenökologische Forschungsgesellschaft mbH (KÜFOG), Alte Deichstr. 39, D-27612 Loxstedt-Ueterlande, Germany, Tel.: ++49 (0) 4740/ 1071, e-mail: info@kuefog.de

[2] Alfred Wegener Institute of Polare and Marine Research, Benthic Ecosystems, Columbusstraße, D-27515 Bremerhaven, Germany.

Abstract

The macrobenthic community of a tidal channel system in the Weser estuary (Germany) was investigated with a dense grid of Van Veen grab samples and dredge trawls. Spatial distribution of species was analysed and related to abiotic parameters, such as riverbed morphology, salinity and sediment type. Diversity measures over different scales such as single samples, transects, habitats and large areas were compared. Despite a high variability in abiotic parameters, species showed preferences for certain habitats. Salinity was a major factor for an along-estuary gradient. Sediment composition, channel morphology and hydrology provided factor combinations for specific benthic colonisation. Small areas of biogenic and lithogenic hard substrates, such as subtidal mussel beds or exposed stone layers provide the most important structures for epibenthic assemblages and increase the large area diversity of the estuarine benthic community.

Keywords: Weser estuary, subtidal macrobenthos, diversity, distribution factors, polyhaline channel, estuarine invertebrates

Introduction

Estuaries are unique areas, providing important feeding grounds for birds and fish, as well as supplying various habitats for benthic species (McLUSKY 1989, BARNES 1994). The importance and function of estuarine biodiversity, especially of benthic communities, is given in recent studies (LEVIN et al. 2001, DAYTON 2003). The variability of abiotic conditions and the permanent change between disturbance and succession characterises an estuarine environment, but at the same time makes an investigation of the relationship between the benthic community and the abiotic distribution factors difficult (BOESCH et al. 1976, RAINER 1981, JONES et al. 1986, McLUSKY 1989). The salinity gradient from the river to the sea separates the estuary into different zones, with certain benthic assemblages (REMANE 1940, REMANE & SCHLIEPER 1958, KINNE 1966, RISTICH et al. 1977). In addition to the salinity, water depth and the sediment type are also relevant factors for benthic estuarine communities (BOYDEN & LITTLE 1973, DÖRJES & HOWARD 1975, DÖRJES 1978, WARWICK & DAVIES 1977, COLEMAN et al. 1978, GRAY 1981).

Several authors have investigated the benthic invertebrates of the Weser estuary with a focus on intertidal mudflats (MICHAELIS 1973, HAUSER & MICHAELIS 1975, DÖRJES & REINECK 1977) or subtidal biotopes of the channels (SCHRÄDER 1941, DITTMER 1981, HEIBER 1988 and GOSSELCK et al. 1993).

In this investigation, the benthic community of the “Wurster Arm”, a main tidal channel in the polyhaline zone of the Weser estuary, is surveyed and described for the first time. In order to get basic information on benthic distribution for an impact assessment the survey was initiated by the Bremen Harbour Authority (HBA). Diversity measures over different spatial scales may provide different pictures of the benthic species richness (WHITTAKER 1972). In order to determine the importance of abiotic parameters for species richness, different scales of diversity measures were applied to the data. Point diversity was compared to large area diversity following the definition of GRAY (2000).

Analysis of composition and distribution of the benthic community may help to manage and preserve important brackish habitats by contributing to a database for an adequate management plan for the Weser estuary and the coastal zone.

Material and methods

Survey area

The tidal channel examined in this survey is located in the polyhaline zone of the Weser estuary (Fig. 1). The investigated area is about 15 km long and up to 4 km wide, depending on the morphology of the channel. A widespread channel system from large intertidal flats in the east leads the ebbing tide into the survey area. The “Robbenplate”, a tidal sandbank in the west of the channel, separates the Wurster Arm from the main shipping lane of the Weser during low tide. Detailed information on the morphology and sediment composition will be given in the results chapter.

The tidal amount of water running through the channel of the Wurster Arm varies between 150 and 260 x 10^6 m³ depending on the time of the year and climatic conditions (WSA Bremerhaven, unpublished data from 1999). The ratio of the amount of water between the surveyed channel (Wurster Arm) and the main channel (Fedderwarder Arm) is about 1:1.8. The maximum velocities of tidal currents reach 1.35 m/s about 1.5 hours after slack water (WSA Bremerhaven, unpublished data, 1996). The turbidity of the Wurster Arm varies between 10 and 100 mg/l suspended matter during a tide with tidal amplitudes of about 3.5 m (ZANKE 1998). The turbidity of the mesohaline zone, further upstream, varies between 250 mg/l and 2000 mg/l (WELLERSHAUS 1981). The position of the turbidity zone in the

Weser depends on the amount of freshwater runoff. In wet years, with a high freshwater runoff, the turbidity zone shifts downwards to the south of the Wurster Arm channel (GRABEMANN & KRAUSE 2001).

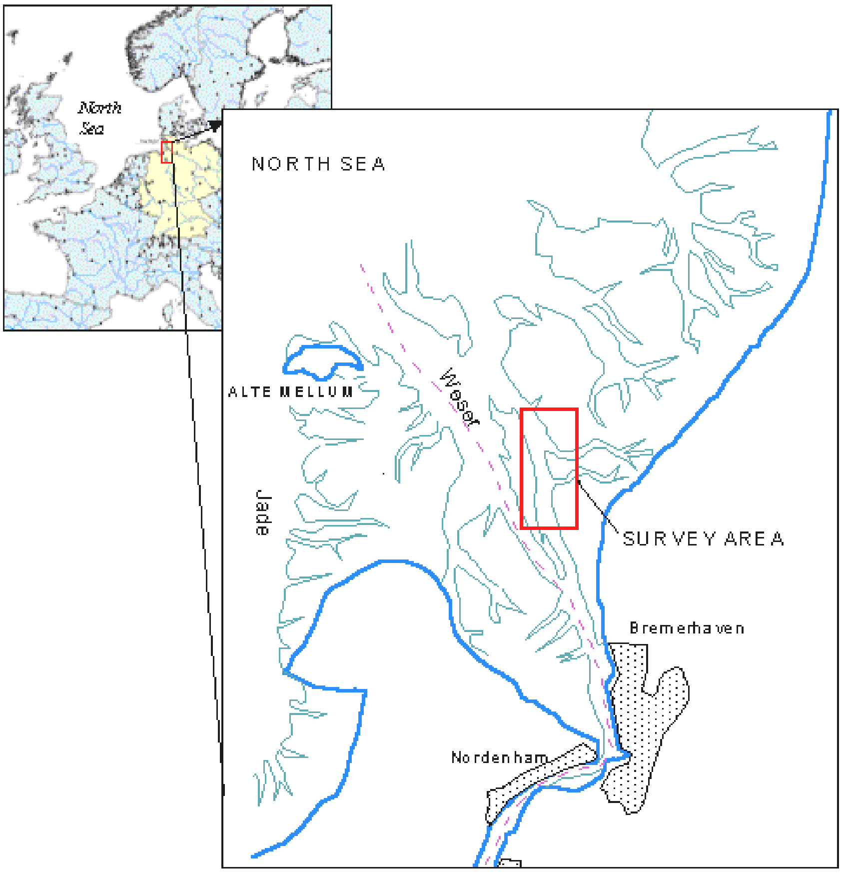


Fig.1 Survey area in the Weser estuary (broken line indicates shipping lane).

Field and laboratory methods

The investigation was carried out between the 22nd and 30th of October 1997. Thirty transects were positioned across the tidal channel with a distance of about 500 m in between. A total of 150 Van Veen grab samples and 45 dredge trawls cover the area from river point km 80 to km 95 (Fig. 2). On each transect 5 grab samples were collected using a Van Veen grab (0.1 m²). On every second transect 3 dredge hauls of 100m length were taken using a frame dredge (1m width, 5 mm mesh size). The outer sampling sites of each transect were positioned on the 4m depth line, thus transects differ in length due to the riverbed morphology (Fig. 2).

Grab samples were sieved in the field using a sieve of 1-mm mesh size and the residue was transferred in seawater containers to the laboratory. After separating animals from the sediment they were stored in buffered formalin (5%) and identified to the lowest possible taxonomic level (normally species). Dredge samples were sorted on board with the storage of animals for identification purposes as described before.

Salinity, pH, temperature and dissolved oxygen of the bottom water (1 m above sediment surface) were recorded at the central position of each transect. Position and water depth of sampling sites were registered by GPS and echosounder of the vessel. An additional grab was taken at the central sites to provide a sediment sample in order to measure the grain size composition and to analyse the total organic matter by the loss of weight on ignition method (BUCHANAN 1984).

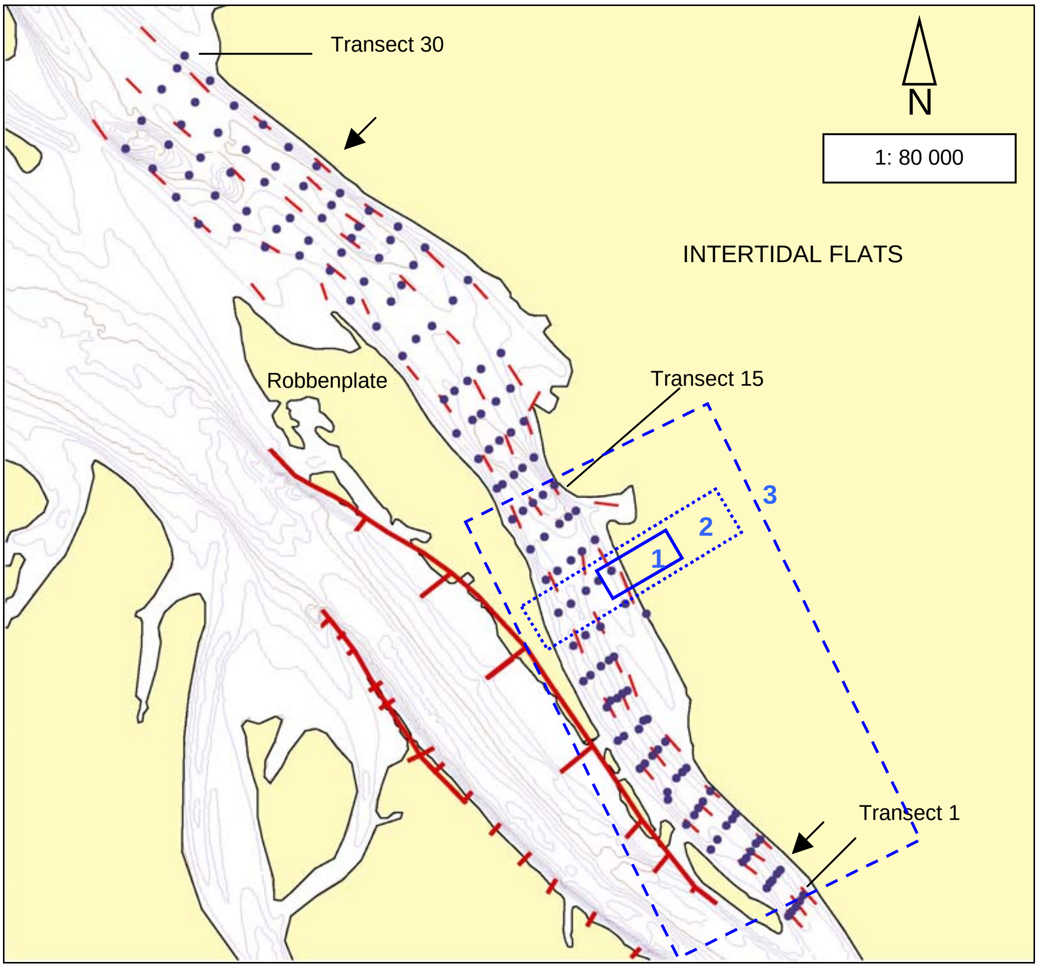


Fig. 2 Surveyed channel Wurster Arm with positions of grab sampling sites (dots) and dredge haul sites (lines), broken frames indicate different spatial scales (s. text), depth contours are given every 2 m, arrows indicate transects 2 and 25 of Fig. 4.

Data analysis

For analysing the endobenthic community grab sample data were used after separating vagile epibenthic species from the data set. Dredge-sample data were used to investigate the epibenthic macrofauna. Pelagic species were excluded from further analysis.

Abiotic data of environmental variables such as salinity, morphology and sediment composition were compared with the faunal data. Ecological classification of species was taken from the literature (HAYWARD & RYLAND 1990, TARDENT 1993, HARTMANN-SCHRÖDER 1996). Cluster analysis and non-metric multidimensional scaling (MDS) were used to identify patterns in the species distribution (CLARKE & WARWICK 1994). Fourth root transformation was applied to species abundance to reduce the influence of dominant species before calculating inter-sample similarity by the Bray-Curtis coefficient (BOESCH 1977). The dredge data were transformed to presence/absence data. Statistical analyses were accomplished using the statistic software PRIMER, v 5.2 (CLARKE & WARWICK 1994, CLARKE & GORLEY 2001).

The number, abundance, presence and dominance of species were compared on different spatial scales. Species number (S), species richness (d) (MARGALEF 1954) and equitability using Pielou`s evenness (J`) (PIELOU 1976) were calculated. Shannon’s diversity index (H`, based on $\log_2$) was used for a comparison of the diversity. Following the terminology of GRAY (2000) 3 different scales of diversity measures were compared (broken frames 1-3 in Fig. 2). First level (1) is the point diversity (single sample, alpha diversity sensu WHITTAKER 1960), second (2) is the sample diversity (in this case the diversity of a transect with 3 to 5 sample units) and third (3) is the diversity of a large area (northern and southern part of the entire channel).

Results

Physical water measurements

The bottom water was well oxygenated in all areas and at all times during the survey with oxygen saturation between 83% and 127% (7.8 to 12.3 mg O_2/l). Neither a gradient nor a relevant oxygen minimum was found in the channel. The temperature of bottom water varied between 12.2 and 13.4°C and the salinity from 17‰ to 30‰. Despite the strong tidal currents a gradient with increasing salinity from the south to the north was identified. The variability between the samples was high, due to sampling at different tides. Fig. 3 shows salinity data from the central stations of each transect.

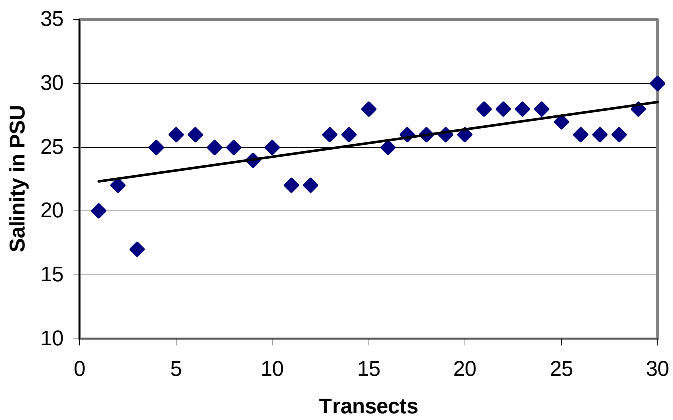


Fig. 3 Salinity of bottom water in the Wurster Arm during the survey.

Morphology

The riverbed is formed by the erosive action of strong currents in the tidal channels, which transport sediments. Consequently, the river morphology and its sediment distribution change continuously (ZANKE 1998). The most common morphological structures in the Wurster Arm channel are the flat, sandy embankments. The northern part of the channel is wider with less steep banks than the southern part, which is narrowed by the nearby Robbenplate sandbank and the intertidal flats. The depth of the channel varies in most parts between 7 and 12 m. Deeps are washed out of the riverbed reaching water depths of up to 18 m. These deeps vary in diameter between 50 and 700 m and may change position and extension during time.

The lateral erosion in places where strong currents hit the embankment creates steep edges of clay or stony surfaces. The depth lines in Fig. 2 (2 m distance) indicate the riverbed morphology. The cross-sections of two transects are shown in Fig. 4. Transect 25 represents the situation in the north with a shallow western slope. Transect 2 represents the channel morphology in the south with steep intertidal edges. The difference in the cross sections from north to south force a high amount of water from the wide and deeper channel in the north through a narrow morphology in the south during flood, which may result in high currents which affect the sediment composition.

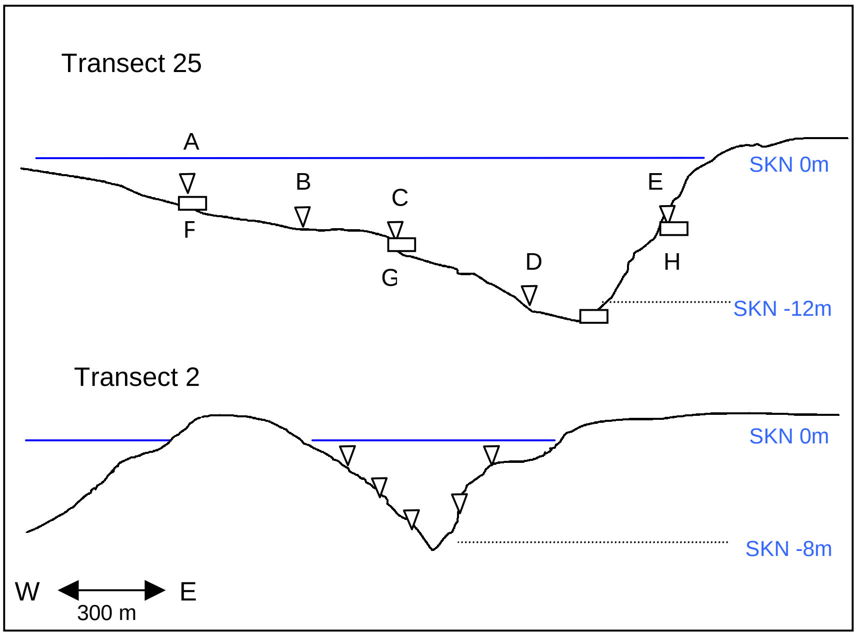


Fig. 4 Schematic cross sections of the survey area at transect 25 in the north and transect 2 in the south (triangles - grab samples, rectangles - dredge hauls).

Sediments

The sediments of the central transect stations were analysed by grain size analysis while sediments of all other stations were classified visually. Results of the grain size analysis present a higher median in the south than in the north (Fig. 5). The percentage of sites characterised by their dominant substrate (Fig. 5) shows that all stony substrates were found in the southern part of the channel. Sites with shells or silt as a major component were more often represented in the north, while sites with clay and coarse sand were more numerous in the south.

Results of the sediment classification have been transferred to a map. In Fig. 6 the most southern part of this map is presented as an example. For the presentation, minor components of the sediments had to be ignored. Most areas had sediments of fine sand with differing percentages of silt. Alternating layers of sand and mud were found at sites with dynamic sediment transport. The centre of the tidal channel, with its strong tidal currents, showed sandy sediments with occasional pebbles or stones. Muddy sands were found along the slope toward the intertidal edges in a water depth of around –4 m SKN. The sediments of the central channel stations were usually coarser than sediment from the shallow sites.

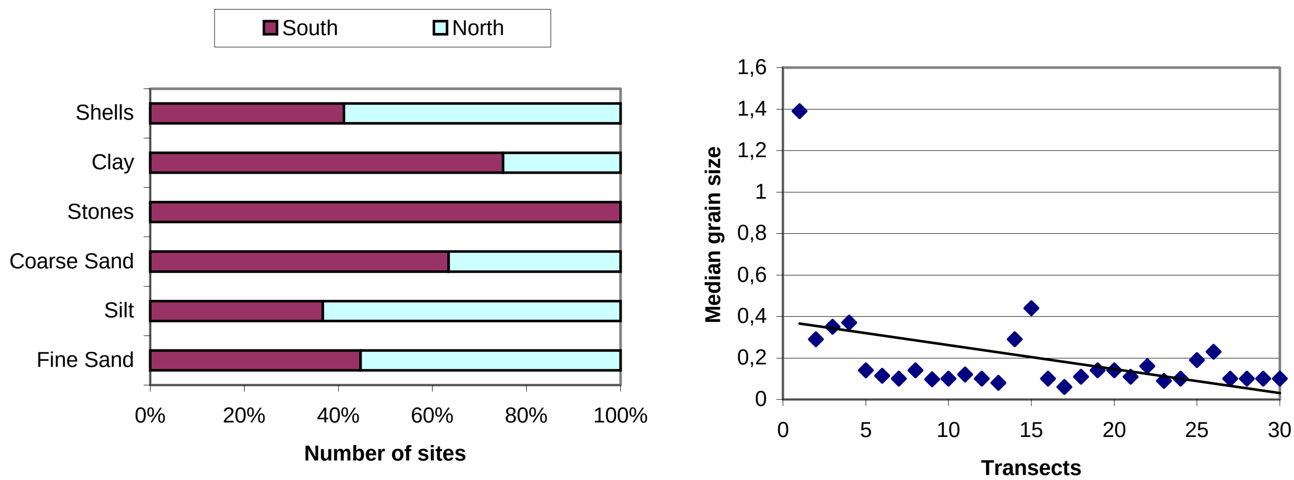


Fig. 5 Distribution of dominant substrates (left - all sites, sediment classification of grab samples, n= 150, south - transect 1-15, north - transect 16-30), median grain size (all transects, central sites 1-30).

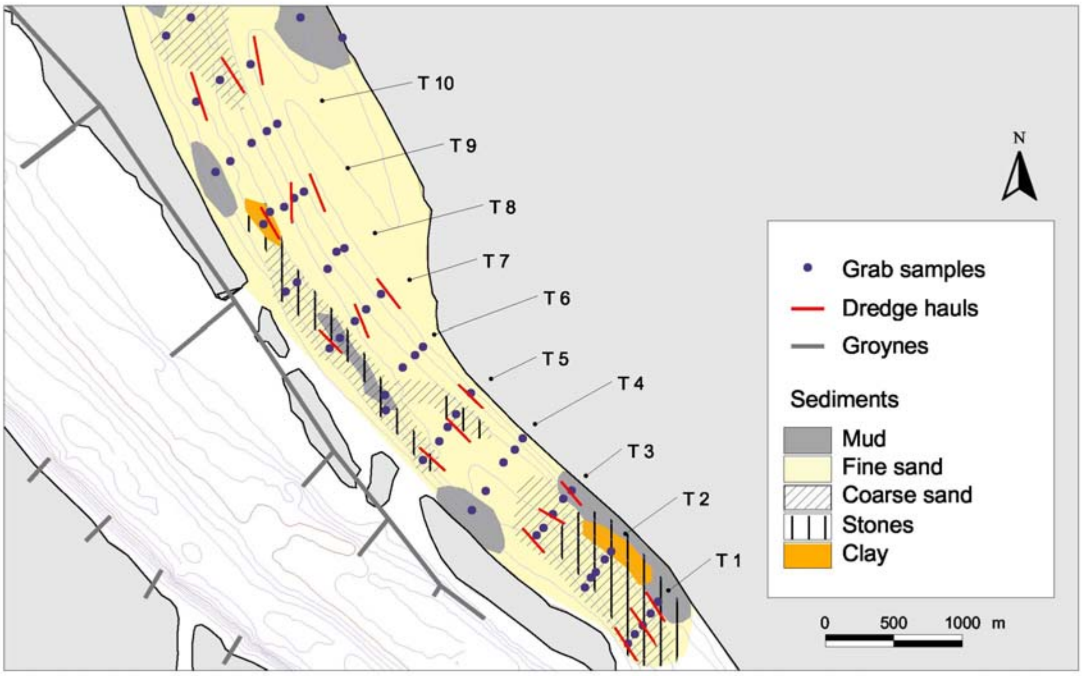


Fig. 6 Distribution of substrates in the southern survey area (transect 1-10).

The macrobenthic community

A total of 119 species were collected during the survey, including 101 species of benthic macrofauna and 18 fish species (Appendix Tab. A-1). Polychaetes yielded 34, crustaceans 25, hydrozoans 13 and molluscs 9 species. Others, such as Bryozoa, Anthozoa, Pantopoda and Nemertini were represented by few taxa only. The diagram in Fig. 7A shows the percentage of each taxonomic group of the total number of species. Looking at the preferred salinity zones, most of the species (65%) are euryhaline marine species with a high tolerance to changing and lower salinity conditions (Fig. 7B). Marine species contribute 29% and genuine brackish water species were represented by 8 species (6%). Different types of mobility of the identified species are shown in Fig. 7C. 53% of all species were sessile and 38% can be considered as mobile (vagile). About one third of all species were related to hard substrates as a substrate to settle or feed on. The importance of lithogenic and biogenic hard substrates in estuarine channels will be referred to in the next chapter.

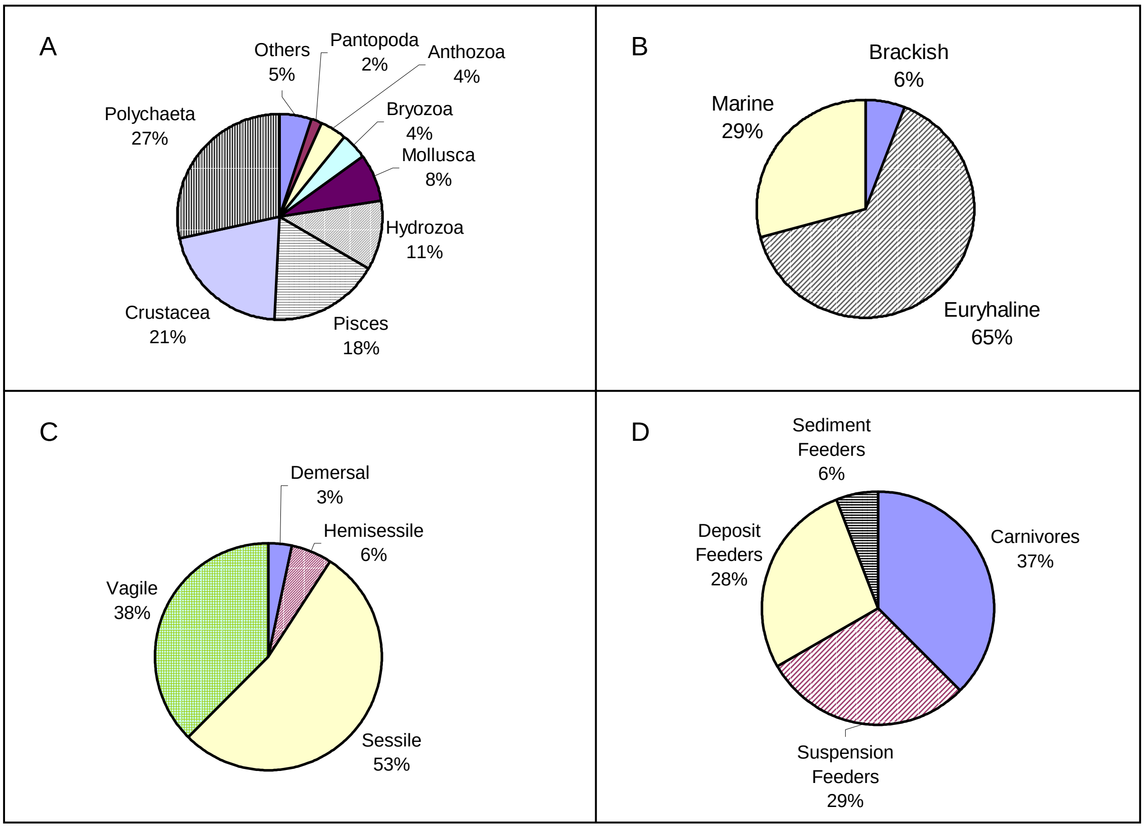


Fig. 7 Total species number (n = 120) classified by taxonomic group (A), salinity (B), mobility (C), and feeding type (D).

Fig. 7D shows the feeding types of all species. More than one-third of all species are carnivores, almost one-third are suspension feeders and deposit feeders, respectively. Only 6% can be classified as sediment feeders. 8 species (5%) are listed in the Red List of Threatened Species (RACHOR 1998, Appendix, Table 1).

Spatial distribution of benthic invertebrates

For an overview of faunal data interaction and possible relationships to abiotic data the MDS plot (Fig. 8) shows the endobenthic data set of central grab stations. A clear south to north gradient was presented by the ordination of the samples, most probably reflecting the salinity increase and differences in substrates towards the north. The further analysis will treat a southern more brackish part of the survey area, and a northern marine influenced part, separately.

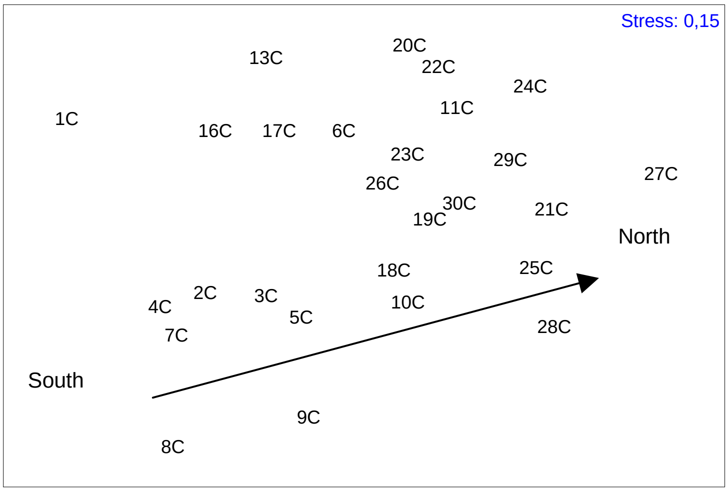


Fig. 8 MDS plot of grab sample data (central sites, numbers of transects from south (1) to north (30).

In Table 1 some main characteristics of benthic invertebrates of the southern part (transect 1-15) and the northern part (transect 16-30) of the channel are given.

Table 1 Main characteristics of endobenthic data (grab samples), species number (S), mean abundance in Ind./m² (N), species richness (d), evenness (J´) and diversity (H´, log_2) of different scales (sites, transects and large areas, s. text), standard deviation (SD).

	S	***N***	***d***	***J'***	***H'***
Total, n=150	38	3336	4.56	0.57	3.0
Mean / Site	3.48	22.24	1.13	0.72	1.15
SD (+/-)	1.93	36.56	0.66	0.26	0.80
North, n=15	25	1453	3.30	0.62	2.87
Mean / transect	10.40	97.67	2.21	0.68	2.28
SD (+/-)	2.29	82.42	0.55	0.17	0.58
Mean / Site	4.24	63.01	1.28	0.75	1.34
SD (+/-)	4.35	381.96	0.77	0.24	0.79
South, n=15	32	1883	4.10	0.45	2.25
Mean / transect	12.73	226.67	2.33	0.58	2.07
SD (+/-)	5.85	240.91	0.85	0.20	0.80
Mean / Site	3.17	25.11	1.01	0.68	0.99
SD (+/-)	1.93	38.74	0.64	0.27	0.80

All indices show higher point values (per site) in the north than in the south. The southern part has a higher total species number, individual number and species richness at the higher spatial scales of transects and large areas. The diversity measures in the northern part of the survey area is higher than in the south within endobenthic data (Table 1).

Dominance structure of endobenthic species (grab samples) in the north and south is presented in Table 2.

Table 2 Along channel differences of selected endobenthic species (mean abundance in ind. /m², +/- standard deviation (SD), numerical dominance (DOM) and presence (PRE) in %, n = 75 stations).

Taxon	**South** *(Transect 1-15) n= 75*				**North** *(Transect 16-30), n= 75*			
	Ind./m²	**+/-SD**	**DOM**	**PRE**	**Ind./m²**	**+/-SD**	**DOM**	**PRE**
Marenzelleria viridis	7.9	16.1	29.7	41.3	0.0	0.0	0.0	0.0
Gammarus salinus	0.3	1.2	1.0	8.0	0.0	0.0	0.0	0.0
Heteromastus filiformis	13.3	36.1	49.9	54.7	4.5	28.8	22.3	39.7
Neanthes succinea	1.4	4.5	5.2	22.7	0.4	2.1	1.9	8.2
Bathyporeia pelagica	0.1	0.4	0.4	5.3	5.5	19.9	27.4	30.1
Nephtys caeca	0.5	0.9	2.0	28.0	1.9	2.1	9.4	69.9
Ensis directus	0.0	0.0	0.0	0.0	4.1	8.7	20.5	49.3

Table 3 Main characteristics of epibenthic data (dredge hauls) by species number (S), mean abundance in ind./m² (N), species richness (d), evenness (J´) and diversity (H´, $\log_2$) of different scales (sites, transects and large areas, s. text), standard deviation (SD).

	S	***N***	***d***	***J'***	***H'***
Total, n=48	57	59799	5.9	0.29	1.79
Mean/ Site	10.38	1244	1.42	0.30	1.06
SD (+/-)	4.68	1403	0.71	1.72	0.71
North	48	28358	5.17	0.17	0.95
Mean/ Site, n=24	10.08	1180	1.38	0.28	0.95
SD (+/-)	4.18	1346	0.68	0.17	0.71
Mean / Transect, n=8	22.25	3544.75	2.67	0.23	1.05
SD (+/-)	4.30	2428.06	0.61	0.14	0.70
South	50	31441	5.40	0.37	2.20
Mean/ Site, n=24	10.67	1308	1.47	0.34	1.17
SD (+/-)	5.20	1485	0.75	0.17	0.72
Mean / Transect, n=8	23.63	3930.13	2.78	0.30	1.39
SD (+/-)	4.19	2139.31	0.55	0.14	0.71

The northern part is dominated by *Bathyporeia pelagica, Heteromastus filiformis* and *Ensis directus,* which are marine species. In the south *Heteromastus filiformis* and *Marenzelleria viridis are* the dominating species. The brackish water species *Marenzelleria viridis* and *Gammarus salinus* did not occur in the northern part of the channel. Marine species, such as *Ensis directus* were found only in the northern part. Most of the other species are euryhaline and do not show a particular south to north difference in dominance, abundance or presence.

The epibenthic macrofauna shows higher indices at all spatial scales in the south (Table 3). In opposite to the endobenthic data the point, transect and large area diversity is higher in the south.

In Fig. 9 the abundance from south to north of some selected epibenthic species is presented. The marine species, *Liocarcinus holsatus* and C*rangon crangon,* show an increasing abundance towards the north. The brackish water crustacean *Balanus improvisus* showed a decline along the channel towards the north. A similar situation was found for the hydrozoan *Eudendrium ramosum.* For both species, the natural range is restricted to low salinities and hard bottom substrates to attach to.

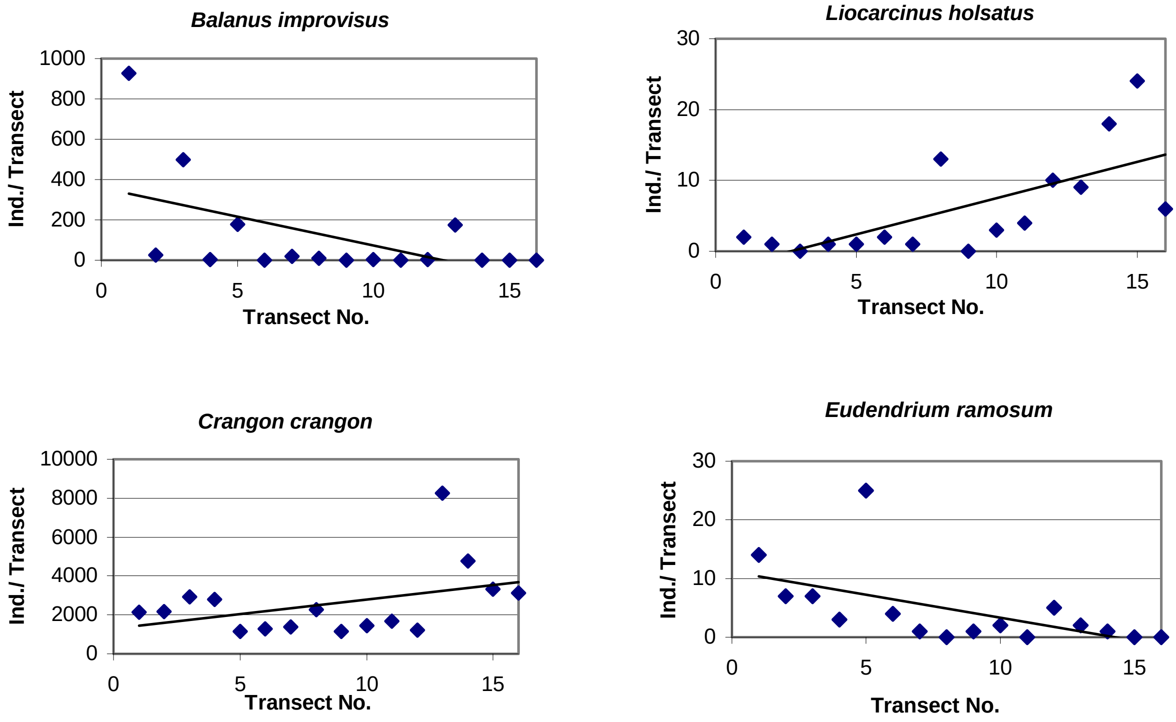


Fig. 9 Along-channel patterns of selected epibenthic species from the polyhaline channel (abundance in individuals per transect, T1-15, linear regression).

Morphology

When comparing the benthic fauna at the slopes with the deep central channel, differences in the species number and abundance are obvious. Shallow water areas (slope sites, position E) were inhabited by more endobenthic species and individuals than the deep-water areas (central sites, position C). Regarding the epifauna, more individuals but fewer species occurred on the slopes than in the deep channel areas (Table 4).

Table 4 Comparison of grab sample data from deep channel sites (position C, in Fig. 2) and the eastern slope (position E, in Fig. 2).

	Channel			***Slope***		
Endofauna, n=30 (grab samples)	**Total**	**Mean per site**	**+/- SD**	**Total**	**Mean per site**	**+/- SD**
Species number	36	5.0	2.8	46	5.2	3.3
Individuals	1216	40.5	82.8	1665	55.5	27.8
Epifauna, n=16 (dredge hauls)						
Species number	45	18.5	8.4	44	14.8	5.3
Individuals	15112	944.5	1497.3	43212	1227.4	665.7

The hydrozoan *Hartlaubella* sp., the bryozoan *Electra crustulenta*, the bivalve *Ensis directus* and the amphipod *Bathyporeia* spp. occurred with more individuals in deep habitats (Fig. 10). The crustaceans *Gammarus salinus, Corophium volutator*, the gastropod *Hydrobia ulvae* and the polychaete *Scoloplos armiger* preferred sites at the slope (Fig.10). The epibenthic crustaceans *Crangon crangon*, *Carcinus maenas* and the hydrozoan *Obelia longissima* showed a clear preference for slope sites. *Ensis directus* and *Metridium senile* occured more often in the deep channel. The mussel beds (*Mytilus edulis*) and the associated fauna did not show any preference regarding the riverbed morphology.

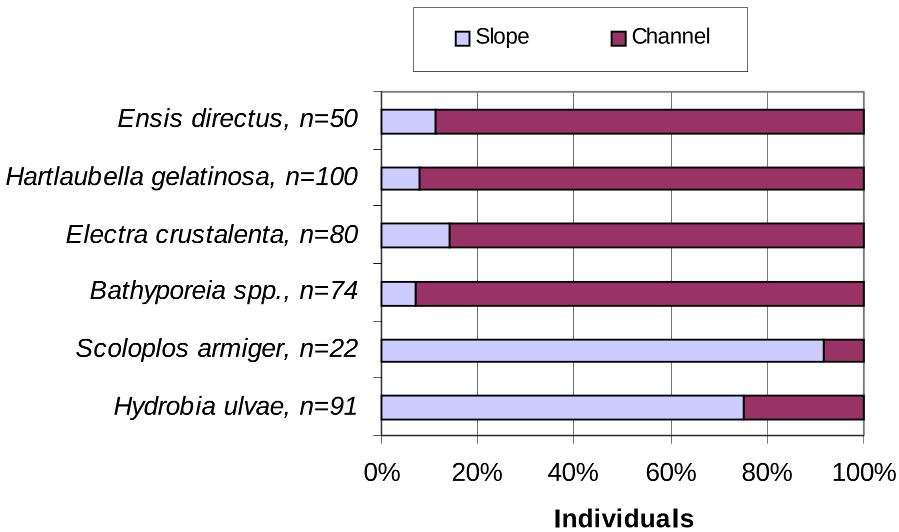


Fig. 10 Habitat preference of selected species (n= total individual number, all grab samples corrected for the number of sites, slope = 60, channel = 30).

In Fig. 11 selected species from sand and mud sites are presented by abundance and presence data. The polychaete *Heteromastus filiformis* is significantly more abundant and more often present in mud than in sand sediments. While in sandy habitats *Marenzelleria* *viridis, Bathyporeia* spp. occurred with higher abundance and presence, *Corophium volutator* preferred mud sediments significantly.

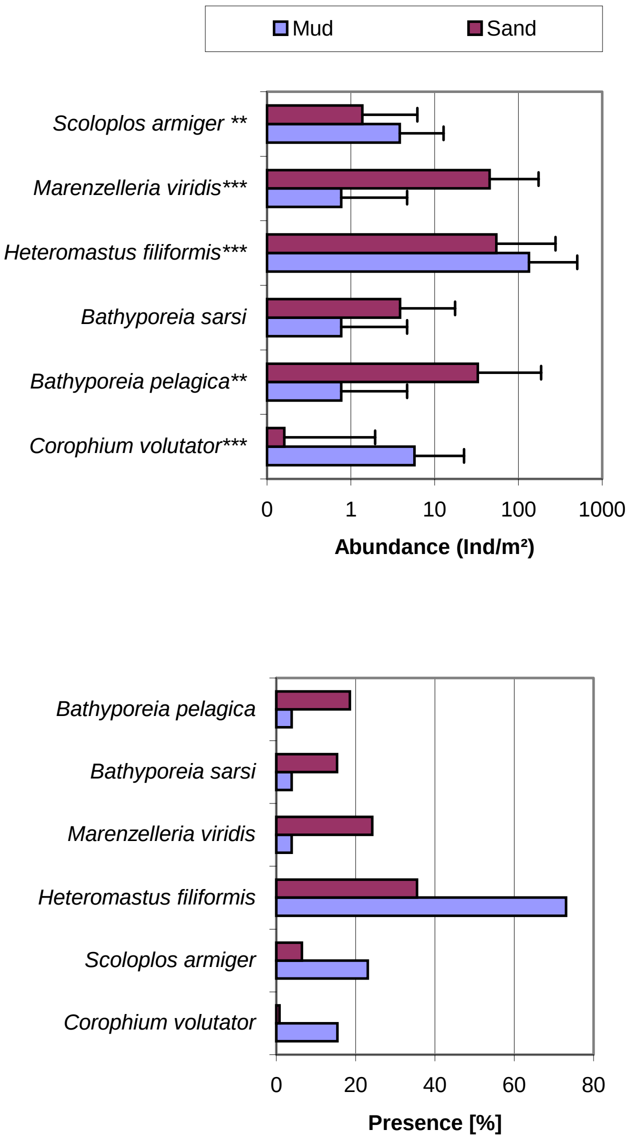


Fig. 11 Abundance (+/- SD) and presence (in %) of selected species at sand and mud sites (Mann Whitney, *-p<0.1,**<0.05,***<0.01, n= 150 sites).

The multivariate analysis techniques exclude the influence of the salinity gradient. Some results are given for the most southern part of the survey area by MDS plots (Fig. 12). The clusters from cluster analysis, indicated in Fig. 12 by circles, divide the data into 4 groups with different sediments and different riverbed morphology. The station with clay sediment (4A) is clearly separated from all others. The fauna is poor and only a few polychaetes were found (*Nepthys* spp., *Neanthes succinea*). The eastern steep slope with enriched sands and varying amounts of silt is represented by another cluster. These stations include areas with a high abundance of *Heteromastus filiformis* together with other polychaetes such as *Nepthys* spp., *Neanthes* sp., *Tharyx killariensis* or *Marenzelleria viridis.* Sites of fine and medium sands, with less silt, represent the western slope area. *Marenzelleria viridis* is dominant at these stations, accompanied by *Capitella capitata* or *Bathyporeia* spp. The fourth group is characterised by musselbeds of *Mytilus edulis* and its biogenic hard substrates with a stable surface for epibenthic settlement. At these sites *Balanus improvisus* and hydrozoans occur in high abundance besides *Mytilus edulis* and its associated fauna.

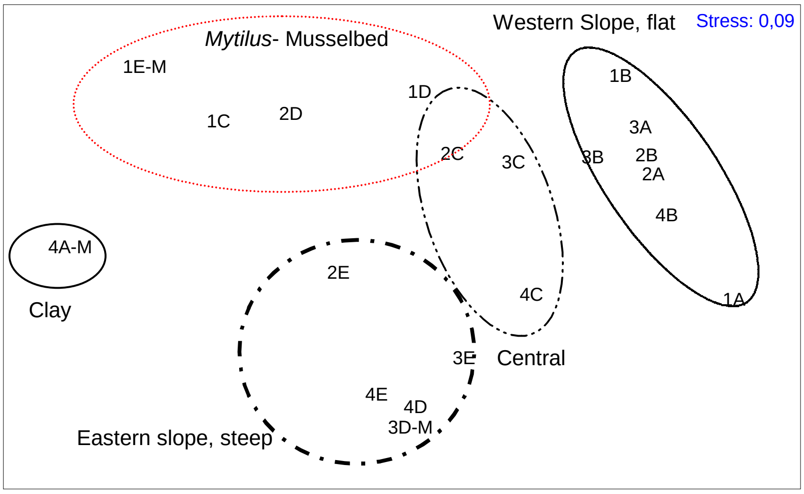


Fig. 12 MDS plot from endobenthic data of the most southern part of the survey area (transect 1-4, 20 grab samples, √√ transformed data, Bray-Curtis similarity).

The MDS plots of epibenthic data (Fig. 13, transect 1-9) showed similar clusters to endobenthic data with *Mytilus* sites, channel centre and sandy slopes.

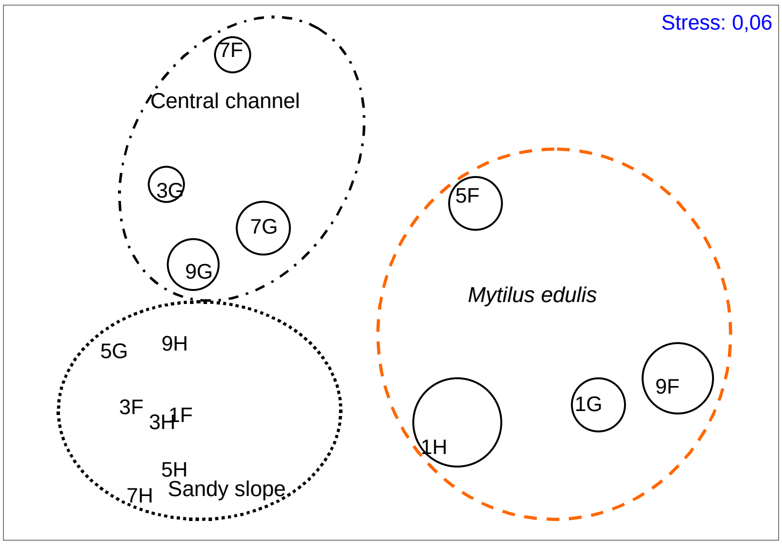


Fig. 13 MDS plots of epibenthic samples (transects 1-9, 15 samples, presence/ absence transformed data, Bray-Curtis similarity, with superimposed Shannon`s diversity (circles).

Higher values of species number, individuals and diversity were concentrated on the Mytilus beds and channel sites, while the slopes were inhabited by large numbers of mainly two species such as *Crangon crangon* and *Carcinus maenas*. Besides *Mytilus edulis, Balanus improvisus*, hydroids such as *Obelia longissima, Hartlaubella gelatinosa*, anthozoans such as *Metridium senile* or *Sagartia troglodytes* have been caught at these sites. The sites 5F and 7F are closely related to the mussel beds, but both only with few individuals of *Mytilus edulis*.
Besides the soft sediments, there are hard substrates with importance for benthic species. These substrates were found in deeps and steep edges, created by erosive currents. Three different types of hard-bottom substrates were found:

Stones and pebble layers provide a stable surface in areas which are exposed to currents and therefore without sedimentation. Epibenthic suspension feeders, such as hydrozoans, anthozoans, bryozoans and balanids, occurred in these exposed areas. Dense covers of *Hartlaubella gelatinosa* or *Obelia longissima* provided habitats for a diverse associated fauna. The gastropod *Aeolidia papillosa* and pantopods, such as *Nymphon gracile* or *Callipene brevistoris*, were feeding on hydrozoans, while amphipods like *Gammarus* spp. and small polychaetes used the structures to hide.

Clay layers and peat appeared on steep slopes as substrates. Here they resisted erosion longer than the surrounding soft sediments. The clay and peat sediments were unsuitable for quantitative sampling by the van Veen grab. Information on these endobenthic and epibenthic habitats was therefore derived from dredge hauls only. The bivalve *Petricola pholadiformis* was found in both substrates, along with the polychaete *Polydora* spp. Epibenthic fauna on these substrates was comparable to other hard substrates, but with lower abundances.

Subtidal mussel beds of *Mytilus edulis* provided the most important substrates for other species. Epibenthic species such as *Obelia* spp., *Metridium senile, Balanus improvisus, Asterias rubens* and various amphipods were found in high abundances at sites with *Mytilus edulis*. Additionally, there was an associated fauna living between the shells in the faeces-enriched mud comprising *Nereis virens*, *Polydora* spp., *Nepthys* spp. and *Corophium volutator.*

Shells of different molluscs can provide large, hard substrate areas when currents keep them free from sedimentation. In this study they were mixed with medium sands and a stable shell layer, as a typical habitat, was not registered. The colonisation by sessile epibenthic species depends on the stability of these layers. Most of the time the stability is short term and colonisation by anthozoans or hydrozoans occurs at an early stage, and is consequently sparse. Amphipods like *Bathyporeia* spp. or *Gammarus* spp. use the shells to hide in.

The substrates show different community indices of endobenthic and epibenthic data. The highest species number of all dredge sites (24 species, site 9F, mussel bed) was coupled with a diversity index of 1.95. The highest diversity index of the whole survey area was 2.84 at site 23H, which was also situated in a mussel bed. The highest diversity index in the southern part (transect 1-9) was 2.36 at site 7G. In Fig. 14, epibenthic diversity of sites with different substrates is demonstrated. The sites with mussel beds provide the highest species numbers and the most diverse habitats of the tidal channel.

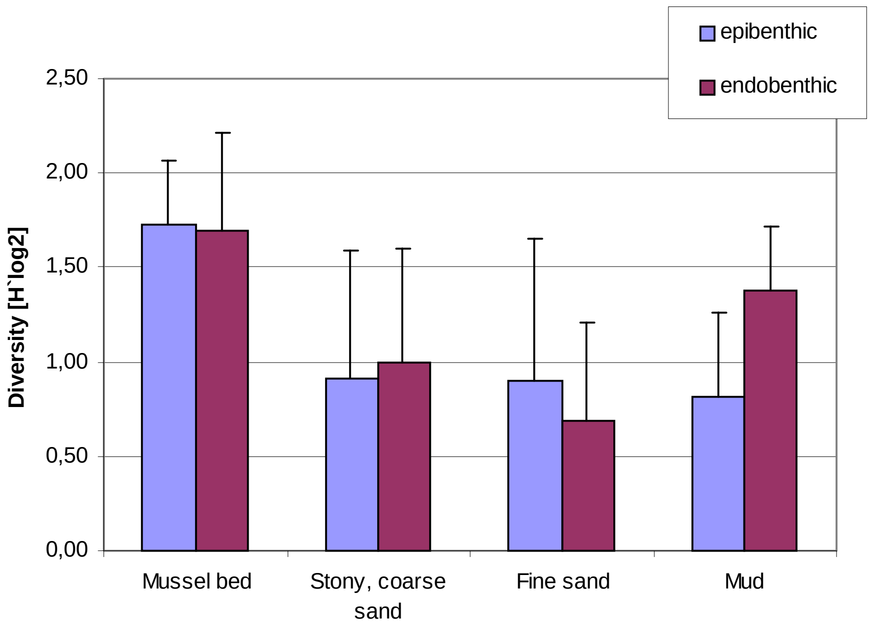


Fig. 14 Diversity (H`) of endobenthic and epibenthic macrofauna of different substrates (southern survey area. transect 1-15, column represents mean, bar indicates standard deviation).

Discussion

Quantitative studies of benthic invertebrates in estuaries were carried out by several authors such as DÖRJES & HOWARD (1975), RISTICH et al. (1977), COLEMAN et al. (1978) and JONES et al. (1986). The strong influence of seasonal and annual variations to the estuarine benthic community was emphasised in POORE & RAINER (1979), RAINER (1981), ELLIOT & O´REILLY (1991) and MEIRE et al. (1994).

In this study the spatial variations in the faunal community have been investigated, whereas temporal variability was not an objective. The benthic invertebrates of the Weser estuary were investigated by SCHRÄDER (1941), MICHAELIS (1973, 1981) and DITTMER (1981). However, the patterns of benthic distribution in the sub-tidal areas were rarely described. GOSSELCK et al. (1993) examined the benthic distribution in the main channel of the Weser estuary, focussing on the along-estuary gradient. HEIBER (1988) quantified the interchange between the fauna of a tidal channel and neighbouring intertidal flats. The benthic community in the investigated polyhaline channel, with 101 species, is divided into a more brackish part in the south and a more marine part in the north. Several typical euryhaline species from this investigation, including *Nephtys hombergi, Nephtys cirrosa, Hydrobia ulvae, Macoma balthica* and *Bathyporeia* spp. have been found in many estuaries of Northern Europe. However, they have a different range of occurrence and maximum densities in most of the estuaries due to individual abiotic features of each river (BOYDEN & LITTLE 1973).

DÖRJES & HOWARD (1975) described a similar situation in the Ogeechee estuary on the east coast of the United States (Georgia). Among the most important of a total of 109 species in the polyhaline area of the Ogeechee estuary were *Spiophanes bombyx*, *Bathyporeia* sp., *Solen viridis* and *Tellina* sp., which could be compared by feeding habits to *Marenzelleria viridis*, *Bathyporeia pilosa*, *Ensis directus* and *Macoma balthica* collected here. Although a comparison of different communities by feeding habits is considered to be controversial because of the difficulties in exactly classifying the feeding types (MAURER et al. 1979), similarities of ecological functions in the estuarine communities are obvious.

Salinity

In this study salinity was found to be the major distribution factor of the investigated benthic community, which supports results of BOESCH et al. (1976), WARWICK & DAVIES (1977) and JONES et al. (1989).

Most species were classified as euryhaline marine species with different tolerance of low salinities. Because of this specific tolerance the range of the species into the upper reaches of an estuary differs and the benthic composition shifts from a marine into a brackish community. As described by SCHLIEPER & REMANE (1958) and DÖRJES (1978), the brackish water species have their main range in the oligohaline and mesohaline zone of an estuary and only a few occur in the polyhaline zone. Only 8 brackish water species were identified in the investigated channel. GOSSELCK et al. (1993) found brackish water species (except *Balanus improvisus*, which occured from fresh to almost marine conditions) in the main channel up to km 95. This is approximately the same range as mentioned in this study. DITTMER (1981) found a faunal break in the main channel of the Weser at km 85 with a strong increase in species number towards the north. In contrast to that, the along-estuary gradient in this survey was determined by a change in species composition with less species in the north. This was attributed to morphological features such as hard substrates and mussel beds of *Mytilus edulis*, which provide habitats for associated epibenthic species in the southern part of the channel. The variation of substrates therefore caused a higher diversity against a typical distribution of an along-estuary gradient. BOYDEN & LITTLE (1973) did not find an increase in the number of endobenthic species along the estuarine gradient compared to a strong one in hard-bottom assemblages. That emphazises the importance of epibenthic assemblages within a spatial analysis of estuarine communities and the need of a consideration of others than just salinity as a distribution factor.

Sediments and riverbed morphology

Fine sedimentary deposits are characteristic features of estuaries. Sedimentary material is transported into the estuary from rivers or the sea, or is washed in from the land surrounding

the estuary. In most North European estuaries the main source of sedimentary material is the sea, which carries the material into the estuary either as suspended flux or as bed load transported by the bottom currents (McLUSKY 1989).
The deposition of sediments within the estuary is controlled by the speed of the currents and the particle size of the sediments. Not only grain-size composition but also exposure, movement and stability of the sediment are important factors for benthic colonisation (GRAY 1981, BARNES 1994).
Extensive studies on the interaction between sediments, morphology and benthic distribution in estuaries were carried out by BOYDEN & LITTLE (1973), WARWICK & DAVIES (1977) and JONES et al. (1986). DÖRJES et al. (1969) and DÖRJES (1978) analysed sediments and resulting benthic distribution of the neighbouring Jade system. Because of the nearby location, and the similar salinity, the conclusions concerning the distribution of the benthic invertebrates will be compared with this study. As a main morphologically based distribution aspect DÖRJES et al. (1969) separated the *Macoma balthica* community into subdivisions of intertidal flats and subtidal channels. Furthermore, the channels were classified by their hydrology, morphology, different water energy (currents) and the resulting sediments. In Fig. 15 the main distribution factors of a benthic community in subtidal channels are compiled.
The scheme shows the possible factor combinations that are important for the habitat characteristic. In this survey 7 types of substrates were characterised and related to a certain benthic community (Table 5). 3 types of sediments (mud, muddy sand, fine sand) and 4 types of hard substrates (peat, clay, stones, mussel beds) were differentiated.

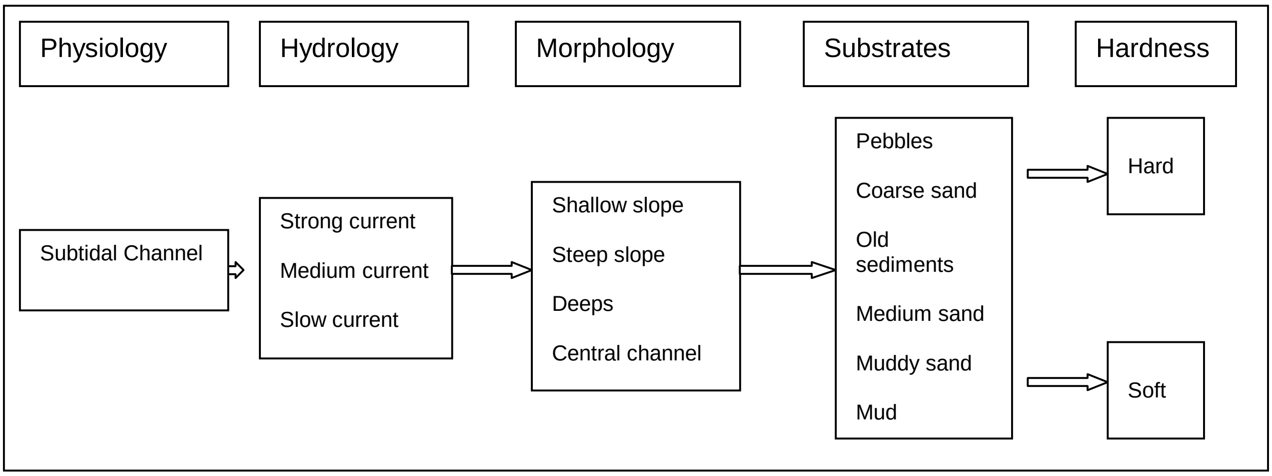


Fig. 15 Abiotic factors for the distribution of benthic species in subtidal channels (modified after DÖRJES et al.1969).

For a comparison the classification of DÖRJES et al. (1969) and WARWICK & DAVIES (1977) is added in Table 5. It is obvious that although the different systems have individual abiotic and biological features, a similar type of species characterises the same habitat.

Partly the same species were found; partly the same genera or at least the same ecological function could be recognized.

Coarse sand and pebbles as sediment types were not registered in the Weser channel. In this survey, clay and peat were found to host generally the same species (Table 5).

The hydrology of a channel can be differentiated into sheltered habitats and exposed habitats, which influence grain size of sediments but also riverbed morphology. The sheltered areas with less current contain soft sediments with high stability, which are habitats for deposit feeders and sediment feeders.

Table 5 Classification of substrates and related benthic species in estuarine channels (characteristic species bold).

Substrate / Biotope	This study	Dörjes et al. (1969), Jade channels	Warwick & Davies (1977), Bristol Channel
Soft mud	*Tubificoides benedeni* ***Heteromastus filiformis*** *Corophium volutator*	*Tubificoides bendeni* *Heteromastus filiformis* *Retusa obtusa* *Eteone longa*	*Tharyx marioni* *Nephtys hombergi* *Tubificoides benedeni*
Muddy sand	*Hetromastus filiformis, Neanthes succinea, Gammarus salinus, Hydrobia ulvae,* ***Nephthys caeca***	***Magelona papillicornis*** *Pygospio elegans, Spiophanes bombyx, Phyllodoce mucosa*	*Abra alba* *Scalibregma inflatum* *Pectinaria koreni* *Nephtys hombergi*
Fine sand	*Marenzelleria viridis,* ***Ensis directus*** *Bathyporeia pelagica, Bathyporeia sarsi*	***Magelona papillicornis*** *Bathyporeia robertsoni* *Angulus fabula*	***Tellina (Angulus) fabula***, *Bathyporeia gulliamsonia* *Magelona palpillicornis* *Ensis ensis*
Coarse sand, pebbles	Not found	***Ophelia limacina*** *Nereis longissima* *Glycera capitata*	***Spisula elliptica*** *(In loose sands)*
Stony surfaces	Epibenthic species like balanids, hydrozoans, anthozoans, *Lanice conchilega*, *Mytilus edulis* and associated fauna	Sessile epibenthic species	***Modiolus modiolus,*** *Pagurus bernhardus* *Lepidonotus squamatus* *Ophiura albida* *Asterias rubens* *Sargartia troglodytes*
Peat	*Petricola pholadiformis, Polydora* spp., epibenthic species like balanids, hydrozoans, anthozoans	***Petricola pholadiformis*** *Lepidonotus squamatus* *Mytilus edulis*	--
Clay, hard (consolidated) mud	*Petricola pholadiformis, Polydora* spp., epibenthic species like balanids, hydrozoans, anthozoans	***Petricola pholadiformis*** *Autolytus prolifer* *Harmothoe impar*	
Mussel bed	*Nereis virens, Polydora* spp., *Corophium volutator, Gammarus* spp., epibenthic species like balanids, hydrozoans, anthozoans	--	***Modiolus modiolus,*** *Pagurus bernhardus* *Lepidonotus squamatus* *Ophiura albida* *Asterias rubens* *Sargartia troglodytes*

The species from the Bristol Channel listed in WARWICK & DAVIES (1977) have similar ecological functions compared to species of this study. Deposit feeders prefer muddy sands, epibenthic suspension feeders were found mostly at hard-bottom sites, mobile burrowing species characterise unstable sands. These basic characters of benthic spatial distribution were found in a similar way in most estuaries (POORE & RAINER 1979, COLEMAN et al. 1978, RAINER 1981). A precise regional characterisation of benthic distribution is intended to improve biological assessments at the species level.

Endobenthic faunas showed more individuals on the shallow slope than in the deep channel. Higher abundance may be explained with the increasing silt amount and decreasing grain size. This may be correlated to a higher sediment stability for burrowing species. The higher nutrient content of muddy sands provides a better food supply for endobenthic species, especially deposit feeders (PEARSON & ROSENBERG 1977, RAFFAELLI & HAWKINS 1996). Most of these species are tolerant to organic enrichment and oxygen deficiency (PEARSON & ROSENBERG 1978). The percentage of about one third of the species being classified as suspension feeders and one third as deposit feeders is similar to the situation in Swedish and Scottish estuaries at certain depths (PEARSON & ROSENBERG 1978). Grazers in these studies were rare, due to light conditions in a certain water depth and missing algae on the sediment surface. In this study the high turbidity may keep light off the deeper sediment surface and therefore phytobenthic activity is probably restricted to very shallow waters and the intertidal areas.
The epibenthic fauna achieves higher species numbers at the centre of the channel compared to the slopes. Vagile epibenthic species were not attributed to certain sediments due to their mobility. Further analysis of epibenthic sediment relationship (dredge samples) is limited because of the non selective sampling method. Sessile epibenthic species occurred on exposed but stable hard substrates, in areas with stronger currents. Unstable or continuously moving sandy sediments hosted only few species (e.g. *Bathyporeia* spp.). Haustorid amphipods, *Nepthys* spp. and *Ensis directus* are considered to be typical for sandy unstable or moving sediments, because of their capability of burrowing (MAURER et al. 1979). These unstable fine sands were found quite often in central exposed sites of the channel and might be the reason for earlier biologists considering the estuarine channel systems to be sparsely colonized or even devoid of benthic fauna (SCHRÄDER 1941).

DÖRJES et al. (1969) found similar relationships in the Jade channel system, but with some major differences. Firstly, the key species of the Jade *Ophelia limacina* and *Magelona papillicornis* did not occur in the investigated channel of the Weser. Finer grain size and the occasionally lower salinity in the Weser channel might be the reason for the absence of *Ophelia limacina.* However, the sediment characteristics for the key species *Magelona papillicornis* were definitely present in this study. WARWICK & DAVIES (1977) mentioned the same species as typical of the fine sand areas in the Bristol Channel (*Tellina fabula* sub-community). The reason for this species being absent from the present study might be due to a sometimes strong fresh water run off, which is missing in the Jade system since the river was separated by a weir. The Jade system therefore appears to be more strongly influenced by the salt water of the sea while the channel investigated in this study had strong estuarine features, despite equal salinity means. This is supported by the fact that no brackish water species were collected in the Jade system, demonstrating that the *Macoma balthica* association has an estuarine variation, which is not characterised by the key species of DÖRJES et al. (1969). The data from GOSSELCK et al. (1993) and HEIBER (1988), which were collected in the northern part of the Weser estuary, contained both species.

In the listed surveys (Table 5) many species were not clearly linked to specific substrate characteristics because of sampling methods, their general low abundance, their mobility or high tolerance to any kind of substrates. In Table 5 the characterising species of exposed hard substrates are therefore presented on a taxonomic group level, with less differentiation to substrate preference. When epibenthic species find favourable conditions (stable hard substrates) they attach to it and the associated fauna follows with the stages of succession.

Spatial scales of benthic diversity

Small scaled structured biotopes as a result of the strong gradients and tidal currents within an estuary are reflected by the benthic communities. Spatial variance of benthic communities in estuaries therefore can be higher than seasonal and interannual variance (EDGAR & BARRETT 2002). For an analysis of benthic communities it is therefore important to consider different spatial scales. Brackish benthic communities have a natural low diversity with strong abiotic control of species distribution (e.g. salinity). In these biotopes point diversity may be low while large area diversity is relatively high (compare GRAY 2000). The benthic community indices of endobenthic data in this study vary at different spatial scales (Table 5). While the northern part shows higher index values at single sites (e.g. point diversity), the southern part has a higher species number and species richness at the transect level and large area level (endobenthic data). The grab samples show differences in habitat variation on a larger scale only.

The epibenthic data show higher indices at all spatial scales in the southern part of the survey area and therefore gives a better response to habitat variation. The higher diversity and species richness of epibenthic data in the south is due to the higher habitat variety in the form of different types of hard-bottom substrates in the southern brackish part. Dredge samples reflected these differences more clearly especially at single sites, because single dredge samples collect epibenthic species from a dredge haul length of 100 m. This covers a much wider area and gives a better picture than a single grab sample. A highly variable survey area influenced by abiotic features, such as salinity, sediment distribution and morphology as presented by an estuarine channel therefore needs larger sample units than less structured marine areas. A combination of endobenthic and epibenthic methods and an analysis on different spatial scales is important for an appropriate reflection of species richness and diversity.

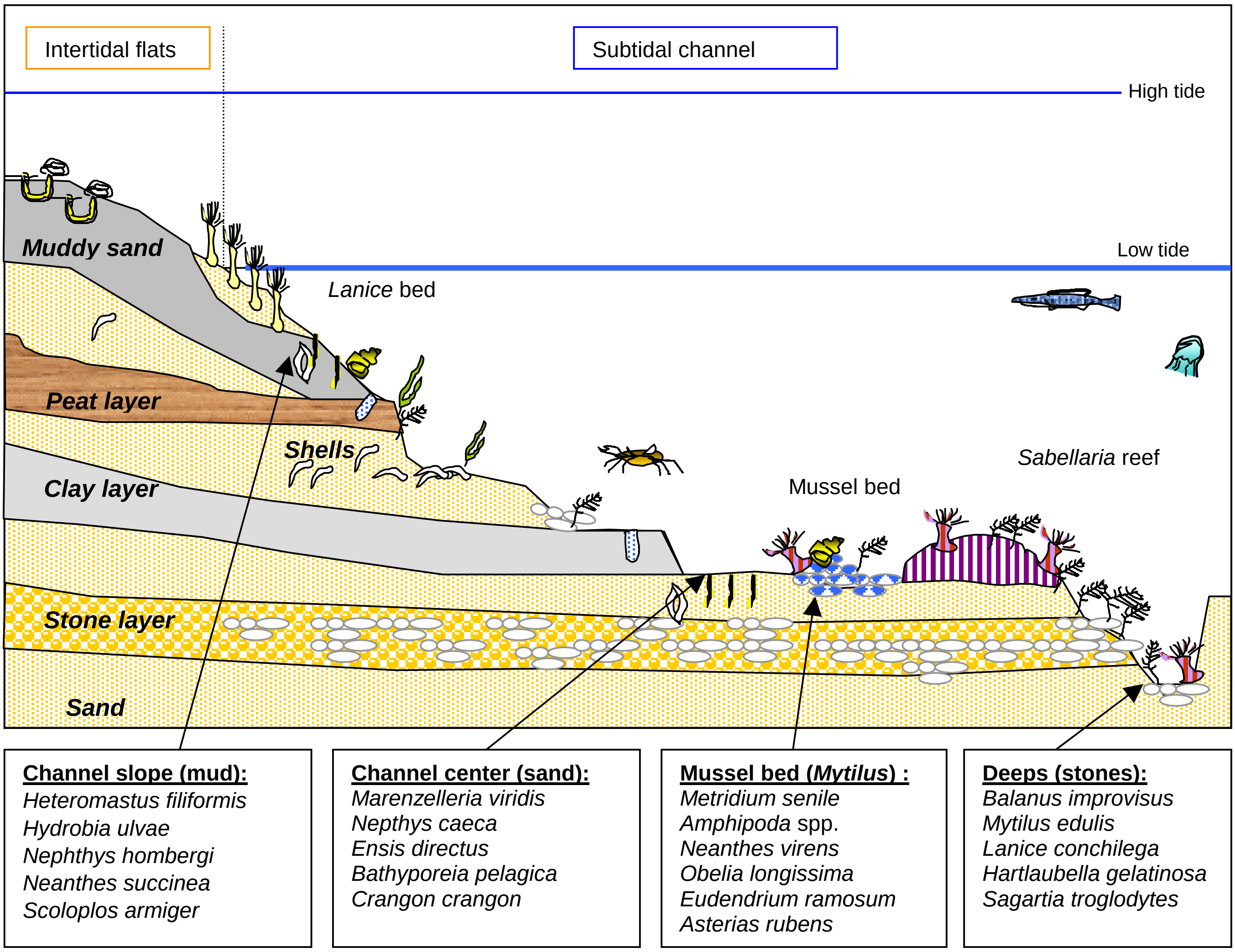


Fig. 16 The benthic community of a polyhaline channel in relation to different substrates (schematically).

In Fig. 16 the community of the estuarine channel is pictured schematically. Because most typical structures are presented in one cross section the tidal channel appears unrealistically rich. The Sabellaria-reef is added from a study of the main channel (BUHR 1979) to demonstrate the variety of biogenic hard structures in estuarine channels although it is missing in the survey at hand. The different layers of peat, clay or stones make steep edges and wash outs structural diverse biotopes. In flat slope areas these structures are covered by sands and habitat diversity is low at all spatial scales.

Most studies tend to overestimate soft-bottom substrates and underestimate hard-bottom substrates because of the method of sample collection (WARWICK & DAVIES 1977). The high species richness of hard substrates in tidal channels in relation to the surrounding soft sediments should be emphasised. The fact that epibenthic data contribute major aspects for the evaluation of the estuarine community supports the need of new sampling techniques to integrate quantitative epibenthic data in the community analysis as done by WARWICK & DAVIES (1977). Grab samples alone fail to provide sufficient data for ecological assessment of the diversity in subtidal systems.

The subtidal mussel beds of *Mytilus edulis* provide structures of high importance to associated species and for the diversity of the channel system. Furthermore, the diversity of an estuarine channel is closely connected to the structural variety of subtidal structures. The sensitivity of such structures towards dredging and dumping activities demonstrates a need for an integrated management plan for estuaries and coastal areas. The inventory of such estuarine habitats can be an important first step towards such a concept. An effective strategy should be implemented to monitor the biological changes within the channel system and the intertidal flats in the estuaries in order to protect them, and to ensure their integrity is maintained for the future.

Acknowledgements

We thank the harbour authority of Bremen (bremenports GmbH, Bremerhaven, formerly HBA) namely Mr. U. von Bargen and Dr. U. Burghardi for supporting this paper and for the data release. Many thanks to the crew of the bremenports-vessel “Hol Deep” and to the KÜFOG-Team being a great help during the surveys, in the field and in the laboratory.

Apendix

Table A-1 Species list with total individual number (A), average abundance per site (B), numerical dominance of species (C) and presence of species in % (D). B- brackish water species, RL- Red List status (RACHOR 1998): P potentially threatened, 3- threatened.

Dredge trawl species list

Taxon	A	B	C	D
Plathyhelminthes				
Planaria indet.	1	0.0	0.0	2.1
Hydrozoa				
Bougainvillia ramosa	9	0.2	0.0	12.5
Bougainvillia sp.*	1	0.0	0.0	2.1
Clythia hemisphaerica	4	0.1	0.0	6.3
Eudendrium ramosum	72	1.5	0.1	35.4
Hartlaubella gelatinosa	96	2.0	0.2	35.4
Laomedea flexuosa	2	0.0	0.0	2.1
Laomedea sp.	21	0.4	0.0	20.8
Obelia longissima	2099	43.7	3.5	81.3
*Rhizostoma octopus**	1	0.0	0.0	2.1
Sertularia cupressina, RL 3	48	1.0	0.1	33.3
Tubularia bellis/ indivisa	15	0.3	0.0	6.3
Anthozoa	0	0.0	0.0	0.0
Diadumene cincta	1	0.0	0.0	2.1
Metridium senile, RL P	428	8.9	0.7	45.8
Sagartia troglodytes	185	3.9	0.3	27.1
Urticina felina	16	0.3	0.0	16.7
Urticina eques, RL P	17	0.3	0.0	6.3
Bryozoa				
Aeta anguina	2	0.0	0.0	2.1
Conopeum seurati	3	0.1	0.0	6.3
Electra crustulenta, B	33	0.7	0.1	25.0
Electra pilosa	7	0.1	0.0	8.3
Farella repens	60	1.3	0.1	41.7
Pantopoda				
Pycnogonum littorale	1	0.0	0.0	2.1
Polychaeta				
Arenicola marina	2	0.0	0.0	4.2
Eumida sanguinea	3	0.1	0.0	4.2
Harmothoe imbricata	18	0.4	0.0	6.3
Harmothoe impar	29	0.6	0.0	8.3
Harmothoe sp.	3	0.1	0.0	6.3
Lanice conchilega	10	0.2	0.0	4.2
Lepidonotus squamatus	17	0.4	0.0	10.4
Marenzelleria viridis, B	2	0.0	0.0	4.2
Neanthes succinea	135	2.8	0.2	25.0
Nephthys caeca	6	0.1	0.0	8.3
Nephtys hombergi	3	0.1	0.0	6.3
Polydora cornuta	4	0.1	0.0	6.3

Grab samples species list

Taxon	A	B	C	D
Hydrozoa				
Clytia hemisphaerica	2	0.1	0.0	0.7
Eudendrium ramosum	2	0.1	0.0	0.7
Hartlaubella gelatinosa	15	1.0	0.2	1.3
Laomedea sp.	4	0.3	0.1	2.0
Obelia longissima	345	23.0	5.4	14.0
Sertularia cupressina, RL 3	2	0.1	0.0	1.3
Anthozoa				
Diadumene cincta	3	0.2	0.0	0.7
Metridium senile, RL P	28	1.9	0.4	4.0
Sagartia troglodytes	19	1.3	0.3	5.3
Urticina felina	7	0.5	0.1	2.7
Bryozoa				
Conopeum seurati	13	0.9	0.2	2.7
Electra crustulenta, B	182	12.1	2.9	14.7
Electra monostachys	1	0.1	0.0	0.7
Electra pilosa	4	0.3	0.1	2.0
Farella repens	3	0.2	0.0	2.0
Nemertini				
Nemertini spp.	2	0.1	0.0	1.3
Polychaeta				
Arenicola marina	5	0.3	0.1	2.0
Capitella capitata	12	0.8	0.2	6.0
Harmothoe impar	1	0.1	0.0	0.7
Harmothoe sarsi	1	0.1	0.0	0.7
Heteromastus filiformis	1270	84.7	19.9	46.7
Marenzelleria viridis, B	563	37.5	8.8	20.7
Neanthes succinea	126	8.4	2.0	15.3
Neanthes virens	9	0.6	0.1	6.0
Nephthys caeca	175	11.7	2.7	48.0
Nephthys longosetosa	11	0.7	0.2	6.7
Nephtys hombergi	22	1.5	0.3	11.3
Nephtys kersivalensis	66	4.4	1.0	26.7
Nephtys sp.	13	0.9	0.2	5.3
Phyllodoce mucosa	2	0.1	0.0	1.3
Polydora cornuta	8	0.5	0.1	2.0
Pygospio elegans	1	0.1	0.0	0.7
Scolecolepis foliosa	1	0.1	0.0	0.7
Scolecolepis squamatus	2	0.1	0.0	0.7
Scoloplos armiger	27	1.8	0.4	12.0
Spio martinensis	5	0.3	0.1	3.3

Table A-1 (continued)

Dredge trawl species list

Taxon	A	B	C	D
Crustacea				
Atylus swammerdami	3	0.1	0.0	4.2
Balanus crenatus	47	1.0	0.1	8.3
Balanus improvisus, B	841	17.5	1.4	25.0
Carcinus maenas ad.	1958	40.8	3.2	97.9
Carcinus maenas juv.	651	13.6	1.1	58.3
Corophium volutator	8	0.2	0.0	4.2
Crangon crangon	41064	855.5	68.1	100.0
Gammarus c.f. *crinicornis*	1	0.0	0.0	2.1
Gammarus locusta	58	1.2	0.1	16.7
Gammarus salinus, B	594	12.4	1.0	20.8
Gammarus sp.	10	0.2	0.0	6.3
Gastrosaccus spinifer	2	0.0	0.0	4.2
Liocarcinus holsatus ad.	95	2.0	0.2	47.9
Liocarcinus holsatus juv.	46	1.0	0.1	31.3
Mesopodopsis slabberi	2	0.0	0.0	4.2
Neomysis integer, B	77	1.6	0.1	20.8
Pandalus montagui	1	0.0	0.0	2.1
Praunus flexuosus	7	0.1	0.0	4.2
Schistomysis kervillei	3	0.1	0.0	2.1
Mollusca				
Aeolidia c.f. *papillosa*	11	0.2	0.0	16.7
Cerastoderma edule	49	1.0	0.1	2.1
Crepidula fornicata	2	0.0	0.0	4.2
Ensis directus	99	2.1	0.2	22.9
Hydrobia ulvae	5	0.1	0.0	4.2
Macoma baltica	5	0.1	0.0	10.4
Mytilus edulis	8868	184.8	14.7	29.2
Mytilus edulis juv.	76	1.6	0.1	39.6
Petricola pholadiformis, RL 3	2	0.0	0.0	4.2
Echinodermata				
Asterias rubens	857	17.9	1.4	35.4
Pisces				
Agonus cataphractus	62	1.3	0.1	52.1
Callionymus lyra	3	0.1	0.0	4.2
Ciliata mustela	3	0.1	0.0	6.3
*Clupea harengus**	1	0.0	0.0	2.1
Eutrigla gurnhardus	1	0.0	0.0	2.1
*Gasterosteus aculeatus**	1	0.0	0.0	2.1
Limanda limanda	375	7.8	0.6	56.3
Liparis liparis, RL 3	3	0.0	0.0	2.1
Myoxocephalus scorpius	4	0.1	0.0	6.3
*Osmerus eperlanus**	48	1.0	0.1	31.3
Platichthys flesus	5	0.1	0.0	6.3
Pleuronectes platessa	251	5.2	0.4	47.9
Pomatoschistus minutus	512	10.7	0.8	81.3
Solea vulgaris	15	0.3	0.0	16.7
*Sprattus sprattus**	1	0.0	0.0	2.1
Syngnathus rostellatus	161	3.4	0.3	72.9
Zoarces viviparus	1	0.0	0.0	2.1

Grab samples species list

Taxon	A	B	C	D
Spiophanes bombyx	1	0.1	0.0	0.7
Tharyx killariensis	6	0.4	0.1	3.3
Oligochaeta				
Tubificoides benedeni	11	0.7	0.2	2.0
Tubificoides sp.	5	0.3	0.1	2.7
Crustacea				
Balanus crenatus	88	5.9	1.4	4.7
Balanus improvisus, B	1567	104.5	24.6	13.3
Bathyporeia pelagica	408	27.2	6.4	17.3
Bathyporeia pilosa, B	3	0.2	0.0	2.0
Bathyporeia sarsi	50	3.3	0.8	14.0
Carcinus maenas	27	0.8	0.4	7.3
Corophium volutator	17	1.1	0.3	3.3
Crangon crangon	53	3.5	0.8	27.3
Gammarus salinus, B	27	1.3	0.4	4.0
Gastrosaccus spinifer	15	1.0	0.2	6.7
Liocarcinus holsatus	1	0.1	0.0	0.7
Mesopodopsis slabberi	10	0.7	0.2	6.0
Neomysis integer, B	57	3.8	0.9	22.7
Parapleustes assimilis	2	0.1	0.0	1.3
Praunus flexuosus	2	0.1	0.0	1.3
Schistomysis kervillei	2	0.1	0.0	1.3
Mollusca				
Aeolidia c.f. *papillosa*	3	0.2	0.0	2.0
Cerastoderma edule	3	0.2	0.0	0.2
Crepidula fornicata, juv.	1	0.1	0.0	0.7
Ensis directus	301	20.1	4.7	24.0
Hydrobia ulvae	142	9.5	2.2	34.0
Macoma baltica	50	3.0	0.8	18.0
Mya arenaria	1	0.1	0.0	0.7
Mytilus edulis	83	5.5	1.3	3.3
Mytilus edulis, juv.	14	0.9	0.2	2.7
Petricola pholadiformis, RL 3	12	1.0	0.2	1.3
Echinodermata				
Asterias rubens	2	0.1	0.0	0.7

* = non-benthic species

The impact of harbour sludge disposal on benthic macrofauna communities in the Weser estuary

Jan Witt[1,2], Alexander Schroeder[2], Rainer Knust[2], Wolf E. Arntz[2]

[1] Küstenökologische Forschungsgesellschaft mbH (KÜFOG), Alte Deichstr. 39, D-27612 Loxstedt-Ueterlande, Germany, Tel.: ++49 (0) 4740/ 1071, e-mail: info@kuefog.de

[2] Alfred Wegener Institute of Polare and Marine Research, Benthic Ecosystems, Columbusstraße, D-27515 Bremerhaven, Germany.

Abstract

During an open water disposal of about 710,000 m³ of harbour sludge in the polyhaline zone of the Weser estuary, Germany, a monitoring programme was carried out to investigate the impact on benthic invertebrates. The macrofaunal communities of 4 sites within the disposal area and 5 sites in a reference area were compared after discharge. The location and extension of the potentially affected area were inferred from a morphodynamic computer model (TIMOR 3, ZANKE 1998). Disposal effects were analysed by comparing species numbers, densities, diversity and faunal similarity by multivariate methods. A loss of diversity and a decline in the abundance of several species in the disposal area were measured. The species number was reduced up to 50% and important habitat structures were absent from the disposal area. Several benthic species indicated an impact of the disposal. The importance of species such as *Mytilus edulis* (Mollusca) and *Lanice conchilega* (Polychaeta) for the diversity of the community and their sensitivity to sediment discharge are analysed. The difficulties of separating dumping effects from natural variation in a dynamic estuarine channel system are discussed.

Keywords Harbour sludge disposal, Dumping effects, Impact assessment, Benthic invertebrates, Weser estuary

Introduction

The effects of sediment disposal on macrofaunal communities in open waters have been investigated by several authors (ROSENBERG 1977a b; WILDISH and THOMAS 1985; MÜHLENHARDT-SIEGEL 1988, 1990; ESSINK et al. 1992). The impact on the benthic communities varies from minimal to severe, depending on the amount and type of material and the modus of discharge. The formation of deposit layers, changes in sediment composition, an increase in turbidity and chemical changes in the water column are the main stress factors to invertebrates after a discharge (ESSINK 1995, 1996; KROST 1996). The high variability of benthic communities in dynamic systems such as estuaries makes it difficult to differentiate between natural variability and man-induced changes (WILDISH &

THOMAS 1985). A reliable impact assessment of sediment disposals in open waters and a standardisation of methods is therefore an international scientific objective (BFG 1992, 1999, PIANC 1998).

For the maintenance of the harbours of Bremerhaven (Germany), dredging is necessary at regular intervals. The sedimentation rate in the harbours varies between 0.3 and 1.6 m/a due to the high suspension load of the river Weser and the sedimentation conditions in the semi-enclosed harbours (WOLTERING 1997). About 550,000 m^3 of muddy sediments from these harbours have been dumped in the polyhaline zone of the Weser estuary each year. This investigation was carried out on behalf of the Harbour Administration of Bremen (bremenports GmbH formerly HBH) in order to assess the effects of harbour sludge disposal on the benthic macrofauna community.

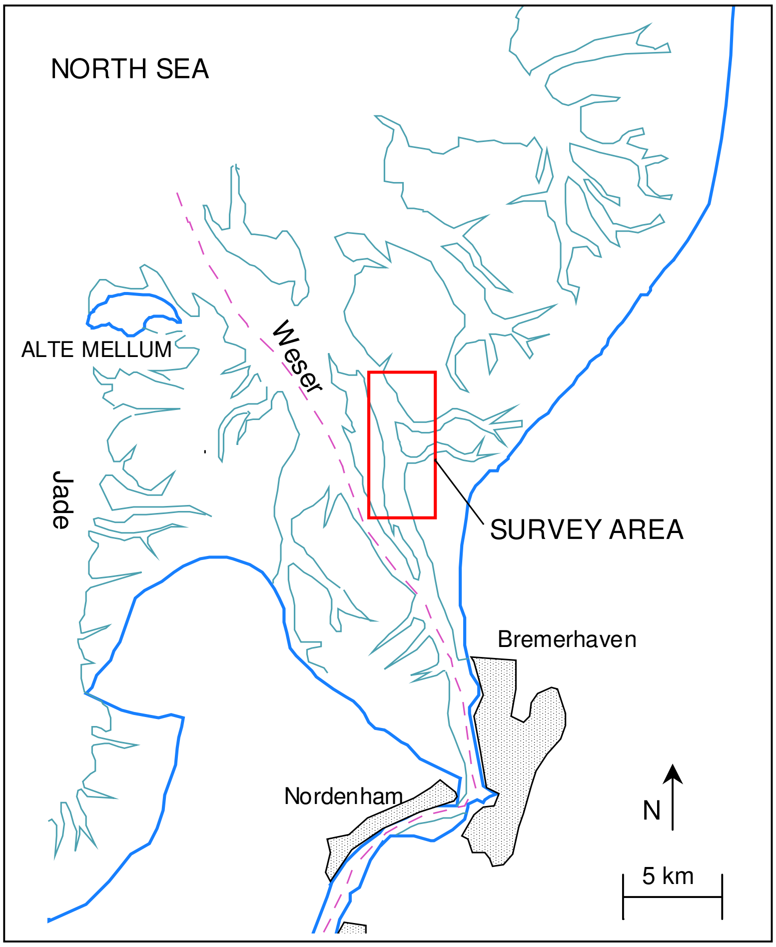


Fig. 1 The Weser estuary with the survey area “Wurster Arm” (broken line indicates shipping lane).

Methods

The Weser estuary is funnel-shaped, with a wide opening towards the North Sea. Due to the tidal amplitude and the volume of freshwater outflow, it has to be considered as partially mixed (WELLERSHAUS 1981; McLUSKY 1989). The main tidal channel of the Weser was built and is maintained as a major shipping lane with a large number of cargo ships using it regularly. The survey area is located at a neighbouring side channel, called the "Wurster Arm", which is used by smaller, often private vessels and for fishery purposes (Fig.1). The disposal area, in the centre of this channel, has been used for sediment discharge since the 1960s.

It has a water depth of 16 m while the average depth of the channel is around 8 m; there is a strong tidal current of up to 1.5 m/s (KÜFOG 1998). The salinity varies between 17 and 30 PSU. The survey area is thus a polyhaline brackish water zone (REMANE 1958; McLUSKY 1989).

Samples were collected at 9 sites (Fig. 2). The stations within the dumping area (I-IV) were in the centre of the channel, about 100 m apart from each other. The reference stations VII and VIII were located south of the disposal area, the reference station IX north of it. The stations V and VI were located close to the disposal area, towards the intertidal flats, in shallower waters (Fig. 2).

The distinction between the potentially affected area and the reference area was made according to a morphodynamic computer model (TIMOR 3, ZANKE 1998). This model was based on field data such as water depth, currents, tidal water exchange, turbidity and sediment composition. Predictions from this model include an increase of turbidity caused by the disposal, the spatial distribution of sediment fractions, and the height and duration of the sediment layer from the time of disposal. The area of main impact was defined as the area with an additional sediment layer of 10 mm or more for a minimum of 25 days per year and with an increased turbidity of more than 35% above the natural rate (Fig. 2). Natural turbidity in the survey area varies with tides between 10 to 100 mg/l of suspended matter (ZANKE 1998).

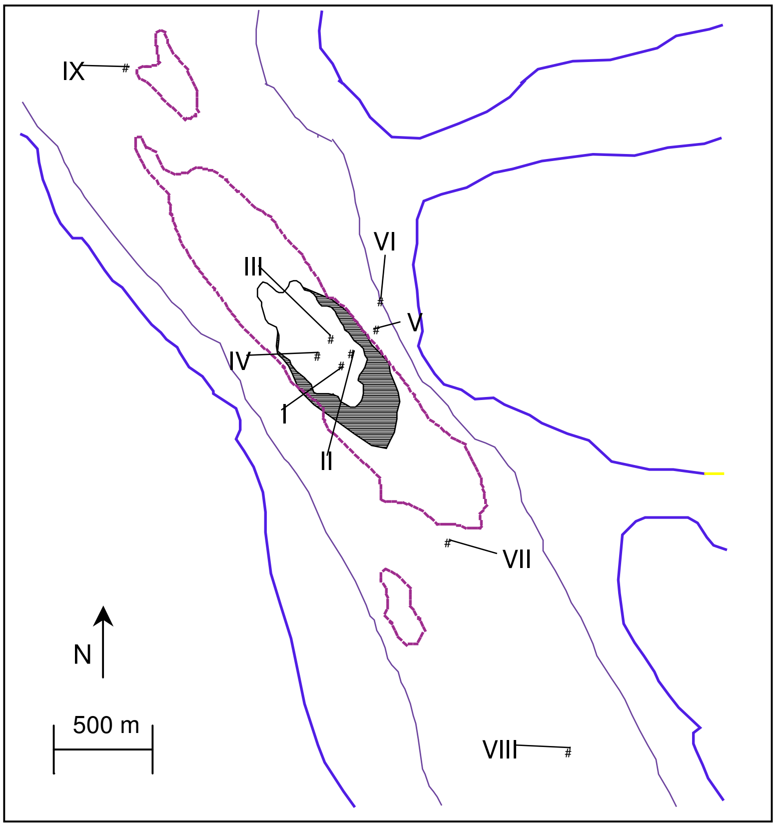


Fig. 2 Location of sampling sites in the survey area (area of maximum sediment deposit- white; area of maximum suspension increase- black lined, based on a sedimentation model of ZANKE 1998).

The periods of dumping and sampling are shown in Figure 3. Samples were collected 2-3 weeks after each disposal period. The amount of discharged sediment varied between 800 and 383,000 m³. The material from the harbours was mainly soft silt sediment which contained a high percentage of organic matter. The area has been used as a disposal site for many years. Therefore, in the absence of any pre-dumping data, it is unknown what the biological situation was before dumping began. The recovery of the benthic community from disposal effects was investigated in August 1999; results will be presented elsewhere. Sampling at each site included 3 replicates of van Veen grabs (0.1 m²) and one dredge trawl (1 m width, 5 mm mesh size). The sediment of the van Veen grab was classified and washed through a sieve with a 1 mm mesh size. The residue was stored in cooled seawater containers; sorted and classified in the laboratory the next day, or it was stored in 80% ethanol (crustaceans) or buffered 5% formalin (polychaetes) for later identification. An additional grab sample was taken at each site for grain size analysis and for measuring organic content by loss of weight on ignition (BUCHANAN 1984).

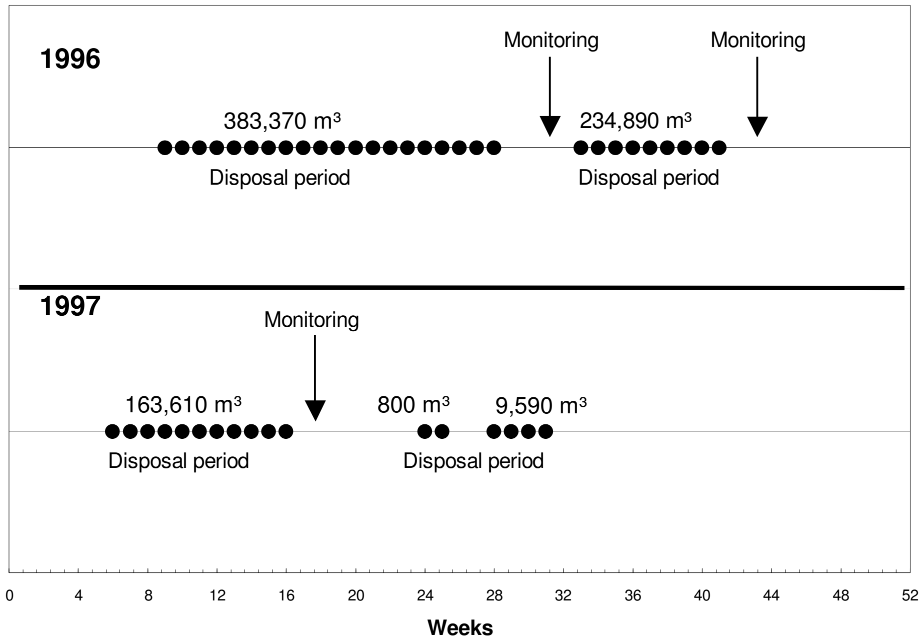


Fig. 3 Time schedule of dumping periods and monitoring surveys (amount of discharged material in m^3).

The dredging direction followed tidal currents, which ensured a steady contact with the bottom. Part of the catch was sorted and classified on board, whilst the remainder was processed as mentioned above. As far as possible, macrofaunal organisms were identified to species level. For faunal analysis a total of 81 grab and 27 dredge samples were taken. The vessel "Hol Deep" of the Harbour Administration of Bremen (bremenports GmbH) was used for the survey.
The analysis of the endobenthic data (grab samples) was based on endobenthic and sessile epibenthic species only. Epibenthic data (dredge samples) were handled separately. Pelagic species such as: *Pleurobrachia* sp., *Bougainvillia* sp. and *Sagitta* sp. were not considered in the analyses. Because station V was located at the boundary between the disposal and reference area, it was not used for direct comparisons (see Fig. 2).

Community structure was analysed by univariate methods for comparisons of species density and community diversity and by multivariate techniques for faunal similarity. Ecological information and feeding behaviour was obtained from the literature, such as HAYWARD & RYLAND (1990), BARNES (1994) and HARTMANN-SCHRÖDER (1996). The diversity indices used included Shannon`s diversity index (H`, based on log2), measurements of evenness (J`) and species richness (SR), as described by PIELOU (1975) and MARGALEF (1958). Differences were analysed by the Mann-Whitney U-test. For statistical analyses of faunal data the software package PRIMER, PML (v5) was used (CLARKE & WARWICK 1994, CLARKE & GORLEY 2001). Non-metric, multi-dimensional scaling (MDS) was used to identify patterns in the community structure (KRUSKAL & WISH 1978). Characteristic species, which contribute most to the similarity of the station groups, were identified using the SIMPER (similarity percentage) analysing tool of the PRIMER software. Data transformation was applied by the fourth root to minimise the influence of dominant species. Similarities were calculated using the Bray-Curtis coefficient (BOESCH 1977).

Results

Sediments

Sediments at the dumping site (stations I-IV) and the reference area (stations VI-IX) differed at all times. Sediments of the disposal area had a higher percentage of silt and organic matter, and a lower median particle size than those of the reference area (Table 1, Fig. 4). The differences between the dumping site and the reference area were small in August 1996, but high in October 1996 and April 1997. The proportion of silt correlated positively with the percentage of organic matter. In April 1997 the percentage of silt was low in the reference area, with a low variation between the stations. High variation in sediment composition over time was noticed at station IV. The reference stations showed more consistent sediment conditions, with a higher proportion of fine sand. Station V, which was located close to the disposal site, had stable sediment conditions with over 90% fine sand and no obvious silt sedimentation from the disposal.

Table 1 Sediment parameters for the disposal and reference area (n= number of stations; Sig.: significance of Mann-Whitney-test *p<0.1, **p<0.05, ***p<0.01).

Survey	Sediment parameter	Sig.	Disposal area (Stations I-IV)	Reference area (Stations VI-IX)
August 96, n=4	Silt (%)		21.8	17.7
	Organic matter (%)		5.8	3.8
	Median grain size (mm)		0.08	0.09
October 96, n=4	Silt (%)	**	58.0	11.50
	Organic matter (%)	**	10.0	3.3
	Median grain size (mm)	**	0.06	0.1
April 97, n=4	Silt (%)	**	43.7	2.7
	Organic matter (%)	**	9.5	1.0
	Median grain size (mm)		0.09	0.10
Over all, n=12	Silt (%)	**	41.1	8.9
	Organic matter (%)	**	8.1	2.6
	Median grain size (mm)		0.08	0.10

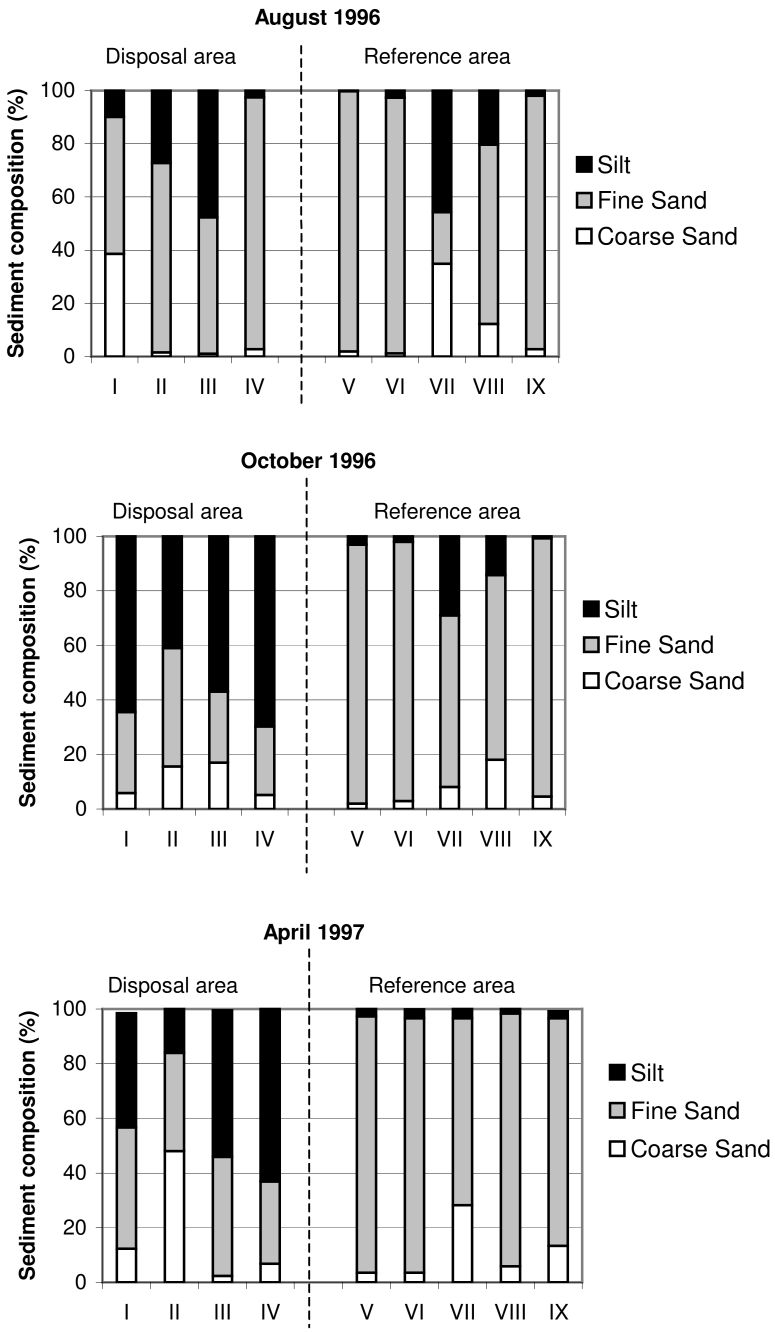


Fig. 4 Results of sediment analysis (% of dry weight) in the disposal area (stations I-IV) and the reference area (stations V-IX).

Endobenthic macrofauna (grab sample data)

A total of 31 benthic species (5.7 per station) were collected by grab in the disposal area, compared to 51 species (10.6 per station) in the reference area. An average of 172.8 individuals per m² were found in the disposal area, and 486.5 individuals per m² in the reference area. Table 2 gives species numbers, individual numbers and community indices of the grab samples (endobenthic and sessile epibenthic species only) from the disposal area (stations I-IV) and the reference area (stations VI-IX).

Table 2 Numbers of species and individuals, and community indices from grab samples in the disposal and the reference area (endobenthic and sessile epibenthic species only; Mean: number of individuals and species per m² and site for all surveys, n=12; SD: standard deviation; Sig.: significance of Mann-Whitney-test *p<0.1, **p<0.05, ***p<0.01)

	Sig.	Disposal area (Stations I-IV, n=12)		Reference area (Stations VI-IX, n=12)	
		Mean	(+/-) SD	Mean	(+/-) SD
Species per site					
Total	**	5.7	4.4	10.6	6.8
Endobenthic only	***	3.8	2.3	7.8	5.2
Cnidaria		0.7	1.1	0.8	1.3
Crustacea	***	0.7	1.0	2.0	1.3
Polychaeta	**	2.5	1.3	5.0	3.6
Mollusca	*	1.4	1.2	2.3	1.1
Individuals per m^2					
Total	*	172.8	224.6	486.5	821.1
Endobenthic only	**	112.6	142.5	381.8	682.0
Crustacea	**	6.8	15.2	85.5	166.9
Polychaeta		96.3	128.8	260.9	512.5
Mollusca	**	53.8	130.4	118.2	175.7
Community indices					
Diversity	*	0.85	-	1.15	-
Species richness	**	0.68	-	1.21	-
Evenness		0.68	-	0.69	-

The average number of 3.8 endobenthic species per station in the disposal area was significantly lower than the 7.8 species per station in the reference area ($p<0.01$, Table 2). A maximum of 22 species was found at station VII in August 1996. The average number of 112.6 individuals per m² in the disposal area was significantly lower ($p<0.05$) than the 381.1 individuals per m² in the reference area. The average diversity (H`) was significantly lower in the disposal area (0.85, $p<0.1$) than in the reference area (1.15). The species richness (0.68) in the disposal area was significantly lower compared to 1.21 at the reference sites ($p<0.05$, Table 2).

There was a clear seasonal influence (Fig. 5): The number of species and individuals were high in August, and low in October and April. The highest diversity was found in August 1996, the lowest in October 1996. The differences in diversity (H`) between disposal and reference sites were high in October (Fig. 5). All data showed a clear difference between disposal and reference area. The evenness (J`) had a maximum of 0.75 in the disposal area in October and 0.82 in the reference area in April 1997.

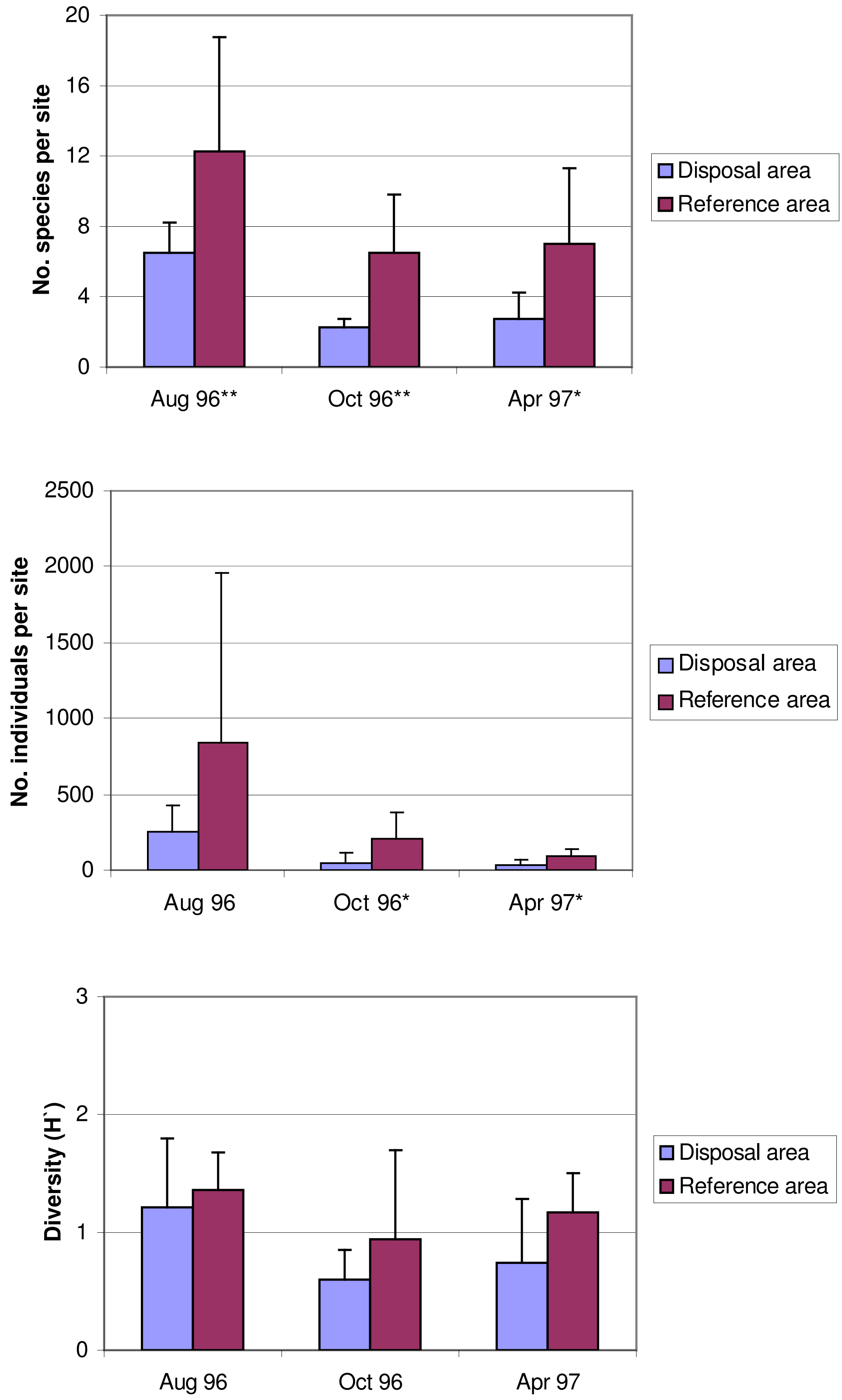
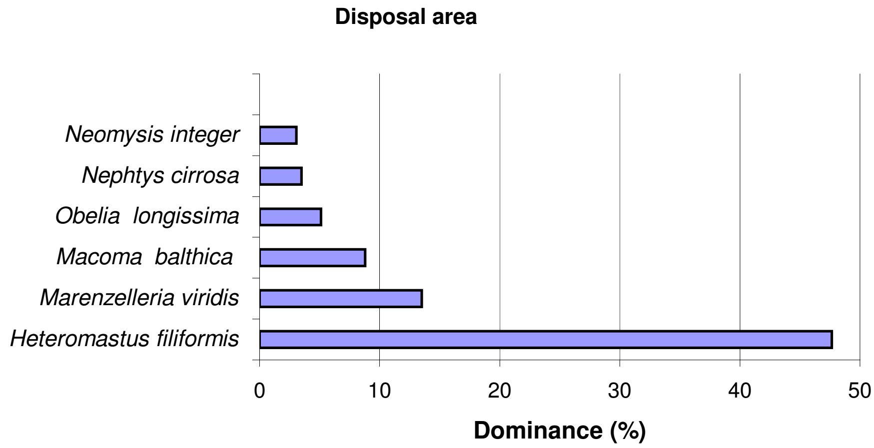


Fig. 5 Numbers of species and individuals per site, and diversity (H`) for the three surveys (grab samples, mean, standard deviation indicated by black line; significance of Mann-Whitney-test *p<0.1, **p<0.05, ***p<0.01).

Comparing both areas on higher taxon level, there were significantly lower species numbers of crustaceans, polychaetes and molluscs in the disposal area (Table 2). The abundance of crustaceans (p<0.05) and molluscs (p<0.025) at the dumping sites was significantly lower than in the reference area. Dominant species in the disposal area were *Heteromastus filiformis* with 47% of all individuals, followed by *Marenzelleria viridis* (13%) and *Macoma baltica* (9%) (Fig. 6). In the reference area *Marenzelleria viridis* dominated with 27%, followed by *Bathyporeia pilosa* (14.6%) and *Eteone longa* (7%).



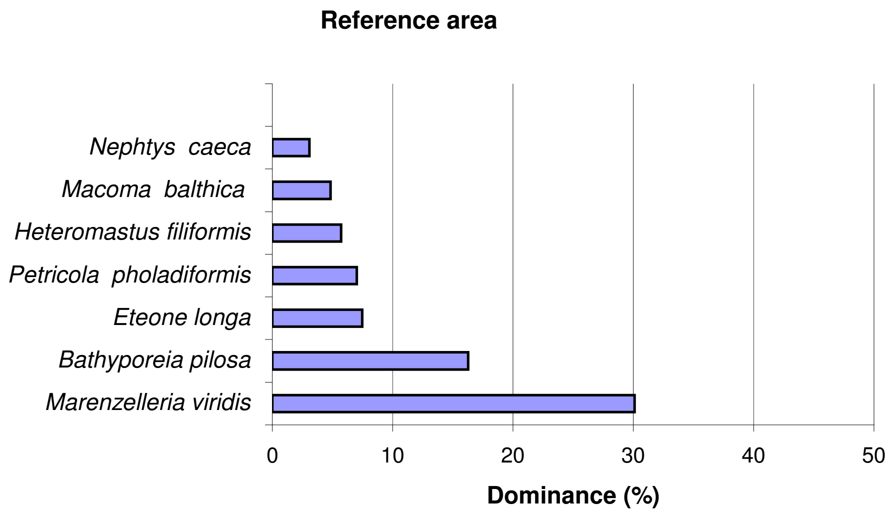


Fig. 6 Numerical dominance of species (%) in the disposal and the reference area (grab sample data, all surveys, species with more than 5% dominance only).

Similarities between grab sample data are presented in the MDS plots in Figure 7. Stations in the disposal area showed clear clusters in all surveys. The stress of all presentations is low, and therefore the plots give reliable pictures of the situation. The separation between the data of the disposal and the reference stations was clearer in April 1997 than in August and October 1996. Stations V and VI, situated in the low water area, showed a high similarity one with another and with the disposal area in August. In April the data of stations V and VI were similar to those of the reference stations.

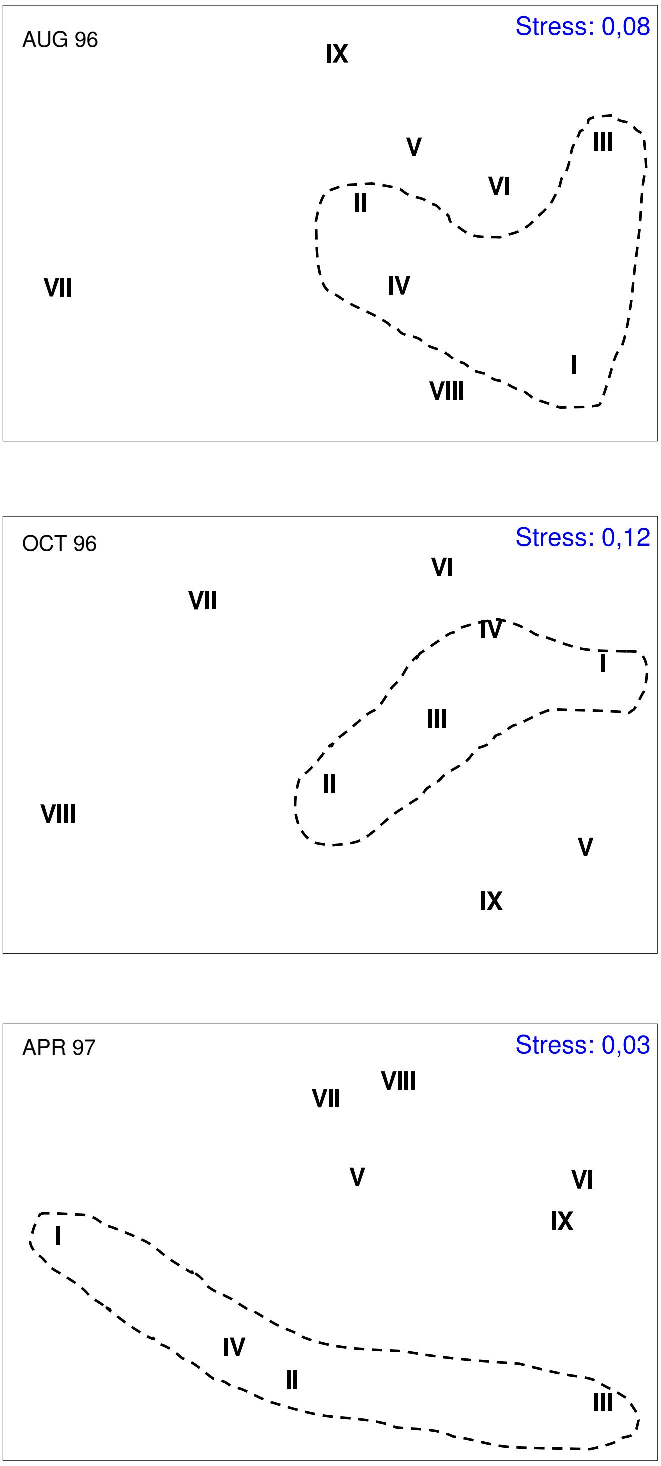


Fig. 7 Results of multidimensional scaling of the endobenthic data (grab samples); MDS plots for the three surveys from August 1996 to April 1997. Stations of the disposal area surrounded by dotted line (Bray-Curtis similarity, 4th root transformed data).

In August station VII showed a very low similarity to the disposal area, which was due to the presence of *Mytilus edulis* in that month. The same could be recognized at station VIII in October 1996. Similarity percentage (SIMPER) analysis of both groups showed an average dissimilarity of 63.4% in August 1996, 83.5% in October 1996 and 74.9% in April 1997. These data are supported by the species listed in Table 3.

Table 3 Average abundances of species contributing with high contribution to the dissimilarity between the disposal and reference area (total dissimilarity in %, SIMPER analysis, √√ transformed grab sample data, n=4).

Survey	**Taxon**	**Average abundance (Ind. /m²)**		**contribution (%)**
		Disposal area	**Reference area**	
August 96	**Total diss.: 63.4%**			
	Heteromastus filiformis	126.7	34.5	12.8
	Polydora caeca	0.0	422.5	12.2
	Marenzelleria viridis	54.3	124.5	12.1
October 96	**Total diss.: 83.5%**			
	Heteromastus filiformis	41.5	8.3	11.6
	Petricola pholadiformis	0.0	53.3	6.9
	Bathyporeia pilosa	0.0	100.0	6.7
April 97	**Total diss.: 74.9%**			
	Nepthys caeca	0.8	23.3	10.7
	Heteromastus filiformis	25.8	13.25	9.9
	Nereis virens	4.0	0.0	8.6

Heteromastus filiformis showed a higher than average abundance at the disposal site in all surveys (Table 3). In the reference area species such as *Petricola pholadiformis*, *Polydora caeca, Bathyporeia pilosa, Marenzelleria viridis* and *Nephtys caeca* were more abundant, yet their respective dominance differed among the survey. To minimize seasonal influences, the average abundances from all surveys (n=12) are given in Table 4.

Crustaceans such as *Balanus crenatus* and *Bathyporeia pilosa,* the polychaete *Nephtys caeca* and the bivalve *Petricola pholadiformis,* showed significantly lower abundances in the disposal area compared to the reference area. The reduction in the abundances of mobile species such as *Neomysis integer*, *Carcinus maenas* or *Crangon crangon* was not significant (see below). Some species that occurred with low abundances in the reference area (*Metridium senile, Sargartia troglodytes, Corophium volutator, Harmothoe* spp., *Pygospio elegans*, *Tharyx killariensis* and *Phyllodoce mucosa*) were missing at the disposal sites. The structurally important species *Lanice conchilega* was not present, adult *Mytilus edulis* were rare in the disposal area (Table 4).

Table 4 Densities of the 15 most abundant species from grab samples in the disposal and reference area (endobenthic and sessile epibenthic species only; Mean: numbers of individuals per m² and site, all surveys, n=12 sites; SD: standard deviation; Sig.: significance of Mann-Whitney-test *p<0.1, **p<0.05, ***p<0.01).

Taxon	Sig.	Disposal area (Stations I-IV, n=12)		Reference area. (Stations VI-IX, n=12)	
		Mean	(+/-) SD	Mean	(+/-) SD
Metridium senile		0.0	0.0	6.7	14.9
Obelia longissima		7.0	21.2	1.9	6.4
Corophium volutator		0.0	0.0	6.5	20.7
Bathyporeia pilosa	*	0.0	0.0	38.6	107.5
Balanus crenatus	*	0.0	0.0	33.8	111.9
Eteone longa		0.3	0.8	15.9	33.6
Marenzelleria viridis		18.3	32.9	43.7	108.3
Nereis virens		1.3	2.8	5.7	14.0
Heteromastus filiformis		64.7	118.7	18.7	24.0
Tharyx killariensis		0.0	0.0	3.1	7.5
Nephtys caeca	***	2.5	7.4	11.0	15.6
Phyllodoce mucosa		0.0	0.0	1.9	5.5
Lanice conchilega		0.0	0.0	1.4	4.7
Macoma balthica		12.0	17.1	12.2	16.1
Mytilus edulis		1.1	2.8	50.8	92.0
Petricola pholadiformis	*	0.0	0.0	20.8	41.3

Epibenthic macrofauna (dredge sample data)

A total of 53 benthic species and 12 fish species were caught in dredge samples: 38 species in the disposal area, and 62 species in the reference area. In Table 5 the number of species and individuals as well as community indices are given for the disposal and reference area. The average species number per site was significantly lower in the dumping area (11.5 species) than in the reference area (17.0 species, p<0.01). The highest species number per site was 29, recorded at station VII in April 1997. The number of individuals decreased in the dumping area with an average of 282 individuals per station, compared to 671 individuals at the reference sites (p<0.05, Mann-Whitney). Diversity showed almost no difference between both areas, although species richness was higher in the reference area (2.8) than in the disposal area (2.3) (Table 5).

Comparing both areas on higher taxon level, there were significantly lower species numbers of cnidarians and molluscs at the dumping sites (Table 5). The abundance of crustaceans and molluscs at the dumping sites was significantly lower than in the reference area. The Cnidaria was the only group with higher numbers of individuals in the disposal area, although filter-feeding, sessile epifauna is supposed to be sensitive to all impacts on the sediment surface (NEWELL et al. 1998).

Table 5 Numbers of species and individuals, and community indices from dredge samples in the disposal and reference area (endobenthic and sessile epibenthic species only; Mean: numbers of species and individuals per sites of all surveys, n=12 sites; SD: standard deviation; Sig.: significance of Mann-Whitney test *p<0.1, **p<0.05, ***p<0.01).

	Sig.	Disposal area (Stations I-IV, n=12)		Reference area. (Stations VI-IX, n=12)	
		Mean	**(+/-) SD**	**Mean**	**(+/-) SD**
Species per site					
Total	***	11.5	3.1	17.0	7.3
Cnidaria	**	2.2	1.3	3.5	1.6
Crustacea		4.7	1.8	5.3	2.2
Polychaeta		0.5	0.9	1.8	2.6
Mollusca	***	0.8	0.7	2.3	1.3
Individuals per site					
Total	**	282.4	388.6	671.3	734.0
Crustacea	**	159.2	188.0	319.6	385.2
Polychaeta		0.7	1.4	27.4	56.9
Mollusca	**	87.6	210.6	186.2	418.4
Echinodermata		0.6	1.0	66.5	116.7
Community indices					
Diversity		1.5	-	1.4	-
Species richness		2.3	-	2.8	-
Evenness		0.6	-	0.2	-

Epibenthic samples from the reference area showed higher numbers of species and individuals for all feeding guilds (Fig. 8). There were significantly higher numbers of species (5.8 species per site) in the reference than in the disposal area (2.2 species per site). Filter feeders and carnivore/omnivore species showed significantly higher numbers of individuals in the reference area compared to the disposal area. In other groups (e.g. deposit feeders) smaller differences between reference and disposal area were recorded, with high variance in the data and therefore no statistical significance (Fig. 8).

The MDS plots of the similarity matrix of the dredge trawls from August 1996 to April 1997 are shown in Figure 9. The disposal sites (stations I to IV) showed clear clusters. Stations V and VI (both in shallower water) were always close to each other, indicating the influence of water depth on the benthic community. The two data groups showed an average dissimilarity of 60.2% in August 1996, 44.2% in October 1996, and 64.2% in April 1997 (SIMPER,

Table 6). The species with the highest influence on this dissimilarity differed during the surveys; seasonal changes were strong as seen in the grab data. Vagile crustacea such as *Praunus flexuosus* and *Schistomysis kervillei* were found with higher abundances in the disposal area. In the reference area species such as *Neomysis integer*, *Asterias rubens* and *Crangon crangon* dominated (Table 6).

Table 6 Average abundances of species contributing with high percentages to the dissimilarity between the disposal and the reference area (SIMPER analysis, √√ transformed data of dredge samples, n=4 sites).

Survey	***Taxon***	***Average abundance (Ind. /m²)***		***Contribution (%)***
		Disposal area	**Reference area**	
August 96	**Total diss.: 60.2%**			
	Praunus flexuosus	14.5	4.8	6.9
	Schistomysis kervillei	8.3	4.3	6.9
	Asterias rubens	0.3	152.8	6.1
October 96	**Total diss.: 44.2%**			
	Balanus crenatus	12.5	11.5	9.2
	Mytilus edulis	0.0	15.5	7.3
	Gammarus salinus	42.5	4.5	6.3
April 97	**Total diss.: 64.2%**			
	Crangon crangon	1.8	21.8	6.6
	Mytilus edulis	3.8	1.5	6.4
	Metridium senile	0.5	20.0	5.0

All surveys taken together, lower average abundances were recorded in the disposal area for species such as *Crangon crangon*, *Metridium senile, Asterias rubens* and *Mytilus edulis. Praunus flexuosus* and *Gammarus salinus* were more abundant in the disposal area. The average abundances of selected species for all surveys is given in Table 7. At the species level there was a significant reduction in the abundances of species such as *Metridium senile*, *Sargartia troglodytes*, *Mytilus edulis, Lanice conchilega* and the associated macrofauna e.g. *Asterias rubens*. Others such as *Hartlaubella gelatinosa*, *Sertularia cupressina, Nereis succinea* and *Hydrobia ulvae* showed declines in abundances which were statistically not significant. The species *Urticina eques, Nymphon* spp.*, Harmothoe imbricata, Mya arenaria*, *Petricola pholadiformis* and *Ensis directus* were not present in the disposal area but could be found in the reference area. Hard substrate species such as *Obelia* spp. and associated macrofauna such as *Gammarus* spp. and juvenile *Mytilus edulis* occurred more abundantly in the disposal area.

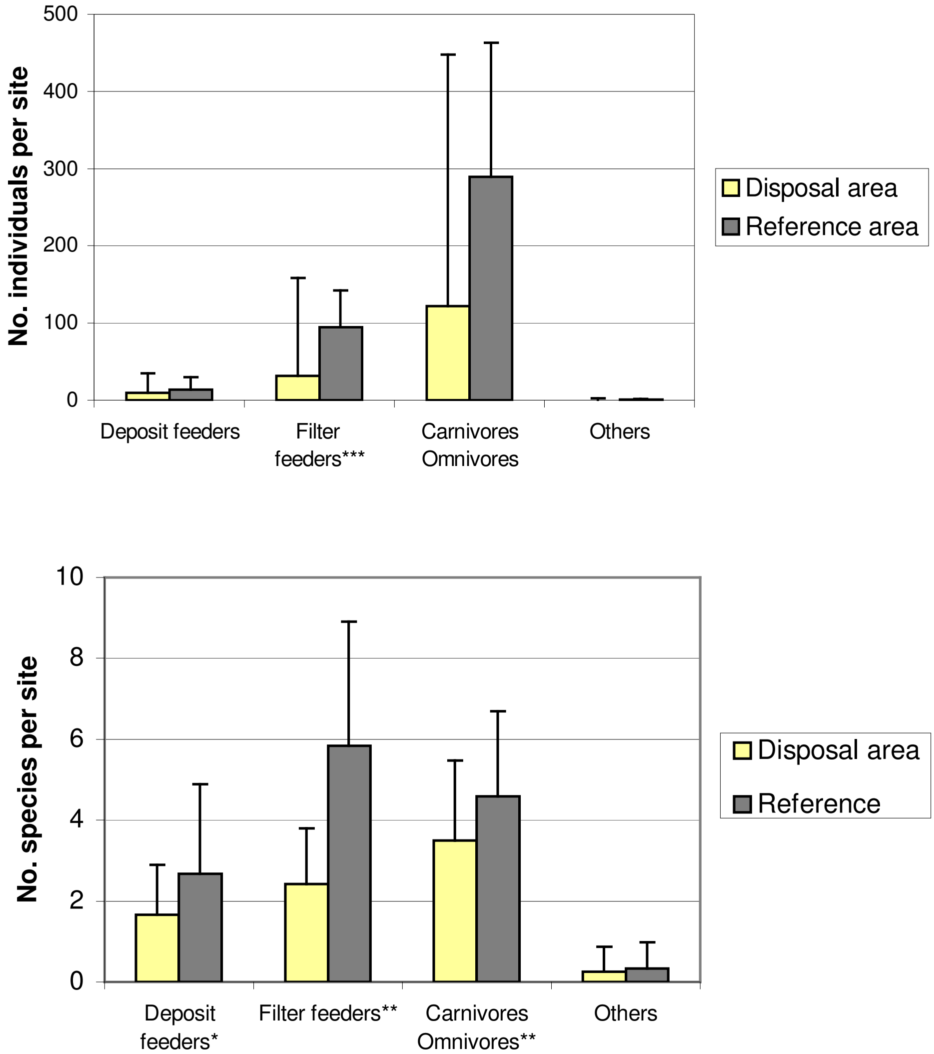


Fig. 8 Number of individuals and species of invertebrates with different feeding modes from the disposal and reference area (all surveys, epibenthic species only, standard deviation indicated by stack line, significance of Mann-Whitney-test *p<0.1, **p<0.05, ***p<0.01).

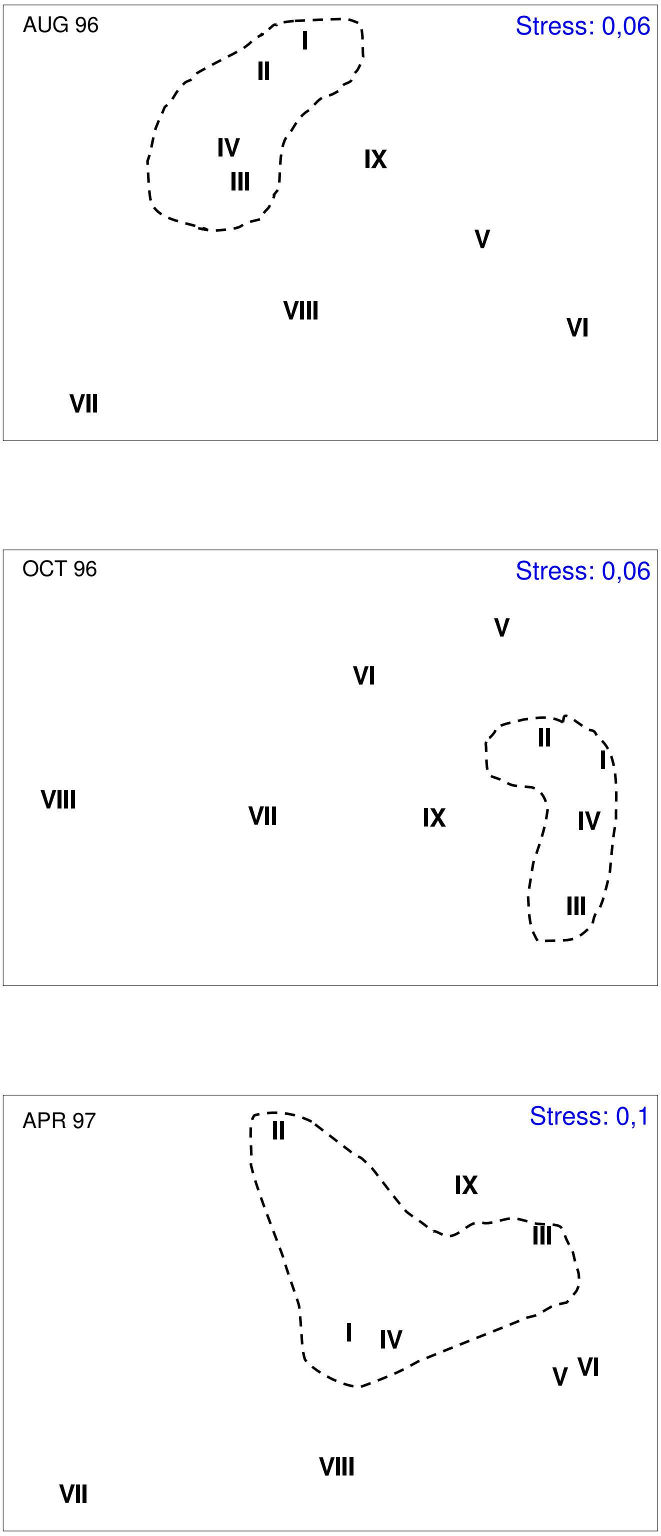


Fig. 9 Results of multidimensional scaling of the epibenthic data (dredge samples); MDS plots for three surveys from August 1996 to April 1997. Stations of the disposal area surrounded by dotted line (Bray-Curtis similarity, presence absence transformed data).

Table 7 Densities of 15 species from dredge samples in the disposal and reference area (Mean: number of individuals per site and m², n=12 sites; SD: standard deviation; Sig.: significance of Mann-Whitney test *p<0.1, **p<0.05, ***p<0.01).

Taxon	***Sig.***	***Disposal area (Stations I-IV, n=12)***		***Reference area. (Stations VI-IX, n=12)***	
		Mean	**(+/-) SD**	**Mean**	**(+/-) SD**
Metridium senile	*	6.3	9.8	38.2	68.4
Sagartia troglodytes	**	0.0	0.0	4.6	6.4
Obelia longissima		23.5	37.0	6.5	11.0
Sertularia cupressina		0.2	0.4	1.3	2.1
Crangon crangon		114.8	170.3	283.8	388.6
Gammarus salinus		14.6	31.0	2.0	2.8
Gammarus locusta		3.9	7.9	1.6	3.4
Carcinus maenas		7.8	12.9	17.5	26.4
Praunus flexuosus		4.9	8.7	2.3	3.7
Nereis succinea		0.0	0.0	7.2	22.0
Lanice conchilega	*	0.0	0.0	11.3	34.9
Harmothoe imbricata		0.0	0.0	1.5	4.4
Mytilus edulis	**	0.1	0.3	148.4	417.2
Petricola pholadiformis		0.0	0.0	0.8	1.9
Asterias rubens	**	0.6	1.0	66.5	116.7

Discussion

The data presented in this study focus on physical effects of open water disposal on macrobenthic invertebrates which are known to indicate changes in sediments and morphology (RACHOR 1982). However, a disposal of sediments can affect pelagic communities as well (SAILA et al. 1972, HAGENDORFF et al. 1996; KOFOD 1997).

There are two main physical impacts of sediment disposal on benthic communities (KROST 1996). First, there is a direct physical disturbance resulting from the formation of a covering layer in the centre of the disposal area from the discharged sediment. MAURER et al. (1986) found a vertical migration and increased mortality depending on the persistence of the covering layer, its depth, and the type of discharged material. Secondly, an increased turbidity can lead to changes in metabolic rates of filter feeders and a reduced larval recruitment and growth (ROSENBERG 1977a,b; DAVIS & HIDU 1988). The impact depends on the amount of discharged sediment, disposal time, water depth, currents, particle size, and other abiotic parameters (VAN DOLAH et al. 1984). Figure 10 summarizes the main effects of sediment disposal in marine or estuarine waters, as considered by various authors (KROST 1996, ESSINK 1996). Currents influence the drift of suspended material, resuspension and sediment advection after the discharge. Therefore the area of impact may be not similar to the disposal area. Exact information of the position and physical impact of the discharge must be gathered before its effects on the benthic fauna can be studied adequately.

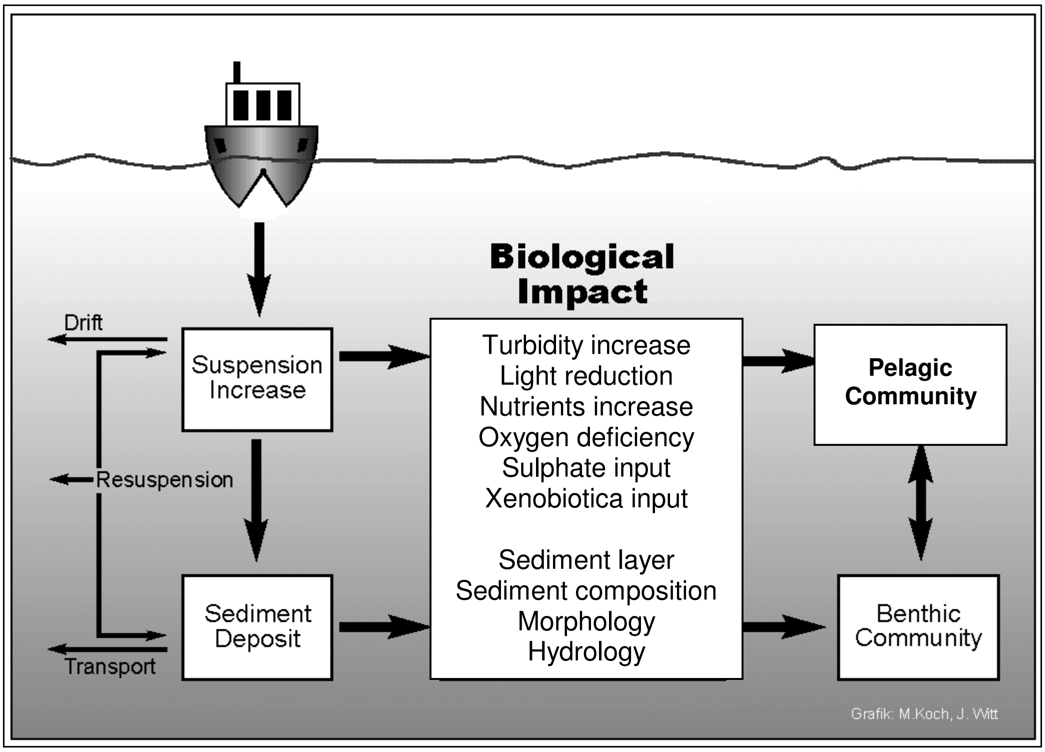


Fig. 10 Diagram summarising potential effects of sediment disposal in open waters.

Sediments

The computer-generated model by ZANKE (1998) predicted that the impact area (Fig. 2) would have a disposal layer of at least 10 mm for a period of more than 25 days. The centre of the dumping area was supposed to have covering layers of 65 mm during the dumping period and for a short time (several hours) afterwards (ZANKE 1998). The results of the sediment analysis confirm the prediction of the computer model as to sediment composition; the higher proportion of silt in the disposal area was caused by the disposal of muddy harbour sludge with a high percentage of organic matter. But the silt fraction was washed into the sediment up to 20 cm depth and did not necessarily form a surface layer. The high variation in the silt proportion at the disposal sites was probably caused by the lateral advection of sediments by the tidal currents. A major part of the sediment discharge was eroded immediately after dumping and carried away by the strong currents. Most of it should stay in the area of the “Wurster Arm” as a thin layer of a few mm according to the computer model (ZANKE 1998). The present study was not intended to verify the prediction, but it was obvious that at least part of the deposit was washed into the sediment, changing its characteristics by silt enrichment. Other investigations found a complete eroding of the discharge layer within hours after dumping (RUMOHR 1996, NEHRING & LEUCHS 1997).

Endobenthic macrofauna

The presented data indicate a clear faunal impoverishment in the disposal area. The endobenthic fauna showed more marked responses in relation to abundance and diversity than the epibenthic fauna. This is due to the higher proportion of sessile and hemi-sessile species in the endobenthic community compared to the more vagile species in the epibenthic assemblage.

At the disposal site numbers of endobenthic and sessile epibenthic invertebrate species were reduced to about 50%. Faunal differences between the disposal site and the reference area were correlated with changes in the sediment composition. The disposal sites had a higher proportion of silt and mud, which influenced species composition. The results showed significant differences at community level, higher taxon level and ultimately, species level which is the most important level for the understanding of ecological interactions (HALL 1994).

The comparison of the dominance structure showed that the impact area was dominated by *Heteromastus filiformis*, *Marenzelleria viridis* and *Macoma balthica.* The polychaete *H. filiformis* prefers mud with a high content of organic matter as a substrate, and the deposit feeder *M. balthica* also may be affected by the nutrient input at the disposal site. Both species appear to respond opportunistically to the disposal of muddy material and nutrient enrichment. Similar to this TESCH & WITT (1998) described an opportunistic reaction of *M. balthica* and *H. filiformis* with highly increased abundances a few months after a disposal of dredged clay in a neighbouring area. Oligochaetes and some polychaetes (*Capitella* sp., *Scolelepis* sp.) showed high abundances in the epicentre of a sewage sludge disposal in Scotland (PEARSON et al. 1986).

Opportunistic species are typical members of the estuarine community of muddy sediments which are subject to frequent disturbances (NEWELL et al. 1998). These communities are well adapted to rapid recolonization and are characterised by large populations of a restricted variety of species. This might fit with most areas of the Weser channel system, but in this case it was the disposal which has transformed sand and stone surfaces into bottoms of fine silt and mud, even in the presence of strong currents. The occurrence of opportunistic species such as *H. filiformis* after the disposal indicates a strong impact of the disposal on sandy habitats.

Marenzelleria viridis was first recorded in the Weser estuary in 1986 and has become dominant in most brackish sediments since then. Although its abundance is doubled in the reference area, this species does not provide a reliable indicator for disposal effects because of its variability in abundance and progressive invasion of all mesohaline sediments (TESCH & WITT 1998).

Crustaceans were reduced in species number and abundance within the disposal area. The strong effect on *Bathyporeia pilosa* which prefers sandy sediments, also seems to be caused by the change in sediment composition after the disposal. *Corophium volutator* was missing in the impact area, although this species is attracted to muddy sediments. This may be due to the lack of a stable sediment surface in the disposal area and the absence of benthic algae such as diatoms as a food resource.

The low abundances of endobenthic polychaetes such as *Tharyx killariensis, Polydora caeca, Phyllodoce mucosa* and *Nephtys caeca* in the dumping area was probably due to reduced oxygen and to an input of sulphide from the discharge, which may stress these species (PEARSON & ROSENBERG 1978). The role of these chemical stress factors for specific species needs to be investigated further. *Nephtys* spp. as a mobile species survived covering layers of several dm in laboratory tests (ESSINK 1996). It is considered an “equilibrium species” indicating a high succession-level of the community (PEARSON & ROSENBERG 1978). *Eteone longa,* a more fragile species, was probably not robust enough to survive the disposal and therefore disappeared completely from the affected area.

The bivalve *Petricola pholadiformis* also appears to be sensitive to disposal. Different from many others, this sessile species can not move to overcome sedimentation and to ensure steady contact with the water column for respiration and filtration. Staying covered by sediment layers for more than a few hours is most likely lethal for *Petricola pholadiformis* (ESSINK 1996). However, its patchy distribution (mostly in clay sediments or peat) reduces the indication value of this clam.

Epibenthic macrofauna

Differences in species composition between the disposal and reference areas were due to the more diverse and abundant assemblage of cnidarians, molluscs and polychaetes in the reference area. Important species for the diversity of the community such as the mussel *Mytilus edulis* and the polychaete *Lanice conchilega*, were absent from the disposal area, as was the associated macrofauna. This supports the results of WIDDOWS et al. (1979) who demonstrated a sensitive response (lowered metabolic rates and morphological deformation) of *Mytilus edulis* to increased turbidity. ESSINK (1996) reported that filtration in *Mytilus edulis* stops when the mussel is covered by only a few mm of sediment. The feeding behaviour of benthic invertebrates is responsible for their individual sensitivity to sediment interference (PEARSON & ROSENBERG 1978; VAN DOLAH et al. 1984; ESSINK 1995). The polychaete *Lanice conchilega* is a sessile, non-selective filter-feeder which shows a strong decline when covered by disposal sediments. Both species can be considered as indicators, due to their sensitive response to disposal activities and their slow recovery.

Table 8 Effects of sediment disposal on selected species, and consequences for the community. Abundance in the disposal area compared to the reference area: ↑- higher abundance, ↓ - lower abundance, ♦- no response, - - absent from data set.

Taxon	Aug 96	Oct 96	Apr 97	Effects on species	Consequences
Dredge sample data					
Mytilus edulis	↓	↓	↓	Reduction, absent in disposal area, sensitive to sediment cover, turbidity	Loss of habitats and diversity (associated fauna)
Lanice conchilega	-	↓	↓	Reduction, partly absent in disposal area, sensitive to sediment cover	Loss of habitats and diversity (associated fauna)
Metridium senile	♦	↓	↓	Significant reduction, sensitive to sediment cover	Reduction of diversity, loss of age structure
Sagartia troglodytes	↓	↓	↓	Significant reduction, sensitive to sediment cover	Reduction of diversity, loss of age structure
Urticina eques	-	↓	↓	Reduction, sensitive to sediment cover	Reduction of diversity, loss of age structure
Sertularia cupressina	↓	♦	↓	Reduction, sensitive to sediment cover	Reduction of diversity, endangered species
Balanus crenatus	♦	↓	↓	Reduction, partly absent, sensitive to sediment cover	Indicates sensitive hard-bottom substrates
Asterias rubens	↓	↓	↓	Significant reduction, associated with Mytilus	Indicates loss of prey (Mytilus)
Gammarus spp.	↑	♦	↓	Associated with Mytilus and Obelia, therefore unspecified	-
Obelia longissima	↑	↑	-	Increase due to hard bottom substrates in the sediment discharge	Probably robust against short-term coverage with mud
Grab sample data					
Nephtys caeca	↓	↓	↓	Reduction, partly absent from the disposal area	Equilibrium species indicates stability and late succession stage
Petricola pholadiformis	↓	↓	-	Complete disappearance under sediment cover	Indicator of sediment deposits in special locations (peat. clay)
Bathyporeia pilosa	↓	↓	-	Reduction, partly absent from disposal area	Indicator of sandy habitats, avoids silt sediments
Eteone longa	↓	-	↓	Reduction, partly absent from disposal area	Generally too low abundance for indication
Macoma balthica	↑	↑	↓	Robust species	Indicates nutrient increase, after a certain period opportunistic
Heteromastus filiformis	↑	↑	↑	Increase of abundance, opportunistic	Indicator of silt and nutrient input, sediment change towards finer grain size

Asterias rubens, as a predator of mussels, is dependent on *Mytilus edulis* and, therefore, was less abundant in the disposal area. *Metridium senile* and *Sagartia troglodytes*, both filter-feeders on hard substrate were less abundant in the impact area and seemed to be sensitive to disposal effects. Although hard substrates were available, *Balanus crenatus* was less abundant in the disposal area. The effects of muddy discharge on this filter-feeding species were more severe than those on other filter-feeders such as *Obelia* spp. which was more abundant in the dump area. This might be due to the differences of the distance between the feeding organs and the sediment surface. Balanids may stop filtration after discharged silt layers of a few mm, whereas flexible stems of *Obelia* spp. rise up to 20 cm above the bottom. On the other hand *Sertularia cupressina*, which has a similar morphology, was strongly reduced in abundance. *Obelia longissima* was the only filter-feeder that survived in the disposal areas without reduction in abundance.

Postlarval *Mytilus edulis* were very often found attached to *Obelia* spp. so that they also occurred with higher abundance in the disposal area. This was similar to other associated species such as *Gammarus salinus* and *Gammarus locusta*, which showed even higher abundances in the disposal area.

Other associated macrofauna such as *Aeolydia pallida* and *Nymphon* spp. appeared to be sensitive to disposal and consequently avoided affected areas. In summary, macrofaunal assemblages of hydrozoans and their associated fauna were not completely destroyed by the disposal, yet their diversity was much reduced.

Epibenthic polychaetes which are active on the sediment surface, seemed to be more sensitive to disposal than others. *Harmothoe* spp., *Nereis* spp., *Eteone longa* and *Lepidonotus squamatus* were less abundant in the disposal area but this was statistically not significant. Epibenthic mobile crustaceans such as *Neomysis integer, Schistomysis kervillei* and *Praunus flexuosus* occurred in higher abundances in the disposal area and may have profited from nutrient input or increased access to its common meiofaunal prey, which often responds opportunistically to disturbances. The observed responses of selected endobenthic and epibenthic species to disposal and their consequences for the community are listed in Table 8.

Conclusions

The effects of sediment discharge on benthic communities in dynamic habitats such as estuarine channels are important for decision makers. An adequate assessment faces serious problems because 1) it may often be difficult to find a reliable reference area within the estuarine gradient, and because 2) the conditions in such habitats are highly variable over time and space. For the present study a morphodynamic computer model was helpful to determine the position and extension of the impact area. The predictions of the computation could be confirmed by the biological data. The study showed that even in dynamic habitats such as estuarine channels, severe effects of sediment disposals can be measured and assessed by biological monitoring. Benthic macrofaunal species were affected differently according to their specific feeding behaviour, mobility or morphology. The effects can be described on the community level, higher taxon level and on the species level with univariate and multivariate methods. The indication values of species to predict or reflect specific effects were discussed. Although the different effects could be explained by the biology of the species, specific laboratory experiments are needed for more detailed information. The knowledge of the species´ strategies to overcome impacts such as sediment covering is still sparse (see GRALL & GLEMAREC 1997).

For a complete impact assessment the recovery of the affected areas has to be investigated. In order to achieve this an additional sampling set was done in August 1999, about 26 months after the disposals were stopped. The results of this study will be presented in a forthcoming publication. Species such as *Mytilus edulis* and *Lanice conchilega* which provide habitats for associated macrofaunal species are important for the community structure, its integrity and species richness. Their sensitivity to physical disposal effects may lead to severe consequences for the community. In addition to these structure-providing species the importance of epibenthic assemblages on hard bottom substrates should be emphasised. Anthozoans such as *Metridium senile* represented a well-developed epibenthic community by old individuals. They reacted sensitively to the discharge and indicated the strong impact of sediment disposals on hard bottom assemblages. Finding more benthic indicators for a precise determination of the different anthropogenic impacts on the benthic community can reduce monitoring and analysis efforts and remains a scientific target in the future.

Acknowledgements

We thank the harbour authority of Bremen (bremenports GmbH, formerly Hansestadt Bremisches Hafenamt Bremerhaven), in particular Mr. U. von Bargen and Dr U. Burghardi for supporting this paper and for the release of data. Many thanks are due to the crew of the bremenports-vessel “Hol Deep” and to the Küfog-Team being a great help not only during field and laboratory works.

4 DISCUSSION AND CONCLUSIONS

In the following chapter the most important results of this thesis will be summarized and discussed. For a more detailed discussion on certain aspects see the attached publications. At first the results of benthic spatial distribution in the mesohaline and polyhaline area of the Weser estuary (publication I and II) will be discussed. From the local distribution aspects towards a benthic inventory and characterisation of all brackish zones the aggregated data from external studies are added and analysed, presenting the first comprehensive picture of benthic assemblages of the Weser estuary (based on chapter 3). The third part concentrates on the sensitivity of benthic communities, actual threats and ways to assess human impacts on estuarine benthic assemblages properly (based on publication III).

Linking the results of benthic spatial distribution to the aspects of benthic sensitivity in the last chapter it will finally be discussed how these results may contribute to the requirements of European environmental directives and how a management plan for the Weser estuary could be based on macrobenthic data. Conclusions will be drawn after each section indicated by a frame.

4.1 Spatial distribution of benthic species in the mesohaline and polyhaline zone (publication I and II)

The analysis of benthic spatial distribution in the brackish water zones of the Weser estuary focused on an along-estuary gradient caused by salinity, a vertical gradient caused by water depth in respect to tidal height and the distribution of substrates. In the polyhaline channel the analysis was restricted to subtidal biotopes (publication II), whereas the analysis in the mesohaline area included subtidal, intertidal and supratidal biotopes (publication I).

The analysis within the mesohaline zone showed that the vertical salinity gradient was reflected by a higher species diversity, a different composition of species and taxonomic groups and a change in feeding strategies from the supratidal to the deeper subtidal areas. The strong differences between the intertidal and subtidal assemblage were additionally caused by the presence of stony substrates on the deep slope of the channel (Fig. 21) and endobenthic species that occurred in the subtidal sediments exclusively. The intertidal benthic community was further separated by muddy and sandy sediments.

The occurrence of taxonomic groups and species of fresh water origin or species with a preference for low salinity in the supratidal habitats was explained by the influence of rain and fresh water from the surface run off. The supratidal areas showed certain small-scaled structures of importance to brackish-water species. Beside natural habitats artificial structures were included in the analysis of habitat function.

In Fig. 21 and Fig. 22, cross sections of the different tidal zones of sediments and groynes in the mesohaline zone are presented schematically compiling most obvious habitat stuctures. The distribution of characteristic species is given referring to the different sediments and substrates.

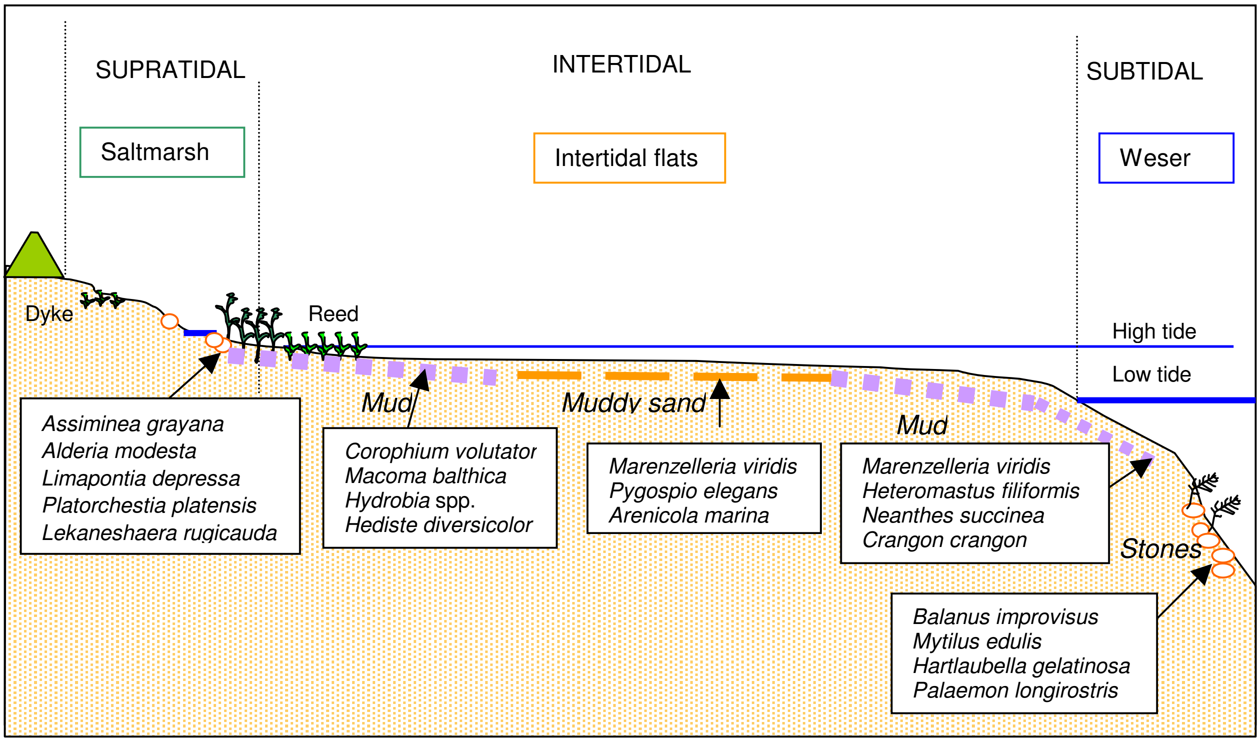


Fig. 21 Benthic assemblages along a cross section of the mesohaline zone of the Weser estuary (habitat of selected species is indicated by its maximal abundance).

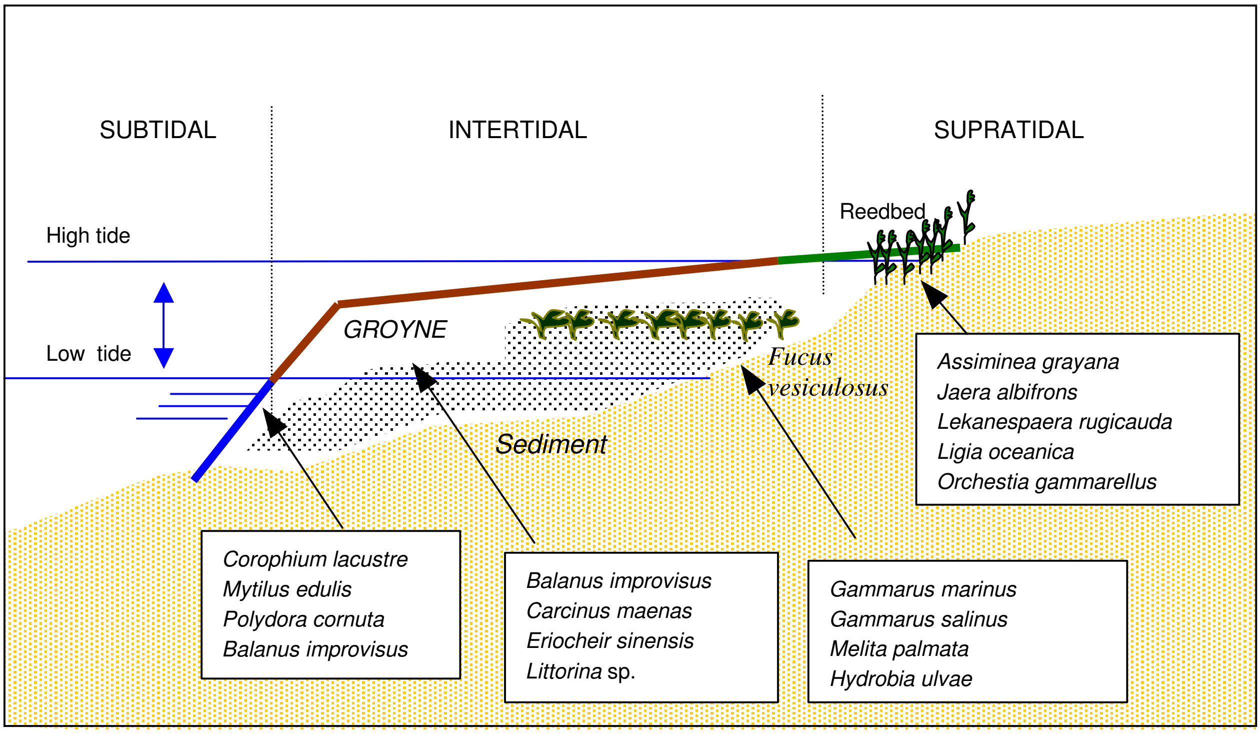


Fig. 22 Spatial distribution of benthic assemblages on a groyne in the mesohaline zone of the Weser estuary (habitat of selected species is indicated by its maximal abundance).

The analysis of species distribution in an estuarine area that is strongly influenced by man reflects a controversial situation within an environmental evaluation. On the one hand the constructions along the shores such as groynes and watershed walls cause a loss of pristine shorelines and reduce natural dynamic processes (SMAAL et al. 1991, MEIRE et al. 1994, LERBERG et al. 2000). In the surveyed intertidal flats the characteristic distribution of sediments within the tidal range as given in REISE (1985) or RAFFAELLI & HAWKINS (1996) was found to be reversed by the influence of the groynes. On the other hand groynes prevent rare mudflats from erosion and provide exclusive habitats to genuine brackish water species and endangered species by their own structure.

In case of artificial salt marsh ditches, which give sheltered tidal areas with reduced salinity to species of former pools and ponds, their substitute function is obvious and a valuable contribution to estuarine diversity conclusive (ARMITAGE et al. 2003). A substitute function of subtidal groynes was limited because although the benthic community was similar to natural stone layers lower species numbers and densities were registered in this case study.

In the intertidal area natural hard structures seem to be restricted to single stones, intertidal mussel beds or shell deposits. A substitute function of intertidal groynes is not apparent. Amphipods, which use dense coverage of algae (*Fucus vesiculosus*) on the intertidal groynes as their exclusive habitat in the Weser estuary may have profited therefore from the ongoing extension of these constructions. Similar algae coverage as a benthic habitat is described from intertidal mussel beds by ALBRECHT & REISE (1994). An assumed substitution of habitat function needs further examination of both structures from the same area. An extensive evaluation of the effects of watershed constructions on the sediment distribution and morphology is beyond the objectives of this study and given in HOVERS (1973). Effects on species and further biological aspects are presented in MEIRE et al. (1994).

KÜHNE & RACHOR (1996) emphasised the importance of hard substrates for benthic diversity in the soft bottom dominated German Bight. The importance of estuarine hard substrates as stated in WARWICK & DAVIES (1977) has been nearly ignored in German estuaries so far due to a lack of data and the obvious dominance of soft bottom substrates.

The analysis of spatial patterns in the polyhaline area shows similar principles of benthic distribution (publication II). As basic distribution factors salinity, water depth, morphology and substrates or sediments were identified.

The combination of benthic distribution factors, as previously described by DÖRJES (1978), COLEMAN et al. (1978) and RAINER (1981), was similar to that found for the mesohaline communities (publication I) but with less obvious anthropogenic influences.

In contrast to the typical decrease of species numbers with lower salinity as stated in BOYDEN & LITTLE (1973) and JONES et al. (1986), it was shown that habitat diversity was higher in the southern part due to a different morphology and higher diversity of substrates.

Subtidal hard bottom substrates and especially mussel beds of *Mytilus edulis* as spots of relatively high diversity contributed to the higher species richness in the southern more brackish part of the polyhaline zone. As mentioned for certain parts of the North Sea in SAIER (2002), DOLMER & FRANDSEN (2002), subtidal mussel beds of *Mytilus edulis* provide similarly important habitats to estuaries. Associated fauna was found to be diverse when dense covers of hydroids provided additional habitat structures.

A low point diversity of the polyhaline community was found to be connected to a relatively high large-scale diversity stressing the need for considering different spatial scales when identifying estuarine diversity (cf. GRAY 2000). Spatial variance of benthic communities in estuaries is generally higher than seasonal and interannual variance, which is often ignored within a monitoring (EDGAR & BARRETT 2002).

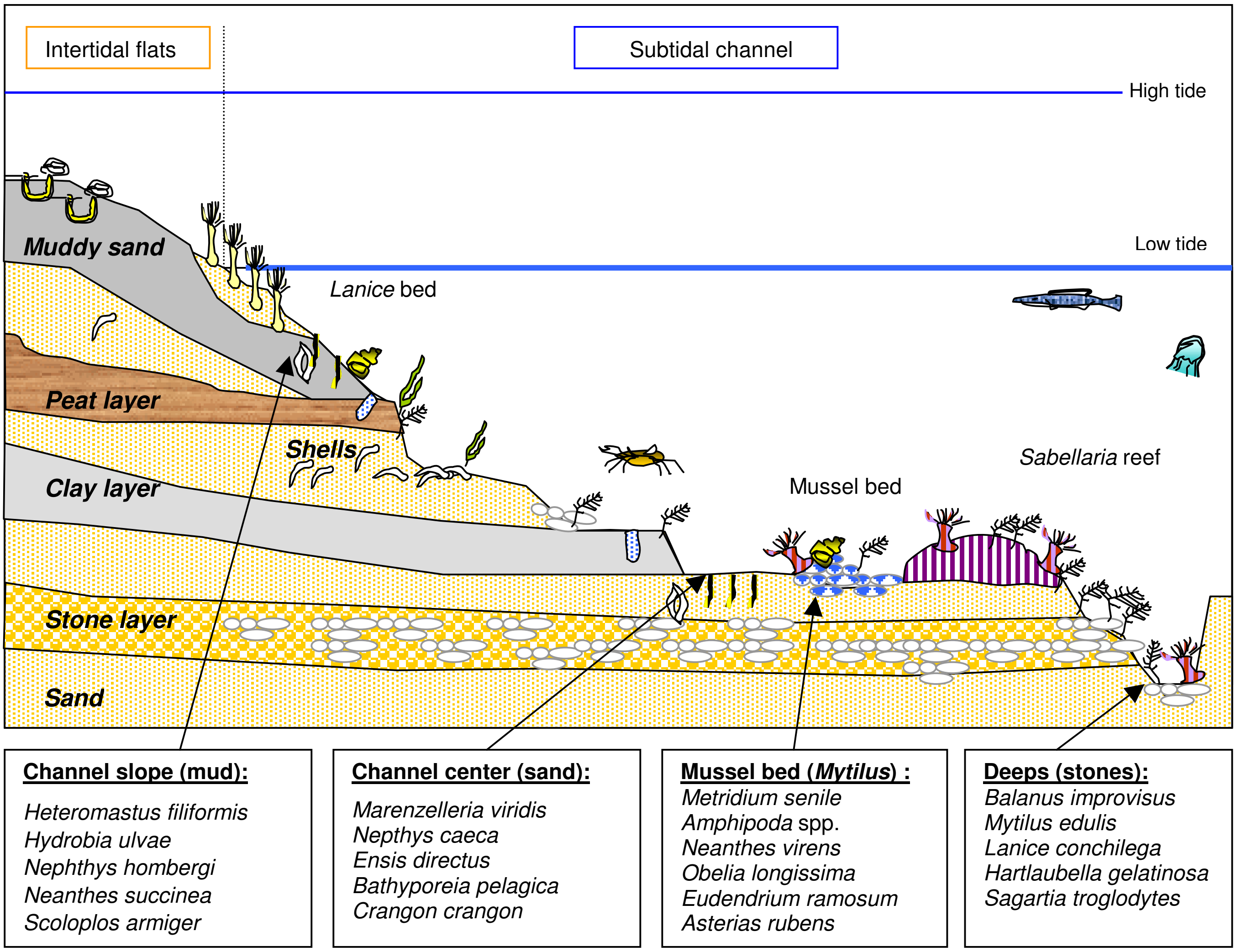


Fig. 23 The benthic community of a polyhaline channel in relation to different substrates (schematic).

The patchiness of habitats and strong variation in abiotic parameters as seen in many borderline environments may represent typical estuarine features (cf. BOYDEN & LITTLE 1973). The importance of diversity for the evaluation of estuarine benthic communities was emphasised in recent studies by COGNETTI & MALTAGLIATI (2000) and LEVIN et al. (2001). An accurate inventory of estuarine inhabitants and the knowledge of spatial distribution is an essential need for protection and restoration efforts (cf. DAYTON 2003).

In Fig. 23 main aspects of species distribution in a cross section of a tidal polyhaline channel are pictured schematically (cf. DÖRJES 1978). The *Lanice* beds and *Sabellaria* reefs within the drawing were not present at the surveyed channel but added from an earlier study in a neighbouring channel (BUHR 1979). DITTMER (1981) emphasised the high diversity of a *Lanice conchilega* assemblage in the outer polyhaline area with many associated species investigated by RIEMANN-ZÜRNECK (1969) and BUHR (1979) at km 100 (Fig. 16). Similar to mussel beds both species provide biogenic structures for fairly diverse benthic assemblages when occurring in high densities.

Conclusions:

Despite the high variation in abiotic conditions the estuarine benthic communities show clear spatial distribution patterns. The analysed benthic distribution of mesohaline and polyhaline communities of the Weser estuary is basically controlled by the same abiotic parameters.

Major factors for benthic settlement in estuaries are longitudinal gradients of salinity as well as water depth and tidal height on a large spatial scale and sediments and substrates on a small spatial scale.

The highly dynamic environment results in a low point diversity that is often related to relatively high large-scale diversity reflecting a high diversity of structures and sediments.

Species distribution reflects several sub-communities, which can be distinguished by species composition, feeding type and salinity tolerance. Natural hard substrates contribute substantially to epibenthic diversity in the subtidal areas. Certain species such as *Mytilus edulis* and *Lanice conchilega* provide additional habitats and have a structural importance for the benthic community.

Artificial structures such as ditches provide important habitats for benthic species, representing, at least partly, substitutes of former natural habitats. The widespread system of groynes and watershed constructions provide artificial habitats for hard bottom communities. Comparisons to natural stone areas recorded less species and lower densities, which may indicate a limitation in their substitute function. The response to new structures shows the strong adaptive skills of the estuarine benthic species on one hand, but indicates a loss of natural habitats on the other.

4.2 Spatial characterisation of the Weser estuary by benthic invertebrates

For a more comprehensive picture of benthic distribution on the large scale of the Weser estuary, main results of the case studies in the mesohaline and poyhaline areas are transferred to the whole brackish water zone of the Weser estuary. Together with additional data from actual baseline studies all different zones of the estuary will be characterised (Table A-1, chapter 3).

4.2.1 Identification of salinity zones

The identification of faunal breaks (discontinuities of faunal composition along the estuary) in an along-estuary gradient gives evidence of true borderlines within benthic colonisation (DITTMER 1981). The results from the analysis of subtidal benthic data as presented in Fig. 12 and Fig. 13 (chapter 3) support basically the classification of salinity zones after the Venice System (CASPERS 1959, REMANE & SCHLIEPER 1971). Except for some new aspects that will be discussed below, they confirm the classification of benthic estuarine sub-zones controlled by salinity as given by several authors before (LÜNEBURG et al. 1975, MICHAELIS 1973, 1981, DITTMER 1981). In Table 9 the positions of boundaries of the salinity zones are compared. The identified zones are the basis for later classification of benthic distribution in this study.

Table 9 Boundaries of estuarine zones by faunal discontinuity and salinity measures.

Boundary of brackish water zone	*Salinity (different authors)*	*DITTMER (1981) (subtidal endofauna)*	*This study (subtidal endofauna)*
Fresh/oligo	Km 45	--	Km 29-45 (uncertain)
Oligo1/oligo2	--	Km 60	Km 55-60 (uncertain)
Oligo/meso	Km 64	--	Km 64
Meso/poly1	Km 81	Km 85	Km 79
Poly1/poly 2	--	Km 99	Km 91
Poly/"marine"	Km 112		Km 112

The endobenthic and epibenthic data show basically a similar clustering of the sections along a salinity gradient (Fig. 12, Fig. 13). As mentioned in DITTMER (1981) the boundary between freshwater and oligohaline salinity is not clearly indicated within the fauna, due to the salt pollution of the fresh water zone as a peculiarity of the Weser estuary (HAESLOOP 1990). Although salt pollution has been strongly reduced since 1990, true freshwater conditions with a total amount of salt less than 0.5 PSU have not been achieved yet.

Another faunal discontinuity was identified by DITTMER (1981) at km 60 (Table 9). In accordance with that, a faunal dissimilarity of the lower oligohaline part (alpha-oligohaline, area from km 60 to 65 south of Bremerhaven) to the sites further up the river was stated in HAESLOOP (1990).

Other discontinuities of the data analysed in this study separate faunal zones more clearly. The borderlines of the mesohaline zone at km 64 and km 79 correspond to earlier investigations and salinity measures (MICHAELIS 1973). In contrast to DITTMER (1981), who describes a faunal break at km 99, in the data set at issue a faunal break was localized at km 91 (Fig. 12). The difference might be based on the different method used by DITTMER (1981) who identified faunal breaks by cumulative plots of upper and lower limits of species distribution. A shift of salinity zones into the estuary is another possibility, but according to the hydrological dynamics of the outer estuary such a shift needs to be analysed in detail. An indication of a shift of intertidal species further into the estuary since 1973, induced by an increased salinity in the inner estuary, has recently been given by KOLBE & MICHAELIS (2001).

Based on the present analysis, the polyhaline area can be subdivided in a more brackish part from km 80 to 91, and a part from km 91 to 112, which is strongly influenced by the sea. Such a change in species composition is similarly found in the neighbouring channel but without a faunal break (publication II). The endobenthic data from km 112 to km 115 (section 9 in Fig. 12) are considered "marine" because they show low similarity with the polyhaline sections (7, 8). The assumed high similarity of section 9 with marine conditions cannot be testified without additional data from true marine areas. As suggested by DITTMER (1981) this area is better considered as marine, because of its high salinity during an average outflow of the Weser.

MICHAELIS (1973, 1981) gives a comprehensive description of intertidal benthic distribution in the Weser estuary, which considers the along-estuary gradient. He suggested 4 sections within the inner brackish water zone with borderlines at km 87, 76, 69 and 64 mainly deduced from intertidal data (MICHAELIS 1981). The subdivision of the mesohaline zone at km 69 into a community of brackish and marine species on one hand and a brackish dominated community on the other hand can not be confirmed by the data at issue. Comparing the data sets from km 73 (publication I) to long term data of an area further up at km 65 (NLÖ 2001, KOLBE & MICHAELIS 2001), the differences indicate rather a gradient than a faunal break. The actual polyhaline intertidal data cannot be used to identify changes in contrast to the much more extensive investigation of MICHAELIS (1973), but the intertidal borderlines still reflect a difference to the subtidal borderlines of several km (Fig. 15). DITTMER (1981) emphasised the different location of faunal breaks in subtidal and intertidal soft sediments. Marine and euryhaline species may be found several km further upstream in subtidal areas compared to their intertidal occurrence (submergent species). This is due to the salinity stratification with higher salinities in the subtidal channels (chapter 3, WELLERSHAUS 1981).

The similarity analysis of benthic assemblages reflecting the salinity gradients along and across the estuary presents 10 estuarine subzones. The supratidal areas do not show a differentiation of mesohaline and polyhaline sections, because the salinity influence drops towards the shore. Within the subzones small size biotopes provide additional habitats.

The GIS supported calculation shows strong differences in the areas of benthic biotopes. While most of the area can be characterised as polyhaline channels (58.4%) supratidal marshes cover minor percentages (oligohaline 0.9%, meso/polyhaline 2.2%). Biogenic structures yield similar small areas but available information of area is restricted to intertidal biotopes only. Seagrass meadows and *Mytilus* mussel beds cover only 0.4 % each of the total intertidal area (35,388 ha). The analysis of areas needs to be integrated in an evaluation of benthic biotopes (see below).

In Fig. 24 a comparison of a simple differentiation of estuarine zones by salinity measures (A, left) and a more detailed approach of a faunal classification including different tidal zones (B) and additional polyhaline subzones from the analysis at hand (C) is pictured schematically. In addition to the mentioned details, all borderlines have to be suspected as variable with a strong shift during seasonal and interannual cycles.

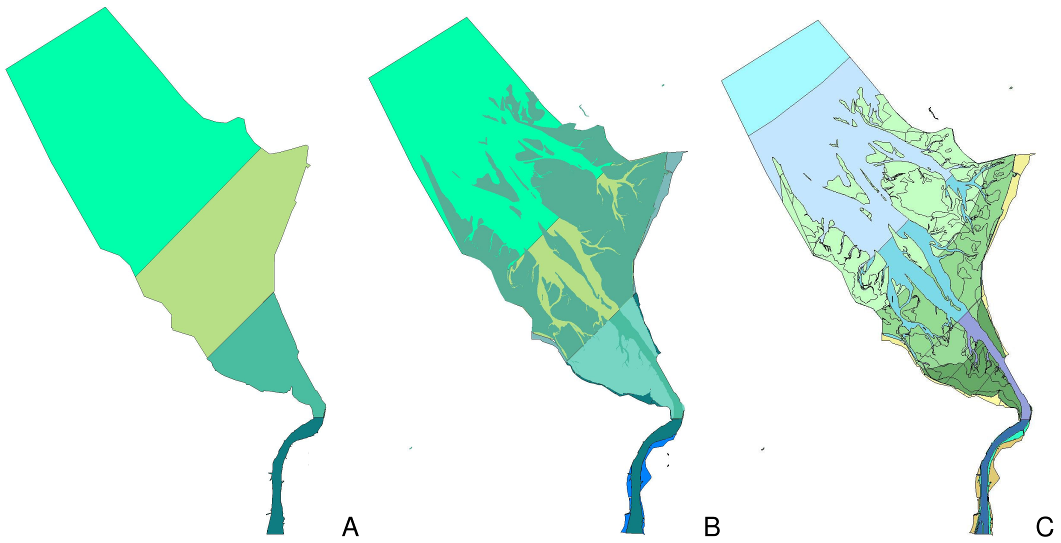


Fig. 24: Salinity zones of the Weser estuary, schematically. A: zones from salinity measurements along the main channel only, B: zones with faunal differentiation of subtidal, intertidal and supratidal areas, C: further differentiation of the polyhaline zone (see Results, Fig.15, chapter 3).

Conclusions:

The analysis of along-estuary gradients shows a clear separation indicated by faunal breaks. Principles of earlier salinity zonation were confirmed and differentiated by integrating intertidal and supratidal biotopes. While intertidal data show high similarities to the subtidal zonation, meso- and polyhaline supratidal areas do not separate into along-estuary patterns.

The inventory of benthic invertebrates represents 10 brackish subzones within the Weser estuary and additional small scale biotopes of certain substrates or special structures. Size of areas are compared by a GIS supported calculation and differ strongly, which has to be considered in an evaluation of habitats.

4.2.2 Species numbers

The present inventory of benthic species in the brackish part of the Weser estuary has yielded many new species in comparison to former basic studies of the area (SCHRÄDER 1941, MICHAELIS 1973, 1981, DITTMER 1981, GOSSELCK et al. 1993). Differences in species number, number of brackish water species, and number of threatened species are presented in Table 10.

Table 10 Studies of benthic inventory of the Weser estuary.

	SCHRÄDER 1941	***MICHAELIS 1973***	***DITTMER 1981***	***GOSSELCK et al.1993***	***This study 2004***
Tidal zones	subtidal	sub-/ intertidal	sub-/ intertidal	subtidal	all
Salinity zones	fresh-poly	oligo-meso	fresh-poly	oligo-poly	oligo-poly
Section of estuary	Km 0-120	Km 50-90	Km 48-112	Km 60-120	Km 45-112
Species total	33	54	92	159	233
Brackish water species	8	13	12	23	40
Threatened species	--	7	6	15	36

The results of this study provide the most comprehensive benthic database for the Weser estuary so far. This was possible by integrating data sets from baseline studies (mainly impact assessment studies from the last 10 years by different authors, see Table A-2, Appendix). In addition the approach of integrating different biotopes of all tidal zones has added many species from the transitory zone between land and water. Not only the total species numbers but also the numbers of threatened species and genuine brackish water species in this study are higher. This is no indication of quality improvement because it is caused by the higher sampling effort (number of sites, samples, replicates), the integration of supratidal zones and various investigation methods.

Although the sampling effort within supratidal biotopes, groynes and ditches is very low (Fig. 25) these areas contribute to a complete picture of benthic distribution with many brackish and exclusive species. With additional investigations more species are expected. The majority of data are obtained from subtidal polyhaline and mesohaline biotopes because these areas were on focus in recent impact studies.

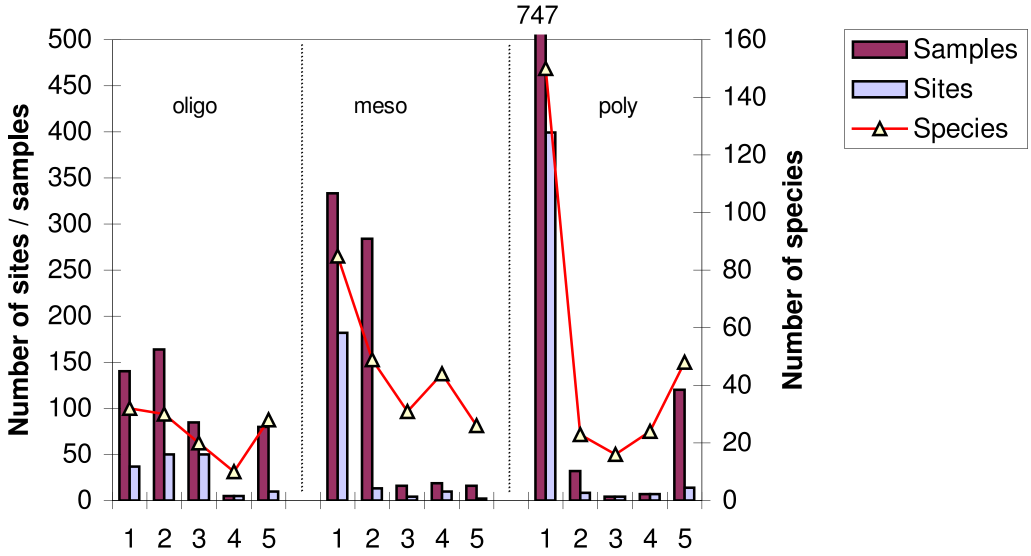


Fig. 25 Sampling effort and species number of different biotopes and salinity zones of the Weser estuary (1- subtidal, 2- intertidal, 3- supratidal, 4- groynes, 5- ditches).

The number of benthic species of the Weser estuary can be compared with that in other studies. A total of 229 species were obtained from the Delta area in the Netherlands (WOLFF 1973) including all tidal zones from freshwater to polyhaline conditions. The list of potentially endemic species for the Elbe estuary presents 195 species (CLAUS 1998) including the fresh water sections and all data from older surveys. From the Hudson River estuary (USA) 105 species were identified including 13 species of chironomids (RISTICH et al. 1977). Although all inventories vary in methods and differences within the database are obvious, they show a lower total species number than the Weser estuary. This is stressed by the fact that in this study the tidal fresh water zone is not considered and additional benthic fresh water taxa have to be expected.

The comparisons between estuaries of the world are mostly focused on abiotic conditions (KETCHUM 1983) or on certain estuarine parts such as mesohaline flats or subtidal channels rather than a comparison of a benthic inventory. However, the principles of distribution and functional relationships on different taxon levels can be compared. Some species actually occur in many estuaries around the world as indigenous cosmopolitans or invasive Neozoa. Some wide-spread species, e.g. *Streblospio benedicti* (Polychaeta) can be found in the Weser estuary (this study), in Norwegian fjords and Scottish estuaries (PEARSON & ROSENBERG (1978) and in Mexican bays and estuaries (TALLEY et al. 2000). Additionally there are often strong similarities at higher taxon levels, such as the genus or family level. For example certain families, such as tubificid oligochaetes, which are known to be associated with high organic sediment content in North Sea estuaries, represent a similar ecological role in Southern Californian estuaries (TALLEY et al. 2000). In contrast to that, the same ecological functions concerning energy and material transfer from nutrients to biomass is fulfilled by completely different taxa in tropical benthic mudflat communities (REISE 1985, 1991).

Compared to marine areas the species number in the Weser estuary is higher than baseline studies of benthic communities in the German Bight, with a total of 219 benthic species (SALZWEDEL et al. 1985) and 149 species (STRIPP et al. 1969). Both studies cover a larger area than the present study, but they are restricted to subtidal habitats and based on a smaller sampling effort. Although the subtidal records allone are higher in the German Bight, the comparison emphasises the benthic habitat function of the Weser estuary on a large scale.

Some species from the early studies of SCHRÄDER (1941) and the inventory of DITTMER (1981) have not been recorded in the compiled investigations since 1980 (Table 11). The absence of these species may indicate a habitat loss. Species with single records were omitted from the Table, because relevance to former benthic community is low or uncertain.

Most of the listed species (Table 11) are marine species with uncertain or low relationship to estuarine biotopes. These species are typical within the benthos communities of the German Bight (SALZWEDEL et al. 1985). They may occur in some years in the outer polyhaline area of the estuary with fluctuating abundances without indicating a change of environmental conditions. The decline of marine molluscs such as *Venerupis pullastra* and *Abra alba* is similarly registered in other coastal areas in Germany (HEIBER & RACHOR 1989).

Table 11 Species listed in earlier studies (DITTMER 1981 with reference to SCHRÄDER 1941, BUHR 1979, 1981 and RIEMANN-ZÜRNECK 1969) with no or single records since 1980 (single findings of DITTMER 1981 omitted*).

Taxa	***Taxonomic group***	***Tidal zone***	***Salinity zone***
Venerupis pullastra	Mollusca	subtidal	Poly
Montacuta ferruginosa	Mollusca	subtidal	Poly
Abra alba	Mollusca	subtidal	Poly
Abra nitida	Mollusca	subtidal	Poly
Mya truncata	Mollusca	subtidal	Poly
Kefersteinia cirrosa	Polychaeta	subtidal	Poly
Notomastus latericeus	Polychaeta	subtidal	Poly
*Sabellaria spinulosa**	Polychaeta	subtidal	Poly
Nototropis vedlomensis	Crustacea	subtidal	Poly
Corophium crassicorne	Crustaces	subtidal	Poly
Psammechinus miliaris	Echinodermata	subtidal	Poly

* although listed as single finding in Dittmer (1981), species was added here because of several findings in the original literature of BUHR (1979).

A degradation or decline of habitat function may be indicated by the polychaete *Sabellaria spinulosa*. The polychaete *Sabellaria spinulosa* was listed as a single record in DITTMER

(1981), but original data from BUHR (1979) showed widespread reefs with living individuals in the area of km 100 to 103. MICHAELIS & REISE (1994) stated that Sabellaria reefs provided the major structure for benthic diversity in 1920 in the Wadden Sea. The extension of former reefs in the Jade area (SCHUSTER 1952, DÖRJES 1978) might similarly describe the importance of these structures in former estuaries. The loss of *Sabellaria* reefs in the trilateral Wadden Sea area within the last century is documented by VORBERG (1995) and DE JONGE et al. (1999).

Only a single record of *Sabellaria spinulosa* is registered in the data at hand (DB Weser, Table A-2) from km 90 in 1992 (station WW 103) but without any reef structures. Small pieces of destroyed reefs were found in several grab samples, but with no indication of living individuals or larger reef structure. Together with a most probably strong decline or loss of this species in the last 3 decades the loss of valuable habitat structures for many associated benthic species has to be registered. Most obvious reasons for degradation of reef structures are physical impacts from fishing gear, disposals and dredging (VORBERG 1995, 1997). Special investigations on actual status, condition, interference and potential change of abiotic conditions are needed.

Similarly to that, the polychaete *Lanice conchilega* provides habitats for other species by stable bed structures, too, and has an important function within the transfer from dissolved nutrients to biomass (BUHR 1979). Although the species is still found frequently within presented data of the inventory, the structure of subtidal *Lanice* beds has not been found since the investigation of BUHR (1979) (Fig. 16). Beside the analysis of their presence, it is therefore even more necessary to include the structural performance of these species within a comparison or evaluation.

4.2.3 Neozoa

Besides certain species which have disappeared from the estuary, many new species records are given in this study (Table A-1). Some of them have been introduced to the estuaries or to the North Sea region by man (Neozoa actualia). An overview of introduced species to the German coastal waters is presented in NEHRING & LEUCHS (1999a). The vehicles of introduction (e.g. ship transport, aquaculture) and information about interference with other species are given in REISE et al. (1999) and WOLFF (1999).

In this study 13 Neozoa have been identified, with different origin and time since introduction (Table A-1, Appendix). The amphipod *Corophium lacustre* for example was already established in the Weser in 1920 (SCHLIENZ 1922).

In comparison to the first baseline study of benthic invertebrates of the Weser estuary by SCHRÄDER (1941) a strong increase of new species was registered for the Lower Weser by HAESLOOP (1990). Today common species such as the crustaceans *Eriocheir sinensis*, *Gammarus tigrinus*, *Palaemon longirostris*, the hydrozoan *Cordylophora caspia* and the gastropod *Potamopyrgus antipodarum* have invaded the estuary since the investigations of SCHRÄDER (1941) in 1929. A loss of several endemic gastropod species in the former fresh water section of the estuary and the introduction of new species is recorded by HAESLOOP & SCHUCHARDT (1995) in comparison to BORCHERDING (1889). A recently introduced species is the polychaete *Marenzelleria* spp., which has been found in North Sea estuaries since 1987 (ESSINK & KLEEF 1988). *Marenzelleria* spp. now dominates most oligohaline and mesohaline soft bottom habitats in the Weser estuary (KOLBE & MICHAELIS 2001).

Impacts of new species on the original fauna and their consideration within evaluation are discussed controversially. While HAESLOOP (1990) stated that most of the indigenous species must have suffered from loss or change of habitats before being replaced by new species, WOLFF (1973) considers the estuaries as young environments with many empty habitats. Especially in estuaries the indigenous species do not fill up all benthic niches thus making it easy for new species to establish. ARMONIES & REISE (2003) found that most macrobenthic species in the Wadden Sea area actually use less than half of the suitable sites. This must be even more evident for estuaries because of the strongly fluctuating abiotic environment and the need for adaptive skills.

Interference competition of *Marenzelleria* spp. with indigenous polychaetes sharing the same feeding habits, such as *Hediste diversicolor,* as stated in ESSINK & KLEEF (1993) and KOTTA et al. (2001), is not confirmed by long-term investigations of KOLBE & MICHAELIS (2001). Although a massive invasion of some new species in the Weser is obvious, ecological damage depicted as a simultaneous decline of indigenous species is not confirmed yet. DAYTON (2003) emphasises that some neozoa have been registered in low numbers for long periods before they suddenly become ecological relevant.

Conclusions:

Although there are obvious changes of estuarine biotopes caused by industrialisation, the number of species of the Weser estuary is still relatively high compared to other estuaries. A comparison to an historic situation (e.g. 1880- before river deepening began) is not possible because of lack of historic benthic data. The comparison to later studies show a strong decline of the polychaete *Sabellaria spinulosa* that was recorded within the present data by single findings only. The importance of Sabellarian reefs for associated species gives this fact a high relevance.

At least 13 new benthic species (Neozoa) have established in the Weser estuary since 1900. A damage to indigenous species is not registered so far because of many assumed empty habitats in young estuarine ecosystems.

4.2.4 Brackish water species

REMANE (1940) defines with reference to VÄLIKANGAS (1933) the genuine (true) brackish water fauna as species that are confined to brackish waters in contrast to euryhaline freshwater species and euryhaline marine species, which have their main range and conditions to reproduce in the river or open sea. All three groups and additional (stenohaline) fresh water and marine species occur in certain combinations in brackish waters. The percentages of the groups shift with a longitudinal and an across-tidal height gradient (see Results, Fig. 15-17). The classification of REMANE (1940, 1969) did not include all estuarine species and less strict definitions from later authors added more species to the "brackish water species group". For example species such as *Balanus improvisus*, *Palaemon longirostris*, *Bathyporeia pilosa*, *Neomysis integer* were considered to be highly (third grade) euryhaline marine in REMANE (1940) but classified as true estuarine species by different authors later on. In accordance with that, and for better comparison, these species were included in the category of brackish water species (Table A-1). On the other hand the oligochaete *Paranais litoralis* (MICHAELIS 1973) and the amphipods *Bathyporeia pelagica* and *Bathyporeia sarsi* (listed in CLAUS 1998) were not considered as brackish water species in this study, because of their frequency in almost all salinity zones and marine areas. Further data-related discussion of these categories seems necessary, but is beyond the objectives of this study.

In the study at hand a total of 40 brackish water species were registered compared to 13 in MICHAELIS (1981) and 23 in DITTMER (1981). Some of these, such as *Leptocheirus pilosus*, were considered to be extinct for the Weser estuary by MICHAELIS et al. (1992). However, it turned out that this species was still quite frequent in certain habitats such as groynes and harbour docks (BFG, KÜFOG unpubl.). Therefore it has to be stressed that small-scale habitat preferences and substrate related distribution have to be taken into account for evaluation of estuarine communities. In addition to that the habitat function of certain substitutes for rare brackish water species becomes obvious.

The identification of characteristic benthic species and the differentiation of benthic communities according to the method of THORSON (1957) as applied by STRIPP (1969) and SALZWEDEL et al. (1985) in the German Bight, failed in the Weser estuary. The high dominance of few euryhaline species with an extremely high variation made determination of communities by that method impossible. The "impoverished *Macoma balthica* community" as stated for the outer polyhaline area by STRIPP (1969) and SALZWEDEL et al. (1985) was found to have pronounced differences in dominance structure and most associated species.

Alternatively, genuine brackish water species were used for differentiating certain biotopes with a species based characterisation. The quantitative data of the different salinity zones (Table 5, 6, 7, 8) show high dominance of the polychaete *Marenzelleria* c.f. *viridis* in three zones. As mentioned before, this species has occupied all brackish soft sediments in the Weser estuary since 1987 and shows extremely high abundance in certain years (GOSSELCK et al. 1993, KOLBE & MICHAELIS 2001). Consequently it has a low value for specific characterisation of certain subzones. Species, which are restricted to a single zone or biotope, have stronger indication values. In Fig. 26 the along-estuary distribution of three brackish water species is given, which occur in the oligohaline zone with relatively high numbers. While *Boccardiella ligerica* is restricted to the oligohaline zone, *Bathyporeia pilosa* is widely spread along the brackish water zone. *Corophium lacustre* has a wide range of occurrence but is quantitatively characteristic of the oligohaline zone.

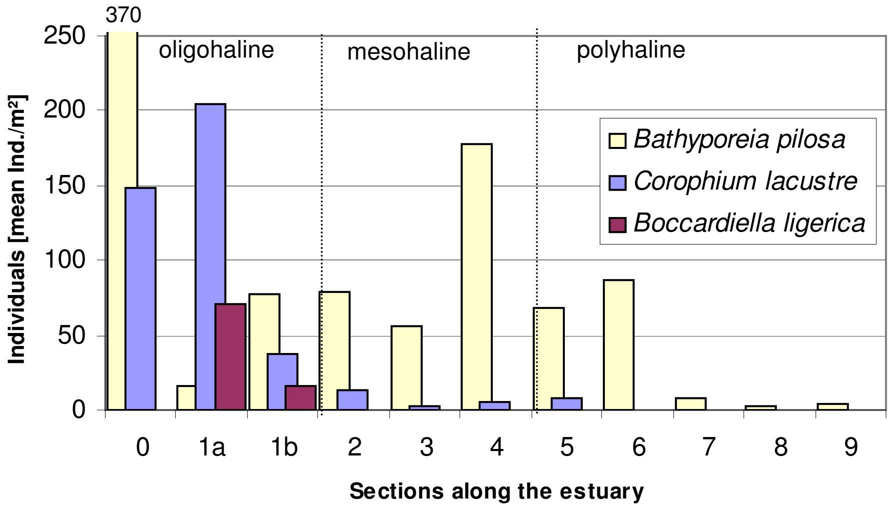


Fig. 26 Different ranges of selected brackish-water species along the estuary (grab samples, DB Weser, main channel 1991-2002, mean abundance in Ind./m² at sites of occurrence, ~5 km sections along the estuary 0-9).

In Table 12 the most frequented habitats of brackish species in the Weser estuary are compiled from personal observations and aggregated literature (Table A-2). Species with indifferent preferences are listed in the last row. The relationship of many brackish-water species to certain structures and habitats is an important base for the evaluation of estuarine environments. Most brackish-water species occur in the oligo-mesohaline environment and have a great tolerance to high variation of salinity. Very few occur in the polyhaline zone exclusively. *Alkmaria romijni* (Polychaeta) and *Idotea chelipes* (Crustacea), for example, were found at only one site in the polyhaline area, which is a too small data base to reflect a natural range. According to REMANE (1940) the polyhaline zone is considered rather a marine than an estuarine area. MICHAELIS (1981) emphasises in the same context that the neighbouring Frisian back barrier intertidal flats have a similar species composition to the polyhaline zone of the Weser estuary. The results given before do confirm this similarity for the outer polyhaline zone (poly 2, Fig. 15). The inner part (km 80-91) provides habitats for several genuine brackish-water species (e.g. *Gammarus salinus*, *Marenzelleria* c.f. *viridis*), which are absent from or less abundant in neighbouring coastal areas.

Table 12 Habitats of genuine brackish-water species in the Weser estuary.

Habitat	***Tidal zone***	***Salinity zone***	***Brackish water species***
Reedbeds	upper intertidal	oligo- meso	*Lekanesphera rugicauda*
	inter-/ supratidal	oligo- meso	*Assiminea grayana*
Reed debris	supratidal	oligo	*Orchestia cavimana*
	supratidal	oligo-poly	*Orchestia gammarellus*
	supratidal	oligo-meso	*Platorchestia platensis*
***Vaucheria* mats**	upper intertidal	meso	*Limapontia depressa*
	upper intertidal	meso	*Alderia modesta*
***Fucus* (-coverage)**	intertidal groynes	mesohaline	*Melita palmata*
Stony beaches	supratidal	meso	*Ligia oceanica*
	supratidal	meso	*Petrobius brevistylus*
Stones intertidal	intertidal	fresh-oligo	*Potamopyrgus antipodarum*
Stones subtidal	subtidal	oligo-marine	*Balanus improvisus*
	subtidal	meso	*Corophium insidiosum*
	subtidal	fresh-oligo	*Corophium lacustre*
	subtidal	fresh-meso	*Palaemon longirostris*
	subtidal	fresh-meso	*Cordylophora caspia*
	subtidal	meso-poly	*Electra crustulenta*
	subtidal	oligo-poly	*Leptocheirus pilosus*
	subtidal	meso	*Cyathura carinata*
Pools, Lagoons	supratidal	meso	*Manayunkia aestuarina*
Ditches	supratidal	oligo-meso	*Palaemonetes varians*
	supratidal	oligo-meso	*Gammarus duebeni*
Mudflats	intertidal	oligo-meso	*Tubificoides hetreochaetus*
	intertidal	oligo-meso	*Tubifex costatus*
	intertidal	meso	*Hydrobia ventrosa*
Muddy sand	inter-/ subtidal	oligo-poly	*Bathyporeia pilosa*
	inter-/ subtidal	fresh-oligo	*Marenzelleria* c.f. *wireni*
	inter-/ subtidal	fresh-oligo	*Corophium multisetosum*
	inter-/ subtidal	oligo-poly	*Marenzelleria* c.f. *viridis*
	subtidal	oligo-meso	*Boccardiella ligerica*
	inter-/ subtidal	meso	*Streblospio benedicti*
	inter-/ subtidal	meso	*Gammarus salinus*
Indifferent	all	all	*Eriocheir sinensis*
	all	oligo-meso	*Gammarus zaddachi*
	all	oligo	*Gammarus tigrinus*
	subtidal	poly	*Heterotanais oerstedi*
	subtidal	poly	*Praunus flexuosus*
	all	all	*Neomysis integer*
	subtidal	poly	*Alkmaria romijni*
	subtidal	poly	*Idotea chelipes*

Some brackish-water species are very specialised and restricted to certain structures. In the case of trophic relationships as documented for specialised gastropods (*Limapontia depressa, Alderia modesta*), which feed on certain green algae (*Vaucheria* spp.) exclusively, the occurrence of these species depends on the occurrence of the algae, which has decreased in area dramatically since 1968 (KOLBE & MICHAELIS 2001). Additionally a mesohaline salinity is preferred by these species, which further restricts their range. Only two habitat sites are actually left for these species in the Weser estuary (Fig. 16). Further investigation and improvement of knowledge about species` ecology and their natural range will simultaneously improve the knowledge of their value for ecological indication.

Conclusions:

Alternatively to prior characterisation by dominant or frequent species a biotope characterisation by brackish-water species is suggested which allows the identification of small structured biotopes.

The strong specialisation of some species to single structures, as given in examples, increases their geographical restriction and potential threat.

The benthic community in the estuarine environment splits into small specialized sub-communities with highly adapted specialists in variable and heterogeneous habitats. This needs to be considered in assessment and evaluation.

4.3 Sensitivity of benthic communities and aspects of impact assessment

4.3.1 The impact of sediment disposal in a polyhaline channel (publication III)

Dredging and sediment disposals are permanent human impacts in German estuaries. The effects to the benthic community are object of recent monitoring programmes (BFG 1999b, 2001, 2003). In publication III an impact assessment of a harbour sludge disposal is presented from a polyhaline area in the Weser estuary. The discussion of this case study leads to a look at impacts on estuarine benthic communities in general and how to analyse them properly. Threats to certain species and indication by sensitive response are discussed further on.

The benthic assemblage of the disposal area was impoverished which was reflected by community indices, certain species and different taxon levels. This was found similarly by e.g. WILDISH & THOMAS (1985) and ESSINK et al. (1992). Species with a certain sensitivity to coverage by deposited sediments, such as filter feeding mussels were absent from the disposal area. Opportunistic species such as *Heteromastus filiformis* achieved higher abundances in the disposal area, which is in agreement with results of NEWELL et al. (1998). According to the specific reaction of benthic species the analysis had to focus on the species level. In publication III some indicator species are given. Some of these species have been considered as indicators for disturbed sediments before in PEARSON & ROSENBERG (1978).

Species such as *Mytilus edulis*, *Lanice conchilega* and *Obelia longissima*, which provide habitat structures for associated macrobenthic species are important for the community structure, its integrity, and species richness (publication III). Filter feeding epibenthic species such as blue mussels, hydroid mats and actiniarians indicate diverse benthic communities (NEWELL et al. 1998). Actiniarians such as *Metridium senile* represented a well-developed epibenthic community and an advanced status of succession by old individuals. Their sensitive reaction to disposals may indicate long-term effects on hard bottom assemblages (WIDDOWS et al. 1979, HALL 1994).

Chemical and physical changes of the water column after an open water disposal as stated in ROSENBERG (1977a,b) and DAVIS & HIDU (1988) affect the pelagic community and thus harm the benthic community indirectly. Such an impact is hard to track within an estuarine monitoring because of the strong drift in tidal currents.

Besides larval stages HEIBER (1988) frequently found adult macrobenthic individuals in plankton samples obtained from tidal sloughs and channels. This may explain the immediate recolonization after perturbation of the respective substrata. Drift as an agent of dispersion appears to have a higher significance in brackish-water systems than previously assumed (e.g. HEIBER 1988, GÜNTHER 1992, ARMONIES 1994). It seems to be an advantage for several species, especially in environments with dynamic sediment movements, to rapidly recolonize new sediments despite the risk of having to leave the substrate.

Besides disposal and dredging for shipping and harbour maintenance the fishing activities (in the Weser: shrimps and flatfish) may cause alteration of benthic habitats by the physical impact of the bottom gear (BUHS & REISE 1997, LINDEBOOM & DE GROOT 1998). Similar obvious is the loss of estuarine habitats and species by the urbanization of watersheds, the separation of the floodplain from the estuary by the dykes and the input of pollutions and nutrients (LEVIN et al. 2001, DAYTON 2003). Long-term degradation or nutrient enrichment is more difficult to detect within an assessment than the physical and direct impact of a sediment disposal.

4.3.2 Biological impact assessment in estuarine waters

Assessment for the European Water Framework Directive has important implications for demonstrating the necessity of programmes of measures. As these will most certainly affect land management, potentially leading to conflict with some stakeholders and legal challenge, robust monitoring procedures across spatial and temporal scales are essential (IRVINE 2004). In the following chapter the special situation of an estuarine environment as given in the publications will be transferred to the needs of monitoring investigations.

Sampling design and methods of data collection

More general design and procedures of marine monitoring are provided by ICES (2001), DAVIES et al. (2001) and CEFAS (2002). The methodological feasibility of impact assessments on benthic communities has been furthermore discussed in FAIRWEATHER (1991) and SMITH (1991).

As a consequence of the highly dynamic estuarine features (MEIRE et al. 1994, WARWICK et al. 2002) not only the spatial but also the temporal variability within an estuarine benthic community can be large. The seasonal cycle in the abundance of a species is affected by e.g. temperature, reproductive cycles, predation, competition and food availability (ARNTZ 1980, ARNTZ & RUMOHR 1982, SCHROEDER 2003). The phenology of many species follows a characteristic annual cycle in abundance and biomass but recruitment success varies extremely (e.g. JAKLIN 2003). However, this is usually governed by temperature and may for example shift well into spring after a severe winter (RACHOR & GERLACH 1978, BUHR 1981). Thus a low abundance in spring may not be representative of the abundance for the entire year. For yearly comparisons it is essential to have at least 2 to 4 samplings per year in order to assess the entire year using means of yearly recordings (e.g. KNUST et al. 2001, IRVINE 2004). In this context, long-term data of stations in reference areas become significant because these will reflect the natural variability of species and exceptional yearly cycles.

The BACI concept (before, after, control, impact) proved to be the most appropriate method for the majority of recent investigations (UNDERWOOD 1991, FAITH et al. 1991). This method entails the sampling of an impact area as well as a reference area before and after interference. If it is not possible to carry out preliminary studies the BACI concept needs modification (publication III).

The position and the number of stations used depend on the extent and heterogeneity of the area. The importance of spatial scales within an analysis of estuarine communities usually demands a more dense grid of sites than in marine areas. Before a comparison of different areas can be drawn, it is necessary to analyse the variation in diversity on different spatial scales (GRAY 2000).

The various methods of positioning (e.g. raster-distribution, random distribution) have been extensively discussed in VAN DER MEER (1997). In an example GRAY (1981) noted that 65% of species (total species found in 15 grabs) were recorded in 2 replicate samples, whereas 4 replicates only accounted for 70%. In order to record more species the effort has to be increased non-proportionally. Meanwhile the selection of 2 to 3 samples has been recognised as an acceptable compromise (KNUST et al. 2001). However, the number of replicates depends on the study area and a high heterogeneity of sediments requires a higher sampling effort. SCHROEDER (2003) stated that five replicates were sufficient for comparisons of benthic community parameters in the German Bight, while species related analysis required additional samples.

Reference areas should resemble the area of impact as closely as possible (REINEKING 1998, SMITH 1991). Especially in estuaries it is important that both areas have a similar hydrology (currents, tidal influence, turbidity, salinity), morphology and similar sediment characteristics (grain size, organic material). The reference area should not be influenced by the procedure itself or any other external factors. This is difficult to guarantee in areas exposed to strong currents. For this reason the possibly far reaching effects of dumping (sedimentation, turbidity) during the monitoring (publication III) were simulated in a computer model which takes into account the hydrological and sedimentological variability of the area (ZANKE 1998).

Van Veen grabs were used in this study to obtain endofaunal samples while light frame dredges were deployed for the epifauna. The advantage of using common methods is to facilitate comparisons beyond a regional level and to include results into long-term studies (RUMOHR 1999). A problem of the Van Veen grab is the low penetration depth in consolidated fine sands, which limits information on deep-living species or adult individuals of certain bivalves and polychaetes. According to HALL (1994) the epifauna is particularly sensitive to interference in the benthic system and is inadequately accounted for in bottom-grabs. The frame-dredge, however, serves to assess sessile and vagile epifauna and thus contributes to a comprehensive description of species communities (c.f. BUHS & REISE 1997).

Analysis of data

Comprehensive procedures on the treatment and analysis of benthos data are provided by CLARKE & WARWICK (1994) and CLARKE & GORLEY (2001).

A fundamental problem in quantitative comparisons and particularly when using statistics, is the focussing on frequently occurring species from the entire range of species (Fig. 27). Only 55 (54%, all endofauna) of the 101 observed macrobenthic species in the surveyed polyhaline channel (publication II) were quantitatively collected by the described methods. Of these about 20 species occurred regularly and in sufficient numbers to enable a quantitative comparison of abundance (Fig. 28). Thus a statistical analysis, which is based on only a few species from the entire range, makes the drawing of conclusions for the entire community questionable. Although small, short-lived endobionts are quantitatively recordable in the sediment, they cannot serve as indicators in this specific context as they are adapted to dynamic sediment conditions and return within a few weeks after a perturbation (NEWELL et al. 1989, HALL 1994).

On the other hand species belonging to the sessile epibionts such as the sea anemone *Metridium senile* are sensitive to dumping measures and could thus serve as indicators of substrate perturbation (HALL 1994, ESSINK et al. 1992, ESSINK 1995). However, they cannot be used for statistical purposes, since they can only be determined qualitatively or occur in very low numbers thus making a statistical comparison impossible. In most investigations, this problem is seldom identified. The development of quantitative epibenthic sampling methods and their implementation within estuarine monitoring programmes would improve the data base.

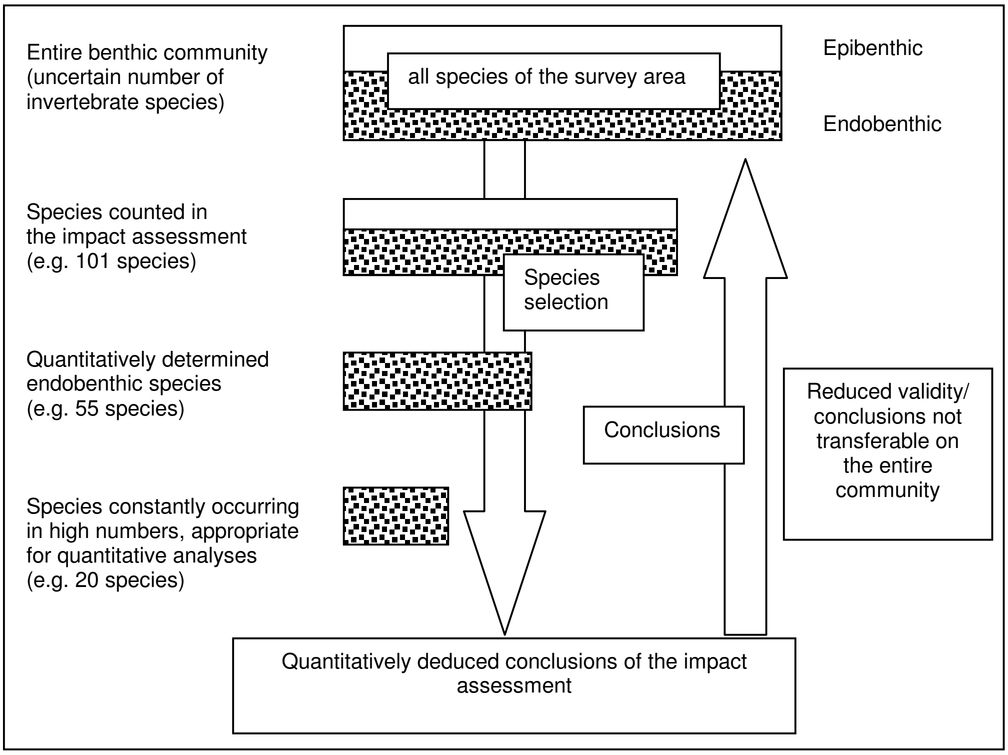


Fig. 27 Reduction of the species numbers by selection for quantitative analysis and conclusions on biological impact in benthic systems (example of species numbers from a polyhaline channel, publication **II**).

4.3.3 Recommendations for future impact assessments in estuarine areas

The discussion on methodological approaches used in impact assessments included pragmatic experience gained from investigations in the Weser estuary. The derived aspects focus on estuarine issues as summarized below:

- The expected results of a monitoring have to take into consideration the different spatial scales, the dynamics and variability of an estuarine survey area. The more heterogeneous the habitat the more dense the sampling grid and the higher the sampling effort need to be.
- The strong seasonal variation within an estuarine community should be considered within the sampling design e.g. by time of investigation and repeated sampling.
- The selection of a reference area with similar hydrological and morphological features is of special importance but difficult to find even when prior knowledge is sufficient.
- Endofauna and epifauna constitute an entity and should consequently be treated as such in estuarine impact assessments. A solely quantitatively derived interpretation

distorts the biological coherence and undermines the significance of the epibionts, which are difficult to investigate quantitatively.

- For the appropriate positioning of stations the documentation of the spatial demarcation of the interference and the impact is fundamental (e.g. soundings, sedimentation model).

In this context it would be desirable to request a monitoring of estuaries, which is independent from impact surveys. Additional to the present federal estuarine monitoring programme with 5 subtidal sampling sites per estuary (NEHRING & LEUCHS 1999b), all tidal zones, the different substrata and the stated small-scale biotopes need to be monitored. These are essential in order to catch the spatial variability in the macrobenthic composition and thus obtain data for a benthic database for comparative purposes in different projects. The compulsory reporting required by the European Habitat Directive and the European Water Framework Directive provide the legal foundation for such monitoring and evaluation by biological criteria.
In conjunction with impact minimisation efforts, it is of particular importance that features such as subtidal mussel beds and diverse epibenthic hard bottom fauna are identified prior to any impact to have a chance to safeguard them against interference.

Conclusions:
Impacts of sediment disposal on estuarine benthic habitats and species can be quantified by biological assessments. In response to the amount and modus of discharged sediments, species react with decline in abundance or avoidance of the impact area corresponding to their habitat preference, feeding behaviour and mobility. Epibenthic sessile filter feeders suffered from disposal effects while most endobenthic show low sensitivity. Opportunistic response to interference is characteristic for some estuarine species and can be used for interpretation as well.
Effects on sensitive species with importance for associated fauna, such as *Mytilus edulis and Lanice conchilega*, may result in severe loss of benthic habitats.
The high variability of the estuarine environment requires certain methodological adaptions of a monitoring as suggested. The importance of the quantification of epibenthic sessile species and biogenic structures within a monitoring and a consideration within analyses is emphasised.

4.4 Evaluation of estuarine biotopes by benthic invertebrates

An environmental evaluation transfers biological data to a classification system with certain criteria of values. However, biological values of an estuary are hard to define generally. What is a valuable biotope, habitat or species of an estuary? Is there a need to preserve estuarine benthic habitats or species at all? The loss of certain species or habitats in an estuary would most probably not result in an ecological collapse. Besides general environmental aspects as stressed from recent European directives, the biological functions of an estuary are substantial and important not only for the benthic community in the estuary itself but for neighbouring coastal, marine and freshwater ecosystems (DAYTON 2003). The keystone position within the complex chain of material and energy flux is represented by the benthic invertebrates as mentioned in KETCHUM (1983) and McLUSKY (1989). Not only major food resources of fish and migrating birds are provided by benthic species but also major sedimentary processes such as perturbation of sediments, nutrient transfer and microbiological decomposition of pollutants are closely connected with the benthic activity (ARNTZ et al. 1999). Water quality within coastal areas, which has a tremendous economical and ecological value, depends to a large extent on the vital functions provided by the estuarine macrobenthos (McLUSKY 1989).

Brackish habitats in estuaries are generally endangered by loss of area and coastline (HEIBER & RACHOR 1989). Attention within an evaluation of an estuary should be drawn to the genuine brackish water species and their habitats, because of they exhibit a close relation to genuine estuarine features as contrary to dominant euryhaline species. A decrease in abundance or presence of certain species and their restriction to few isolated small areas may also reflect a sensitivity to general interference or stage of degradation. The status of brackish water species on the Red List of threatened species (RACHOR 1998) and brackish biotopes (SSYMANK & DANKERS 1996) supports this aspect. Due to the lack of long-term studies integrating all estuarine biotopes an exact documentation of the decline of certain species is missing.

In the inventory at hand 36 species were listed on the Red List of threatened species (RACHOR 1998). From this number, 16 species, belong to the genuine brackish water fauna (Table A1, Appendix). It is obvious that the percentage of threatened species (13.9%) is low compared to other, e.g. terrestrial, biotopes. But for most species knowledge of former abundance and natural range is sparse or missing and although the species is rare, a decline and its cause cannot be documented by data to reveal an actual threat. About half of the presented estuarine species are restricted to few sites only and occur in low abundance; the actual trend of their population size or development is still unknown. Reference data from undisturbed estuaries of the same latitude or from undisturbed former periods are missing. In contrast to thoroughly documented fish data and few invertebrate species, which were used commercially, benthic invertebrates were not investigated in terms of a species inventory before major ecological changes had been initiated. Therefore the present lists of endangered estuarine species suffer from lack of historic data and have to be regarded as preliminary with a need of further development.

From the inventory data of this study and calculated areas (chapter 3) a priority list of biotopes and species, which claim a certain importance for evaluation aspects is given (Table 12). The following criteria are suggested:

- Biotopes of a small area with importance to estuarine species
- Biotopes or species with actual threat
- Biotopes or species with obvious decline in area or abundance
- Unidentified biotopes which are substituted by artificial structures

In Table 12 such a priority list for the Weser estuary that considers the general threats of estuarine biotopes as given in SSYMANK & DANKERS (1996) is suggested.
The typical brackish-water species with a potential indicator value are given, but biological data to confirm the development of the biotope are missing. Further analysis and quantification is needed to get a valid data base for precise evaluation of the actual status and for detecting trends of development. In Fig. 16 the locations of small area biotopes with a special importance to the estuarine community are presented. The polyhaline biotopes such as *Sabellaria* reefs, *Lanice* beds, seagrass meadows and mussel beds, which belong to the estuary as well, are included within Table 12. They might be similarly integrated into a priority list of coastal waters because of their occurrence in neighbouring coastal areas.
The mentioned biotopes carry out more functions than just providing habitats for brackish or endangered invertebrate species. The subtidal stones or mussel beds with dense hydroid coverage (e.g. *Hartlaubella gelatinosa*), for example, act as nursery areas for young fish and provide a substrates for spawning (publication I). Besides the key position within the foodweb these structures are habitats for many other sessile epibionts and therefore generally important sites of benthic diversity (SSYMANK & DANKERS 1996).

Table 12 Proposal for a list of priorities of most important and threatened biotopes in the Weser estuary and their characteristic brackish-water species (*threats as given in SSYMANK & DANKERS 1996).

Biotope	***Estuarine species***	***Trends of biotope development***	***Threats***
Oligohaline			
Mudflats (together with brackish intertidal flats in general)	*Tubificoides costatus* *Tubificoides heterochaetus* *Monopylephorus irroratus*	Decline	*Coastal constructions *Water regulation *Fishing, agriculture *Shipping *Pollution, eutrophication Shift of salinity zones
Reedbeds, natural shorelines	*Assiminea grayana* *Orchestia* spp.	Decline	*Water regulation *Agriculture Shift of salinity zones Coastal constructions
Natural subtidal stones	*Cordylophora caspia* *Leptocheirus pilosus*	No quantification Groynes as substitutes	Dredging and disposal *Fishing *Pollution

Table 12 (continued)

Mesohaline			
Vaucheria mats	*Alderia modesta* *Limapontia depressa*	Strong decline	Uncertain
Natural subtidal stones, subtidal mussel beds	*Palaemon longirostris* *Electra crustulenta* *Cyathura carinata*	No quantification Uncertain locations	Dredging and disposal *Fishing *Pollution
Tidal pools, lagoons, ditches	*Manayunkia aestuarina* *Palaemonetes varians*	No quantification Lagoons replaced by ditches	Coastal constructions *Water regulation
Muddy sands	*Streblospio benedicti* *Hydrobia ventrosa*	No quantification	*Water regulation *Fishing, agriculture *Recreation *Pollution, Eutrophication *Agriculture
Natural stony beaches	*Liga oceanica* *Petrobius brevistylus*	Only substitutes present: Destroyed old groynes, shore walls	New construction techniques, complete sealing
Fucus coverage	*Melita palmata*	No quantification Area has probably increased Groynes intertidal	--

Polyhaline			
Sabellaria reefs	--	No quantification	Fishing Pollution, eutrophication Dredging, disposals
Lanice fields	--	No quantification	Fishing Pollution, eutrophication Dredging, disposals
Seagrass meadows	--	Quantification by aerial photography	Recreation Pollution, eutrophication Dredging, disposals
Mytilus beds intertidal	*Balanus improvisus*	Quantification by aerial photography	Recreation Pollution, eutrophication
subtidal	*Electra crustulenta,* *Gammarus salinus*	No quantification	Fishing Pollution, eutrophication Dredging, disposals

Conclusions:

An evaluation system of the different estuarine biotopes that considers the size and the threat is suggested. Based on analysis of areas and the documented decline from the literature, a ranking list is compiled presenting characteristic species. It is obvious that small-sized biogenic biotopes are most threatened and require a special consideration within monitoring and spatial planning procedures.

4.5 Integrated estuarine management

The list above provides first notes for an environmental management, which is based on benthic data and integrates economic interests and environmental necessities in a long term spatial planning. Nowhere else within the marine and coastal areas are conflicting interests of environment and economy more apparent and more closely interrelated than within the industrialised estuaries. Environmental management principles of marine and estuarine areas as described by LEWIS (1980), McLUSKY (1989), WILSON (1994), CLAUS (1998), REILLY et al. (1999) and HIRST (2003) are based on a most precise knowledge of biological features, their spatial distribution and potential threat by human activities.

For an implementation of an environmental management plan the scientific analysis, as given in the study at hand, needs to be integrated within an interdisciplinary adjusting process and discussion of all stakeholders. The statement of CARTER (1988): “Estuarine management can be divided into three broad areas; policy, planning and practice” describes the different aspects of such an implementation beyond this approach. Besides pollution “the excessive land reclamation especially of intertidal flats is still the greatest single threat to estuarine conservation, destroying forever the habitat” (McLUSKY 1989).

LEWIS (1980) emphazised the need of a large size of protected areas that include a representative range of habitats instead of particular single sites. This implies an identification of all biotopes and small size habitats and their spatial distribution as a first step to claim an adequate, large area for protection which includes all different biotopes in a second step.

As mentioned before the European Water Framework Directive (WFD) is presently defining major biological quality targets for estuaries at present and ways to improve and control them (TUENTE et al. 2002, CIS 2003). Economic interests have to be integrated and adjusted to achieve compliance with these targets. In its consequences this will influence not only economies which have obviously a close interrelation to the estuarine biotopes, such as fishery and harbours, but also economies with more subtle and indirect influence such as agriculture and general coastal land use. An effective consultation with interested parties and stakeholders is an explicit requirement of the WFD (IRVINE 2004).

In case of the European Habitat Directive the required compulsory reports on the protected estuaries within the NATURA 2000 network additionally stress the importance of biological criteria to define an ecological target status and methods of monitoring and evaluation. On the background of the study at hand macrobenthic features may contribute to these targets substantially (compare BACKHAUSEN 2002, IRVINE 2004).

The requirements of both directives give evidence to the fact that an estuarine management based on biological criteria has a high topicality within the present European environmental situation.

The following aspects for such a management may be stressed from the background of this study for further discussion:

- Identification of interests and spatial demands of all stakeholders and analysis of spatial overlap with conflicting interests
- Development of an environmental motivation list of priorities concerning species and biotopes as suggested above
- Development of an economic motivation list of priorities concerning economic development, coastal protection, shipping, land use, reclamation for industries and cities.
- Identification and charting of small-scale biotopes and structurally important species, strict preservation within larger areas (preferable to single site preservation) and monitoring control, as there are:
    - *Sabellaria* reefs
    - *Lanice* beds
    - Subtidal/intertidal mussel beds
    - Sub-/intertidal seagrass beds
    - Subtidal stone fields
    - Hydroid coverages
    - *Vaucheria* mats
    - *Fucus* coverages
    - Brackish reedbeds
    - Tidal ponds, ditches
- Implementation of a reference area without any interference and commercial usage including all tidal zones and salinity zones
- Restoration and development efforts directed to environmental top priorities

Most of the mentioned biotopes are outside of National Parks or nature reserves and therefore without any protection. Subtidal biotopes within the reserves are still subject to intense fishery with all consequences for the benthic communities. Irrespective of their belonging to the estuaries a preservation of those structures should be a general aim of an integrated coastal zone management.

General conclusions:

From the presented analysis of the spatial distribution and sensitivity of benthic species and assemblages we have gained precise knowledge of the actual situation. The Weser estuary is strongly influenced by human activities, which is reflected by the quality of benthic habitats and performance of benthic communities. In addition to the high natural variability of these communities, a relatively low diversity is related to great adaptive skills to withstand extreme abiotic environmental features. Human impacts in an industrialised estuary have to be assessed by scientific monitoring methods. Examples of this and the feasibility of benthic investigations are provided in this study. In the future the technical development of the waterways and harbours will proceed and further impacts on the estuary are to be expected. In order to ensure ecological quality and biological functions we recommend the spatial separation of economic and environmental interests within a long-term management. Such a management should consider estuarine macrobenthos as a major issue for monitoring, impact assessment and evaluation.

5 REFERENCES

ADOLPH, W., S. JAKLIN, M. MEEMKEN & H. MICHAELIS (2003): Die Seegrasbestände der niedersächsischen Watten (2000-2002). NLÖ-Forschungsstelle Küste, Norderney, Dienstbericht 01/03, 19 pp.

ALBRECHT, A. & K. REISE (1994): Effects of *Fucus vesiculosus* covering intertidal mussel beds in the Wadden Sea. Helgoländer Meeresunters. 48: 243-256.

ANGER, K. (1978): Development of a subtidal epifaunal community at the island of Helgoland. Helgoländer Meeresunters. 31: 457-470.

ARBEITSGEMEINSCHAFT ZUR REINHALTUNG DER WESER (2001): Wesergütebericht 2001. Jahresbericht der ARGE Weser, Wassergütestelle des Niedersächsischen Landesamtes für Ökologie, Hildesheim, 85pp.

ARMITAGE, P.D., K. SZOSZKIEWICZ, J.H. BLACKBURN & I. NESBITT (2003): Ditch communities: a major contributor to floodplain biodiversity. Aquatic Conserv. Mar. Freshw. Ecosyst. 13: 165-185.

ARMONIES, W. (1994): Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. Helgoländer Meeresunters. 48: 291-297.

ARMONIES, W. & K. REISE (2003): Empty habitat in coastal sediments for populations of macrozoobenthos. Helgol. Mar. Res. 56: 279-287.

ARNTZ, W.E. (1980): Predation by demersal fish and its impact on the dynamics of macrobenthos. In: Tenore, K.R. & B.C. Coul (eds.): Marine Benthic Dynamics. University of South Carolina press, Columbia: pp. 121-149.

ARNTZ, W.E. (1981): Biomass zonation and dynamics of macrozoobenthos in an area stressed by oxygen deficiency. In: Barrett, G. & R. Rosenberg (eds.): Stress Effects on Natural Ecosystems. John Wiley and Sons, Chichester, pp. 179-200.

ARNTZ, W.E. & H. RUMOHR (1982): An experimental study of macrobenthic colonization and sucsession and the importance of seasonal variation in temperate latitudes. J. Exp. Mar. Biol. Ecol. 64(1):17-46.

ARNTZ, W.E., J.M. GILI & K. REISE (1999): Unjustifiably ignored: reflections on the role of benthos in marine ecosystems. In: GRAY, J.S. (ed.): Biogeochemical Cycling and Sediment Ecology. Kluwer Academic Publishers, The Netherlands, pp. 105-124.

BACHELET, G., X. DE MONTAUDOUIN, I. AUBY & P.-J. LABOURG (2000): Seasonal changes in macrophyte and macrozoobenthos assemblages in three coastal lagoons under varying degrees of euthrophication. ICES J. Mar. Sci., 57: 1495-1506.

BACKHAUSEN, I. (2002): FFH-Lebensraumtyp Ästuar: Untersuchungen zu ausgewählten Tiergruppen der Wesermündung. Ein Beitrag zur Erfassung des Erhaltungszustandes im Rahmen der Berichtspflicht. Fachhochschule Osnabrück, Diploma Thesis, 101pp.

BÄTHE, J. (1992): Die Makroinvertebratenfauna der Weser. Ökologische Analyse eines hochbelasteten, anthropogenen Ökosystems. Thesis, Ekopan Witzenhausen, 261pp.

BALZER, S., D. BOEDECKER & U. HAUKE (2002): Interpretation, Abgrenzung und Erfassung der marinen und Küsten-Lebensraumtypen nach Anhang I der FFH-Richtlinie in Deutschland. Natur und Landschaft 77: 20-28.

BARNES, R.S.K. (1994): The Brackish Water Fauna of Northwest-Europe. Cambridge University Press, Cambridge, 287pp.

BEHRE, K.E. (1978): Die Geschichte des Jadebusens und der Jade. In: Reineck H.-E. (Hrsg.): Das Watt. Lebens und Ablagerungsraum. Verlag W. Kramer, Frankfurt am Rhein, 178pp.

BEHRE, K.E. (1985): Die ursprüngliche Vegetation in den deutschen Marschengebieten und deren Veränderung durch prähistorische Besiedlung und Meeresspiegelbewegungen. Verh. Ges. Ökologie, Bd. 13: 85-96.

BEANLAND, L. (1940): Sand and mud communities in the Dovey Estuary. J. Mar. Biol. Ass. 24: 589-611.

BERGHAHN, R. & R. VORBERG (1998): Schwierigkeiten bei der Auswahl und der Bewertung von Referenzgebieten. SDN-Kolloquium 1998, Schriftenreihe der Schutzgemeinschaft Deutsche Nordsee e.V., Nr. 2, 106pp.

BOESCH, D.F. (1977): Application of numerical classification in ecological investigations of water pollution. Virginia Inst. Mar. Sci. Spec. Sci. Rep. No. 77, 113pp.

BOESCH, D.F., L. WASS & R.W. VIRNSTEIN (1976): The dynamics of estuarine benthic communities. In: WILEY, M. (ed.): Estuarine Processes, Vol. I, Uses, Stresses and Adaption to the Estuary. Acad. Press, New York, pp.177-196.

BORCHERDING, F. (1889): Das Tierleben auf und an der Plate bei Vegesack. Abh. Naturw. Ver. Bremen 11: 265-279.

BOYDEN C.R. & C. LITTLE (1973): Faunal distributions in soft sediments of the Severn Estuary. Estuar. and Coast. Mar. Sci., 1: 203-223.

BUCHANAN, J.B. (1984): Sediment analysis. In: Holme, N.A. & A.D. Mc Intyre (eds.): Methods for the Study of Marine Benthos. IBP-Handbook 16, Oxford; Blackwell Scientific Publications, pp. 41-65.

BUHR, K.J. (1979): Eine Massensiedlung von *Lanice conchilega* (Polychaeta: Terebellidae) im Weser-Ästuar. Veröffentl. Inst. Meeresforsch. Bremerh. 17: 101-149.

BUHR, K.J. (1981): Die Auswirkungen des kalten Winters 1978/79 auf das Makrozoobenthos der Lanice-Siedlung im Weserästuar. Veröffentl. Inst. Meeresforsch. Bremerh. 19: 115-131.

BUHS, F. & K. REISE (1997): Epibenthic fauna dredged from tidal channels in the Wadden Sea of Schleswig-Holstein: spatial patterns and a long-term decline. Helgoländer Meeresunters. 51: 343-359.

BUNDESANSTALT FÜR GEWÄSSERKUNDE (BFG) (1992): Handlungsanweisungen - Anwendung der Baggergutrichtlinien der Oslo-Helsinki-Kommission in der Wasser- und Schifffahrtsverwaltung des Bundes (HABAK-WSV). BFG-700, Koblenz.

BUNDESANSTALT FÜR GEWÄSSERKUNDE (BFG) (1997): Faunistische Untersuchungen an einer Buhne der Außenweser (km 73,6). BFG-1061, Koblenz.

BUNDESANSTALT FÜR GEWÄSSERKUNDE (BFG) (1999): Handlungsanweisung für den Umgang mit Baggergut im Küstenbereich (HABAK-WSV). BFG-1100, Koblenz.

BUNDESANSTALT FÜR GEWÄSSERKUNDE (BFG) (1999b): Bagger- und Klappstellen-untersuchungen in der Außenweser. Band I: Untersuchungen und Ergebnisse (HABAK-WSV). BFG-1146, Koblenz.

BUNDESANSTALT FÜR GEWÄSSERKUNDE (BFG) (2001): Bagger- und Klappstellen-untersuchungen im Ems Ästuar, Klappstellen 1-7. BFG-1329, Koblenz.

BUNDESANSTALT FÜR GEWÄSSERKUNDE (BFG) (2003): Bagger- und Klappstellen-untersuchungen in der Jade. BFG-Nr. 1349, Koblenz.

BUSCH, D., M. SCHIRMER, B. SCHUCHARDT & P. ULLRICH (1989): Historical changes of the River Weser. In: PETTS, G.E. (ed.): Historical Change of Large Alluvial Rivers: Western Europe. John Wiley & Sons Ltd.

BUSCH, D., M. SCHIRMER, B. SCHUCHARDT & K. SCHRÖDER (1984): Der Ausbau der Unterweser zum Großschiffahrtsweg und seine Auswirkungen auf das Flußökosystem und die Flußfischerei. N. Arch. F. Nds., 33: 60-80.

CARTER, R.W.G. (1988): Coastal environments. Academic Press, London, 617pp.

CARRIKER, M.R. (1967): Ecology of estuarine benthic invertebrates: A perspective. In: G. Lauff (ed.): Estuaries. American Association for the Advancement of Science, Washington, 442-487.

CASPERS, H. (1948): Ökologische Untersuchungen über die Wattentierwelt im Elbe-Ästuar. Verh. Dt. Zool. Kiel: 350-359.

CASPERS, H. (1958): Biologie der Brackwasserzonen im Elbeästuar. Verh. Int. Ver. Limnol. 13: 687-698.

CASPERS, H. (1959): Die Einteilung der Brackwasserregionen in einem Ästuar. Archo. Oceanogr. Limnol., Suppl. 11: 155-169.

CEFAS (Centre of Environment, Fisheries and Aquaculture Science) (2002): Guidelines for the conduct of benthic studies at aggregate dredging sites. Report of CEFAS, Burnham Laboratory, Essex, 117pp.

CIS (COMMON IMPLEMENTATION STRATEGY) (2003): Guidance on monitoring for the Water Framework Directive. Working Group 2.7 Final Report, 23 January, Brussels.

CLAUS, B. (1998): Ein Ästuarschutzkonzept für die norddeutschen Ästuare im Spannungsfeld zwischen Nutzung und Naturschutz. In: Mitteilungen aus der NNA, 3: 2-6.

CLARKE, K. R., & R.M. WARWICK (1994): Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth: 144pp.

CLARKE, K.R. & R.N. GORLEY (2001): PRIMER v5. User Manual. Plymouth Marine Laboratory, Plymouth.

COGNETTI, G. & F. MALTAGLIATI (2000): Biodiversity and adaptive mechanisms in brackish water fauna. Mar. Poll. Bulletin Vol. 40, No. 1: 7-14.

COLEMAN, N., W. CUFF, M. DRUMMOND & J.D. KUDENOV (1978): A quantitative survey of the macrobenthos of Western Port, Victoria. Aust. J. Freshwater Res., 29: 445-66.

DAHL, F. (1893): Untersuchungen über die Tierwelt der Unterelbe. Ber. Komm. Unters. Dt. Meere 6: 1-24.

DAHL, E. (1956): Ecological salinity boundaries in poikilohaline waters. Oikos, 7: 1-21.

DAVIES J., J. BAXTER, M. BRADLEY, D. CONNOR, J. KHAN, E. MURRAY, W. SANDERSON, C. TURNBULL & M. VINCENT (2001): Marine Monitoring Handbook, UK Marine SACs Projekt, 405 pp.

DAVIS, H.C. & H. HIDU (1988): Effects of turbidity-producing substances in sea water on eggs and larvae of three genera of bivalve mollusks. The Veliger, Vol. 11, No. 4: 316-324.

DAYTON, P.K. (2003): The importance of natural science to conservation. Am. Nat. 162: 1-13.

DEGRAER, S., I. MOUTON, L. DE NEVE & M. VINCX (1999): Community structure and intertidal zonation of the macrobenthos on a macrotidal, ultra-dissipative sandy beach : Summer- winter comparison. Estuaries 22 (38): 742-752.

DE JONGE F., J., BAKKER, C. VAN BERKEL, K. DAHL , N. DANKERS, C. GÄTJE, H. MARENCIC & P. POTEL (1999): Wadden Sea Status Report. Wadden Sea Ecosystem No. 9. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Quality Status Report Group. Wilhelmshaven, Germany.

DEN HARTOG, C. (1961): Die faunistische Gliederung in einem südwestniederländischen Deltagebiet. Int. Rev. Ges. Hydrobiol. 46: 407-418.

DEN HARTOG, C. (1964): Typologie des Brackwassers. Helgoländer wiss. Meeresunters., 10: 377-390.

DEN HARTOG, C. (1971): The border environment between the sea and the fresh water, with special reference to the estuary. Vie et Milieu, Suppl. 22: 739-756.

DITTMER, J. D. (1981): The distribution of subtidal macrozoobenthos in the estuaries of the river Ems and Weser. In: Dankers, N., H. Kühl & W.J. Wolf (eds.): Invertebrates of the Wadden Sea. Marine Zoology (4): 188-206.

DÖRJES, J., S. GADOW, H.-E. REINECK & I.B. SINGH (1969): Die Rinnen der Jade (Südliche Nordsee). Sedimente und Makrobenthos. Senckenbergiana Marit. 50: 5-62.

DÖRJES J. & J. D. HOWARD (1975): Estuaries of Georgia Coast, U.S.A.: sedimentology and biology. IV. Fluvial- marine transition indicators in an estuarine environment- Ogeechee River- Ossabaw Sound. Senckenb. Marit. 7: 137-79.

DÖRJES J. & H.-E. REINECK (1977): Fauna und Fazies einer Sandplate (Mellum Bank, Nordsee). Sedimente und Makrobenthos. Senkenberg. Marit. 9(1/2): 91-155.

DÖRJES, J. (1978): Das Watt als Lebensraum. In: Reineck H.-E. (Hrsg.): Das Watt. Lebens und Ablagerungsraum. Verlag W. Kramer, Frankfurt am Rhein. 178 pp.

DOLMER, P. & R.P. FRANDSEN (2002): Evaluation of the Danish mussel fishery: suggestions for an ecosystem management approach. Helgol. Mar. Res. (2002) 56: 13-20.

EDGAR, G.J. & N.S. BARRETT (2002): Benthic macrofauna in Tasmanian estuaries: scales of distribution and relationships with environmental variables. J. Exp. Mar. Biol. Ecol. 270: 1-24.

ELLIOT, M. & M.G. O´REILLY (1991): The variability and prediction of marine benthic community parameters. In: Elliot M. & J.P. Ducrotoy (eds.): Estuaries and Coasts, Spatial and Temporal Intercomparisons. ECSA 19 Symposium, Univ. of Caen, France, Olsen & Olsen, pp. 231-238.

ENGEL, H. (1995): Die Hydrologie der Weser. In: Gerken, B. & M. Schirmer (eds.): Die Weser. Limnologie aktuell, Gustav Fischer Verlag, Stuttgart, 349 pp.

ESSINK, K. & H.L. KLEEF (1988): *Marenzelleria viridis* (Verill, 1873) (Polychaeta: Spionidae). A new record from the Ems estuary (NL/FRG). Zool. Bijdragen 38: 1-13.

ESSINK, K. & H.L. KLEEF (1993): Distribution and lifecycle of the North American spionid polychaete *Marenzelleria viridis* (Verill 1873) in the Ems estuary. Neth. J. Aquat. Ecol., 27: 237-246.

ESSINK, K. (1995): Ecological effects of dredging and dumping of dredge spoil. Waddensea Newsletter 1995-1: 9-14.

ESSINK, K. (1996): Die Auswirkungen von Baggergutablagerungen auf das Makrozoobenthos - Eine Übersicht der niederländischen Untersuchungen. In: BFG-Mitteilungen: Baggern und Verklappen im Küstenbereich. Nr.11: 12-17.

ESSINK, K., F.H.I.M. STEYFAERT, H.P.J. MULDER, V.N. DE JONGE, T. VAN HEUVEL & J. VAN DEN BERGS (1992): Effects of dredging activities in the Ems Estuary and Dutch Wadden Sea. Netherlands Institute for Sea Research, No. 20: 243-246.

FAIRWEATHER, P.G. (1991): Statistical power and design requirements for environmental monitoring. Aust. J. Mar. Freshwater Res., 42: 555-67.

FAITH, D.P., C.L. HUMPHREY & P.L. DOSTINE. (1991): Statistical power and BACI designs in biological monitoring: comparative evaluation of measures of community dissimilarity based on benthic macroinvertebrate communities in Rockhole Mine Creek, Northern Territory, Australia. Aust. J. Mar. Freshwater Res., 42: 589-602.

FITTKAU, E.J. & F. REISS, (1983): Versuch einer Rekonstruktion der Fauna europäischer Ströme und ihrer Auen. Arch. Hydrobiol., 97(1): 1-6.

FRANZIUS, L. (1888): Die Korrektion der Unterweser. Nachdruck in: Die Küste 51: 39-74 (1991).

FRÄMBS, H., M. KINDER, B. HIELEN, B. BÖHME, C.P. GÜNTHER, E. RACHOR, H. CORDES & D. MOSSAKOWSKI (2002): Renaturierung salzbeeinflusster Lebensräume der Nordseeküste. BfN Skripten 68, 325 pp.

GARRABOU, J., E. BALLESTEROS & M. ZABALA et al. (2002): Structure and dynamics of north-western Mediterranean rocky benthic communities along a depth gradient. Estuar., Coast. Shelf Sci. 55: 493-508.

GOSSELCK, F., J. PRENA, G. ARLT & A. BICK (1993): Distribution and zonation of macrobenthic fauna in the deep channels of the Weser Estuary. Senckenb. Marit. 23: 89-98.

GRABEMANN, I., A. MÜLLER & B. KUNZE (1993): Ausbau der Unter- und Außenweser. Morphologie und Hydrologie. In: Umweltvorsorge für ein Flussökosystem. UVP-Förderverein (Hrsg.), Dortmunder Vertrieb für Bau- und Planungsliteratur, pp. 21-40.

GRABEMANN I. & G. KRAUSE (2001): On different time scales of suspended matter dynamics in the Weser estuary. Estuaries Vol. 24, No. 5: 688-698.

GRALL, J. & M. GLEMAREC (1997): Using biotic indices to estimate macrobenthic community perturbations in the Bay of Brest. Estuar. Coast. Shelf Sci. 44 (Suppl. A): 43-53.

GRAY, J.S. (1981): The Ecology of Marine Sediments. Cambridge University Press 1981, 185 pp.

GRAY, J.S. (2000): The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. J. Exp. Mar. Biol. Ecol. 250: 23-49.

GÜNTHER, C.P. (1992): Dispersal of intertidal vertebrates: a strategy to react to disturbances of different scales? Neth. J. Sea Res. 30: 45-56.

HAESLOOP, U. (1990): Beurteilung der zu erwartenden Auswirkungen einer Reduzierung der anthropogenen Weserversalzung auf die aquatische Biozönose der Unterweser. Univ. Bremen, Thesis 295 pp.

HAESLOOP, U. & B. SCHUCHARDT (1995): Plankton und Makrozoobenthon der gezeitenbeeinflußten Unterweser. In: Gerken, B. & M. Schirmer (Hrsg.): Die Weser. Fischer, Stuttgart, pp. 161-173.

HAGENDORFF, R., LEUCHS, H. & NEHRING, S. (1996): Eine Literaturübersicht zum Thema Auswirkungen erhöhter Schwebstoffgehalte durch Baggern und Verklappen auf Muscheln. In: BFG-Mitteilungen: Baggern und Verklappen im Küstenbereich. Nr.11: 7-11.

HALL, S.J. (1994): Physical disturbance and marine benthic communities: Life in unconsolidated sediments. Oceanography and Marine Biology: Ann. Rev. 1994, 32: 179-239.

HARTMANN-SCHRÖDER, G. (1996): Annelida, Borstenwürmer, Polychaeta. In: Dahl, F. (ed): Die Tierwelt Deutschlands und der angrenzenden Meeresteile. Fischer, Jena, Germany.

HAUSER, B. & H. MICHAELIS (1975): Die Makrofauna der Watten, Strände, Riffe und Wracks um den Hohen Knechtsand in der Wesermündung. Jber. Forsch.-stelle Insel- u. Küstenschutz, 26: 85-119.

HAYWARD P.J. & J.S. RYLAND (1990): The Marine Fauna of the British Isles and North-West Europe. Clarendon, Oxford.

HEIBER, W. (1988): Die Faunengemeinschaft einer großen Stromrinne des Wurster Wattengebietes (Deutsche Bucht). Untersuchungen zur Struktur und Dynamik in Abhängigkeit von Gezeiten und Jahreszyklus und Folgerungen zu Austauschprozessen zwischen Wattenmeer und offener See. Univ. Bonn, Diss., 368 pp.

HEIBER W. & E. RACHOR (1989): Entwicklungen im Gefährdungsstatus mariner Benthos-Invertebraten und ihre Ursachen. Schr.-R. f. Landschaftspflege und Naturschutz, 29: 52-64.

HEINRICH & MÜHLNER (1981): Beurteilung der Röhrichtbestände an der Unterweser im Bereich des Landkreises Wesermarsch im Hinblick auf ihre Schutzwürdigkeit. Landkreis Wesermarsch, Amt für Landschaftspflege (Hrsg.), unpubl.

HIRST, A.J. (2003): Broad-scale environmental gradients among estuarine benthic macrofaunal assemblages of south-eastern Australia: implications for monitoring estuaries. Mar. Freshw. Res., 55: 79-92.

HOLME, N.A. (1949): The fauna of sand and mud banks near the mouth of the Exe Estuary. J. Mar. Biol. Ass. 28: 189-237.

HOVERS, G. (1973): Der Einfluss von Strombauwerken auf die morphologische Entwicklung der Stromrinnen im Mündungsgebiet eines Tideflusses, untersucht am Beispiel der Außenweser. Mitteilungsbl. Bundesanst. Wasserbau, Karlsruhe, 34: 1-116.

ICES (2001): Report of the ICES/OSPAR Steering Group on Quality Assurance of Biological Measurements Related to Eutrophication Effects. ICES CM 2001 / ACME: 5, 73pp.

ICES (2003): Environmental status of the European Seas. Report No. 1123, 75pp. (http://www.ices.dk).

IRVINE, K. (2004): Classifying ecological status under the European Water Framework Directive: the need for monitoring to account for natural variability. Aquatic Conserv. Mar. Fresh. Ecosyst. 14: 107-112.

JAKLIN, S. (2003): Recruitment dynamics of North Sea macrozoobenthos in intertidal soft bottoms: larval availability, settlement and dispersal. Thesis, Univ. Bremen: 136pp.

JONES, A.R., C.J. WATSON-RUSSELL & A. MURRAY (1986): Spatial patterns in the macrobenthic communities of the Hawkesbury Estuary, New South Wales. Aust. J. Mar. Freshw. Res., 37: 512-43.

KETCHUM, B.H. (1983). Estuarine characteristics. In : Ketchum (ed.): Ecosystems of the world 26, Estuaries and enclosed seas. Elsevier Scientific Publ. Com., Amsterdam, 500pp.

KINNE, O. (1966): Physical aspects of animal life in estuaries with special reference to salinity. Neth. J. of Sea Res., 3: 222-244.

KNUST, R., J. HEUERS, A. SCHRÖDER, M. EXO, O. HÜPPOP, C. KETZENBERG, H. WENDELN, K. LUCKE & J. GABRIEL (2001): Empfehlungen zu Mindestanforderungen an die projektbezogene Untersuchung möglicher bau- und betriebsbedingter Auswirkungen von Offshore-Windenergieanlagen auf die Meeresumwelt der Nord- und Ostsee. BMU /UBA Berlin, Projektgruppe Offshore WEA, 52 pp.

KOFOD, M. (1997): Abschätzung der Emission umweltrelevanter Stoffe bei der Unterbringung von belastetem Baggergut im subaquatischen Milieu und deren Bewertung. BFG-Mitteilungen, Unterbringung von belastetem Baggergut im aquatischen Milieu. Nr.6: 48-55.

KOLBE, K. & H. MICHAELIS (2001): Long-term changes of intertidal benthic assemblages in the mesohalinicum of the Weser Estuary. Senkenbergiana Marit., 31(2): 197-214.

KOTTA J., H. ORAV & E. SANDBERG-KILPI (2001): Ecological consequence of the introduction of polychaete *Marenzelleria* cf. *viridis* into a shallow-water biotope of the northern Baltic Sea. J. Sea Res. 46: 273-280.

KROST, P. (1996): Eine Literaturübersicht zum Thema „Auswirkungen erhöhter Schwebstoffgehalte durch Baggern und Verklappen auf Muscheln“. In: BFG-Mitteilungen, Baggern und Verklappen im Küstenbereich. Nr.11: 69-72.

KRUSKAL, J.B. & WISH M. (1978): Multidimensional Scaling. Sage, Beverly Hills, Calif.

KÜFOG (1998): Benthoskundliche Untersuchungen zur Einbringung von Baggergut in den Wurster Arm. Zusammenfassende Darstellung der 1.-3. faunistischen Erhebung, i.A. Hansestadt Bremisches Amt, Bremerhaven, 33pp., unpubl.

KÜHNE, S. & E. RACHOR (1996): The macrofauna of a stony sand area in the German Bight (North Sea). Helgoländer Meeresunters. 50: 433-352.

LERBERG, S.B., F. HOLLAND & D.M. SANGER (2000): Response of tidal creek macrobenthic communities to the effects of watershed development. Estuaries 23 (6): 838-853.

LEWIS, J.R. (1980): Options and problems in environmental management and evaluation. Helgoländer Meeresunters. 33: 452-466.

LEVIN, L.A., D.F. BOESCH, A. COVICH, C. DAHM, C. ERSEUS, K.C. EWEL & R.T. KNEIP (2001): The function of marine critical transition zones and the importance of sediment biodiversity. Ecosystems 4: 430-451.

LINCOLN, R.J. (1979): British Marine Amphipoda: Gammaridea. Natural History Museum, London.

LINDEBOOM, H.J. & S.J. DE GROOT (1998): IMPACT II: The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystem. NIOZ-rapport 1998-1.

LOEBE, K. (1968): Das Weserbuch. Hameln, 188pp.

LÜNEBURG, H. (1954): Vergleichende Wattuntersuchungen im Bereich der Wesermündung. Veröff. Inst. Meeresforsch. Bremerh., 3: 66-125.

LÜNEBURG, H., K. SCHAUMANN, & S. WELLERSHAUS (1975): Physiographie des Weser-Ästuars (Deutsche Bucht). Veröff. Inst. Meeresforsch. Bremerh., 15: 195-226.

MAURER, D., R.T. KECK, J.C. TINSMAN, W. A. LEATHEM, C. WETHE, C. LORD & T. M. CHURCH (1986): Vertical migration and mortality of marine benthos in dredged material: A Synthesis. Int. Revue ges. Hydrobiol. 71: 49-64.

MARGALEF, R. (1958): Information Theory in Ecology. Gen. Syst. 3: 36-71.

McLUSKY, D. S. (1989): The Estuarine Ecosystem, 2nd edition. Blackie Academic & Professional, Glasgow, 215pp.

McLUSKY, D.S. (2001): North Sea estuaries. Senckenbergiana Marit., 31: 177-186.

MEIRE, P.M., J. SEYS, J. BUIJS, J. COOSEN (1994): Spatial and temporal patterns of intertidal macrobenthic populations in the Oosterschelde: are they influenced by the construction of the storm-surge barrier? Hydrobiologia, 282/ 283: 157-182.

MEYBIER & BÖMEKE (1970): Chemische Beweissicherung in der Unterweser (Titanwerk). Nieders. Wasseruntersuchungsamt, 11pp., unpubl.

MEYERDIERKS, J., N. HEMMER & M. SCHIRMER (2003): Die Bodenfauna der Weserwatten zwischen Bremen und Bremerhaven. Abh. Naturwiss. Verein Bremen, 45(2): 455-464.

MICHAELIS, H. (1973): Untersuchungen über das Makrobenthos der Wesermündung. Forschungst. Insel- Küstenschutz d. Nieders. Wasserwirtschaftsverwaltung, Jahresber. 1972, Bd. 24: 103-170.

MICHAELIS, H. (1981): Intertidal benthic communities of the estuaries of the rivers Ems and Weser. In: Dankers, N., H. Kühl & W.J. Wolff (eds.): Invertebrates of the Wadden Sea. Rep. Wadden Sea Working Group. Mar. Zool. (4): 158-188.

MICHAELIS, H., H. FOCK, M. GROTJAHN & D. POST (1992): The status of intertidal zoobenthic brackish-water species in estuaries of the German Bight. Neth. J. Sea Res., Bd. 30: 201- 207.

MICHAELIS, H. & K. REISE (1994): Langfristige Veränderungen des Zoobenthos im Wattenmeer. In: Lozan, J.L., E. Rachor, K. Reise, H. von Westernhagen & W. Lenz (Hrsg.): Warnsignale aus dem Wattenmeer. Blackwell, Berlin, pp. 106-116.

MILLAT, G. & M. HERLYN (1999): Erfassung und Dokumentation des Miesmuschelbestandes der niedersächsischen Watten sowie Untersuchung und Bewertung alternativer Methoden zur Besatzmuschelgewinnung. Abschlußbericht zum Forschungsprojekt der niedersächsischen Wattenmeerstiftung, 169pp., unpubl.

MORGENTHAL, E. (1995): Die Invertebratenfauna (Mollusca, Crustacea) in salzbeeinflussten Kleingewässern und Gräben der Wesermarsch bei Bremerhaven. Univ. Göttingen, Diploma Thesis, 119 pp.

MÜHLENHARDT- SIEGEL, U. (1988): Die Weichbodengemeinschaft vor der Elbemündung unter dem Einfluss der Klärschlammverklappung. I. Die saisonale Veränderung von Arten- und Individuenzahl sowie Biomasse unter Berücksichtigung der Sedimentstruktur. Helgoländer Meeresuntersuchungen 42: 37-65.

MÜHLENHARDT- SIEGEL, U. (1990): Die Weichbodengemeinschaft vor der Elbemündung unter dem Einfluss der Klärschlammverklappung. II. Die Gemeinschaftsstruktur im saisonalen Wechsel. Helgoländer Meeresuntersuchungen 44: 189-217.

MÜLLER, A. (1994): Die Insektenfauna in salzbeeinflussten Kleingewässern und Gräben der Wesermarsch bei Bremerhaven. Diplomarbeit, Univ. Göttingen, Diploma Thesis, 139 pp.

NEHRING, S. & H. LEUCHS (1997): Einsatz der Remots-Sedimentprofilkamera zur Dokumentation von Sedimentationsereignissen nach Verklappung. Mitteilungen der Bundesanstalt für Gewässerkunde, Baggern und Verklappen im Küstenbereich, Nr.11: 65-68.

NEHRING, S. & H. LEUCHS (1999a): Neozoa (Makrozoobenthos) an der deutschen Nordseeküste- Eine Übersicht. Bundesanstalt für Gewässerkunde, Koblenz, BFG-Bericht 1200, 191 pp.

NEHRING, S. & H. LEUCHS (1999b): The BFG-Monitoring in the German North Sea estuaries: Macrozoobenthos. Senckenbergiana Marit. 29 (Suppl.): 107-111.

NEWELL, R.C., L.J. SEIDERER & D.R. HITCHCOCK (1998): The impact of dredging works in coastal waters: A review of the sensitivity to disturbance and subsequent recovery of biological resources on the sea bed. Oceanography and Marine Biology. An Annual Review, 36: 127-78.

NIEDERSÄCHSISCHES LANDESAMT FÜR ÖKOLOGIE (NLÖ) (2001): Dienstbericht der Forschungsstelle Küste. 11/2001, 44 pp.

PEARSON, T.H. & R. ROSENBERG (1978): Macrobenthic succession in relation to organic enrichment and pollution of the environment. Oceanogr. Mar. Biol. Annu. Rev. 16: 229-311.

PEARSON, T.H., A.D. ANSELL & L. ROBB (1986): The benthos of the deeper sediments of the Firth of Clyde, with particular reference to organic enrichment. Proceedings of the Royal Society of Edinburgh, 90B: 329-350.

PETERSEN, G.H., P.B. MADSEN, K.T. JENSEN, K.H. VAN BERNEM, J. HARMS, W. HEIBER, I. KRÖNCKE, H. MICHAELIS, E. RACHOR, K. REISE, R. DEKKER, G.J.M. VISSER, & W.J. WOLFF (1996): Red List of macrofaunal benthic invertebrates of the Wadden Sea. Helgoländer Meeresunters. 50, Suppl.: 69-76.

PIANC (1998): Management of aquatic disposal of dredged material. Report of Working Group 1 of the Permanent Environment Comission, Brüssel.

PIELOU, E. C. (1975): Ecological Diversity. Wiley-Interscience, New York, 165pp.

POORE, G.C.B. & S. RAINER (1979): A three year study of benthos of muddy environments in Port Philipp Bay, Victoria. Estuar. and coast. Mar. Sci., 9: 477-497.

PRITCHARD, D.W. (1967): Observation of circulation in coastal plain estuaries. In: G.H. Lauff (ed.), Estuaries. Am. Assoc. Adv. Sci. Publ., 83: 37-44.

RACHOR, E. (1982): Indikatoren für Umweltbelastungen im Meer. Dechiana Beih. 26: 128-137.

RACHOR, E. (1998): Rote Liste der bodenlebenden wirbellosen Meerestiere. –In: Binot, M., R. Bless, P. Boye, H. Gruttke & P. Pretscher (Bearb.): Rote Liste der gefährdeten Tierarten Deutschlands.- Schriftenreihe für Landschaftspflege und Naturschutz, 55, 434pp.

RACHOR, E. & S.A. GERLACH (1978): Changes of macrobenthos in a sublittoral sand area of the German Bight, 1967 to 1975. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 172: 418-431.

RAFFAELLI, D. & S. HAWKINS (1996): Intertidal Ecology. Chapman and Hall, London, 356 pp.

RAGUTZKI & MEYER (1999): KFKI-Forschungsvorhaben “Sedimentverteilung als Indikator für morphologische Prozesse”. Dienstbericht NLÖ-Forschungsstelle Küste, Norderney, 40pp., unpubl.

RAINER, S. (1981): Temporal patterns in the structure of macrobenthic communities of an Australian Estuary. Estuar., Coast. and Shelf Sci., 13: 597-620.

RAMACHER, H. (1974): Der Ausbau von Unter-und Außenweser. Mitteilg. d. Franziusinstitutes der TU Hannover, 41: 257-276.

REES, C.B. (1940): A preliminary study of the ecology of a mud-flat. J. Mar. Biol. Ass. 24: 185-199.

REILLY, F.J., R.J. SPAGNOLO & E. AMBROGIO (1999): Marine and estuarine shallow water science and management: The relationship among habitats and their management. Estuaries 22 (38): 731-734.

REINEKING, B. (1998): Übersicht über Referenzgebiete im internationalen Bereich. SDN- Kolloquium 1998, Schriftenreihe der Schutzgemeinschaft Deutsche Nordsee e.V., Nr. 2, 106 pp.

REISE, K. (1985): Tidal Flat Ecology. An Experimental Approach to Species Interactions. In: Golley, Lange, Olson, Remmert, Billings (eds.): Ecological Studies 54, Springer, Hamburg, 234pp.

REISE, K. (1991): Macrofauna in mud and sand of tropical and temperate tidal flats. In: Elliott, M. & J.-P. Ducrotroy (eds.): Estuaries and Coasts: Spatial and Temporal Intercomparisons. ECSA 19 Symposium, Caen, France, Olsen & Olsen, pp. 211-216.

REISE, K., S. GOLLASCH & W.J. WOLFF (1999): Introduced marine species of the North Sea coasts. Helgoländer Meeresunters. 52: 219-234.

REMANE, A. (1934): Die Brackwasserfauna. Verh. Dt. Zool. Ges., 36: 34-74.

REMANE, A. (1940): Einführung in die zoologische Ökologie der Nord- und Ostsee In: GRIMPE, G. & E. WAGLER (Hrsg): Die Tierwelt der Nord- und Ostsee. Akademische Verlagsgesellschaft Becker und Erler, Leipzig: pp.1-238.

REMANE, A. (1950): Das Vordringen der limnischer Tierarten in das Meeresgebiet der Nord- und Ostee. Kieler Meeresforsch. 7: 5-23.

REMANE, A. (1958): Die Biologie des Brackwassers (Teil I). In: Thienemann, A. (Hrsg.): Die Binnengewässer. Bd. XXII, E. Schweitzerbart`sche Verlagsbuchhandlung, 348 pp.

REMANE, A. (1969): Wie erkennt man eine genuine Brackwasserart? Limnologica 7: 9-21.

REMANE, A. & C. SCHLIEPER (1971): The biology of brackish water. In: Elster, H.J. & W. Ohle (Hrsg.): Die Binnengewässer. Schweizerbart`sche Verlagsbuchhandlung, Stuttgart, Wiley Interscience Division New York, 372pp.

RIEMANN-ZÜRNECK, K. (1969): *Sagartia troglodytes* (Anthozoa) Biologie und Morphologie einer schlickbewohnenden Aktinie. Veröff. Inst. Meeresforschung Bremerhaven 12, 169-230.

RISTICH, S., S. CRANDALL, M. & J. FORTIER (1977): Benthic and epibenthic macroinvertebrates of the Hudson River. I. Distribution, natural history and community structure. Estuarine Coastal Mar. Sci. 5: 255-66.

ROSENBERG, R. (1977a): Effects of dredging operations on estuarine benthic macrofauna. Mar. Pollut. Bull., 8 No.5: 102-104.

ROSENBERG, R. (1977b): Benthic macrofaunal dynamics, production and dispersion in an oxygen-deficient estuary of West Sweden. J. Exp. mar. Biol. Ecol., 26: 107-133.

RUMOHR, H. (1996): Biologische Sukzession nach physikalischen Störungen am Boden der Ostsee. In: BFG-Mitteilungen, Baggern und Verklappen im Küstenbereich. Nr.11: 69-72.

RUMOHR, H. (1999): Soft bottom macrofauna: Collection, treatment and quality assurance of samples. ICES Techniques in Marine Environmental Science, No. 27,19 pp.

SAIER, B. (2002) : Subtidal and intertidal mussel beds (*Mytilus edulis* L.) in the Wadden Sea: diversity differences of associated epifauna. Helgol. Mar. Res. 56: 44-50.

SAILA, S.B., S.D. PRATT & T.T. POLGAR (1972): Dredge spoil disposal in Rhode Island Sound. Univ. Rhode Island Mar. Tech. Rep. 2, 48 pp.

SALZWEDEL, H., E. RACHOR & D. GERDES (1985): Benthic macrofauna communities in the German Bight. Veröff. Inst. Meeresforsch. Bremerh. 20: 199-267.

SARDA, R., K. FOREMAN, C.E. WERME & I. VALIELA (1998): The impact of epifaunal predation on the structure of macrofaunal invertebrate communities of tidal saltmarsh creeks. Estuar. Coast. Shelf Sci. 46: 657-669.

SCHIRMER, M. (1995): Eindeichung, Trockenlegung, Korrektion, Anpassung: Die Abwicklung der Unterweser und ihrer Marsch. In: Gerken, B. & M. Schirmer (Hrsg): Limnologie aktuell- Die Weser. G. Fischer Verlag, Stuttgart, Bd. 6: 35-54.

SCHIRMER, M. (1996): Die Weser- eine Zustandsbeschreibung. In: Lozan, J.L. & H. Kausch (Hrsg.), Warnsignale aus Flüssen und Ästuaren. Parey, Berlin: pp. 75-83.

SCHLUNGBAUM, G. (1999): Die EU-Rahmenrichtlinie für eine gemeinsame Wasserpolitik aus besonderer Sicht der Ökologie der Ästuare und Küstengewässer. Rostock. Meeresbiolog. Beitr. 7: 5-43.

SCHOLLE, J. & B. SCHUCHARDT (1997): Übersicht über die Benthon-Taxozönosen im limnischen Abschnitt der Unterweser und in seinen Zuflüssen. Bremer Beitr. f. Naturk. u. Naturschutz, 3: 7-24.

SCHLIENZ, W. (1922): Verbreitung und Verbreitungsbedingungen der höheren Krebse im Mündungsgebiet der Elbe. Univ. Hamburg, Thesis.

SCHRÄDER, T. (1941): Fischereibiologische Untersuchungen im Wesergebiet. II. Hydrographie, Biologie und Fischerei der Unter- und Außenweser. Z. Fisch., 39: 527-693.

SCHROEDER, A. (2003): Community dynamics and development of soft bottom macrobenthos in the German Bight (North Sea) 1969-2000. Univ. Bremen, Thesis, 190pp.

SCHUCHARDT, B., M. BECKMANN, R. KNUST & M. SCHIRMER (1984): Eulitorale Uferstrukturen an der Unterweser. Drosera 2: 83-90.

SCHUSTER, O. (1952): Die Vareler Rinne im Jadebusen. Abh. Senckenberg. Naturf. Ges. 486: 1-38.

SMAAL, A.C., M. KOESTER, P. H. NIENHUIS & P.M. MEIRE (1991): Changes in the Oosterschelde ecosystem induced by delta works. In: Elliott, M. & J.-P. Ducrotroy (eds.): Estuaries and Coasts: Spatial and Temporal Intercomparisons. ECSA 19 Symposium, Caen, France, Olsen & Olsen: pp. 375-384.

SMITH, M.P.L. (1991): Environmental impact assessment: the roles of predicting and monitoring the extent of impacts. Aust. J. Mar. Freshwater Res., 42: 603-614.

SÖFFKER, K. (1982): Die eulitorale Bodenfauna zwischen Bremerhaven und Bremen. Jb. Forschungsst. f. Insel- und Küstenschutz. 33: 105-143.

SPOONER G.M. & H.B. MOORE (1940): The ecology of the Tamar estuary. VI. An account of the macrofauna of the intertidal muds. J. Mar. Biol. Ass. 24: 284-330.

SSYMANK, A. & N. DANKERS (1996): II. Red List of biotopes and biotope complexes of the Wadden Sea Area. Helgol. Meeresunters. 50 (Suppl.): 9-37.

STREIF, H.J. (1978): Geologie des Küstenraums. In: Reineck, H.-E. (Hrsg.): Das Watt. Lebens- und Ablagerungsraum. Verlag W. Kramer, Frankfurt am Rhein. 178 pp.

STREIF, H.J. (1996): Die Entwicklung der Küstenlandschaft und Ästuare im Eiszeitalter und in der Nacheiszeit. In: Lozan, J.L. & H. Kausch (Hrsg.): Warnsignale aus Flüssen und Ästuaren. Parey Berlin, pp. 11-19.

STRIPP, K. (1969): Die Assoziationen des Benthos in der Helgoländer Bucht. Veröff. Inst. Meeresforsch. Bremerh. 12: 95-141.

TALLEY, T.S., DAYTON, P.K. & S.E. IBARRA-OBANDO (2000): Tidal flat macrofaunal communities and their associated environments in estuaries of southern California and northern Baja California, Mexico. Estuaries 23: 97-114.

TARDENT, P. (1993): Meeresbiologie- eine Einführung. Georg-Thieme Verlag, Stuttgart, 324pp.

TESCH, A. (2001): Ökologische Wirkungskontrollen und ihr Beitrag zur Effektivierung der naturschutzrechtlichen Eingriffsregelung. Beiträge zur räumlichen Planung Nr. 60. Schriftenreihe des Fachbereichs Landschaftsarchitektur und Umweltentwicklung der Univ. Hannover, Thesis, 266pp.

TESCH, A. & J. WITT (1998): Ergebnisse des CT III-Monitoringprogramms zur Sandentnahme und Verklappung in der Außenweser. Zusammenfassung und vertiefte Auswertung; WBNL, i.A. des Hansestadt Bremischen Amtes, Bremerhaven, unpubl.

THORSON, G. (1957): Bottom communities (sublittoral or shallow shelf). Mem. Geol. Soc. Amer. 67: 461-534.

TUENTE, U., D. WÜBBEN & W. HEIBER (2002): Ansätze zur Ermittlung von Hintergrundwerten chemischer und biologischer Messgrößen der Nordsee. Bodden 12: 33-47.

UNDERWOOD, A.J. (1991): Beyond BACI: experimental designs for detecting human environmental impacts on temporal variations in natural populations. Aust. J. Mar. Freshwater Res., 42: 569-87.

VÄLIKANGAS, I. (1933): Über die Biologie der Ostsee als Brackwassergebiet. Verh. Int. Ver. Limnol. 6: 62-112.

VAN DER MEER, J. (1997): Sampling design of monitoring programmes for marine benthos: a comparison between the use of fixed versus randomly selected stations. J. Sea Res. 37: 167-179.

VAN DOLAH, R. F., D. R. CALDER & D. M. KNOTT (1984): Effects of dredging and open-water disposal on benthic macroinvertebrates in a South Carolina estuary. Estuaries Vol. 7, No. 1: 28-37.

VENICE SYSTEM (1959): Symposium on the classification of brackish waters. Venice, April 8-14, 1958. Arch. Limnol. Oceanogr. 11 (Suppl.): 1-248.

VORBERG, R. (1995): On the decrease of sabellarian reefs along the German coast. Publ. Serv. Geol. Lux., vol. 229, proc. 2nd Europ. Reg. Meet., ISRS, pp. 87-93.

VORBERG, R. (1997): Auswirkungen der Garnelenfischerei auf den Meeresboden und die Bodenfauna des Wattenmeeres. Schriftenreihe Naturwissenschaftliche Forschungsergebnisse Bd. 54, Verlag Dr. Kovac Hamburg, 191pp.

WARWICK, R.M. & J.R. DAVIES (1977): The distribution of sublittoral macrofauna communities in the Bristol Channel in relation to the substrate. Estuar. coastal Mar. Sci. 5: 267-288.

WARWICK, R.M., C.M. ASHMAM, A.R. BROWN, K.R. CLARKE, B. DOWELL, B. HART, R.E. LEWIS, N. SHILLABEER, P.J. SOMERFIELD, J.F. TRAPP (2002): Inter-annual changes in the biodiversity and community structure of macrobenthos in Tees Bay and the Tees estuary, UK, associated with local and regional environmental events. Mar. Ecol. Prog. Ser. 234: 1-13.

WBNL (Wissenschaftliche Beratung Naturschutz und Landschaftsplanung) (1998): s. TESCH & WITT (1998)

WELLERSHAUS, S. (1981): Turbidity maximum and mud shoaling in the Weser Estuary. Arch. Hydrobiol. Bd.92 (2): 161-198.

WETZEL, V. (1987): Der Ausbau des Weserfahrwassers von 1921 bis heute. Jahrb. Hafenbautech. Ges. 42: 83-105.

WHITTAKER, R.H. (1972): Evolution and measurement of species diversity. Taxon 21: 213-251.

WIDDOWS, J., P. FIETH & C.M. WORALL (1979): Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. Marine Biology 50: 195-207.

WILDISH, D. J. & M. L. H. THOMAS (1985): Effects of dredging and dumping on benthos of Saint John Harbour, Canada. Mar. Environ. Res. 15: 45-57.

WILSON, J.G. (1994): The role of bioindicators in estuarine management. Estuaries, Vol. 17: 94-101.

WOLFF, W.J. (1973): The estuary as a habitat. An analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. Zool. Verh. Leiden, 126: 1-242.

WOLFF, W.J. (1999): Exotic invaders of the meso-oligohaline zone of estuaries in the Netherlands: why are there so many? Helgoländer Meeresunters. 52: 393-400.

WOLTERING, K. (1997): Grundlagen für ein Baggergutkonzept für Bremerhaven. Vorstudie, HBH, 34 pp., unpubl.

ZAJAC, R.N. & R.B. WHITLACH (1982): Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonization. Marine Ecology Progress Series 14: 15-27.

ZANKE, C. E. (1998): Modelluntersuchungen Baggergutverbringung Wurster Arm. Institut für Wasserbau TU Darmstadt. Gutachten im Auftrag des HBH Bremerhaven, unpubl.

7 APPENDICES

Table A-1 Benthic invertebrates of the brackish-water zone of the Weser estuary.

Compiled data since 1980, for data origin see Tab A-2, all data from quantitative sampling (grab, corer) in abundance classes as maximum individuals per m², additional dredge data, net sampling and hand collection data as maximum individuals per site, Red List status from RACHOR (1998), PETERSEN et al. (1996).

B - Brackish-water species
N - Neozoa
RL - Red List status
Cr - critical (1)
En - endangered (2)
Vu - vulnerable (3)
Su - susceptible (G, R)

Habitats:
1 subtidal
2 intertidal
3 supratidal
4 groynes
5 ditches, lagoons

Abundance classes:
1 single finding
x 2-10 ind./m² or site
xx 11-100
xxx 101-1000
xxxx > 1000

				Oligohaline zone (km 45-64,9)					**Mesohaline zone (km 65-80,9)**					**Polyhaline zone (km 81-112)**				
Taxa	**RL**	**N**	**B**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Plathyhelminthes																		
Dugesia tigrina												1						
Planaria sp.														x				
Hydrozoa													x					
Bougainvillia ramosa														x				
Clava multicornis									x									
Clytia hemisphaerica														1				
Cordylophora caspia	Su	N	B	xx					1					x				
Coryne tubulosa									x									
Dynamena pumila									x					1				
Eudendrium ramosum									1					1				
Gonothyraea loveni									x					1				
Hartlaubella gelatinosa									xxx			xx		x				
Laomedea flexuosa									x					x				
Obelia bidentata														x				
Obelia dichotoma									xxx			xx		xx				
Obelia geniculata									x									
Podocoryne borealis									x									
Sertularia cupressina	Vu								x			1		x				
Tubularia bellis/ indivisa														x				
Anthozoa																		
Actiniaria sp.																	xxx	
Diadumene cincta														1				
Metridium senile	Vu													xx				
Sagartia troglodytes														x				
Urticina eques	Vu													x				
Urticina felina	Cr													x				
Mollusca																		
Aeolidia papillosa	Su													x				
Alderia modesta	Su		B							x	x							1
Assiminea grayana	Vu		B		x	xx		x		x	xx	x				x		
Barnea candida									x									
Cerastoderma edule									x					x	xx			1
Corbicula fluminea		N		x														
Crepidula fornicata	Su	N												x				
Donax vittatus														xx				
Ensis directus		N							x					xx	x			

Table A-1 (continued)

				Oligohaline zone (km 45-64,9)					**Mesohaline zone (km 65-80,9)**					**Polyhaline zone (km 81-112)**				
Taxa	**RL**	**N**	**B**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Galba truncatula						x		x										
Hydrobia ulvae									x	xxx	x	xx	x	xxx	xxx	x		xxx
Hydrobia ventrosa	Vu		B							x	1	xx	x	1				
Limapontia depressa	En		B							x	xx							x
Littorina c.f. *saxatilis*	Su								x		x	xx						
Littorina littorea																x	x	
Macoma baltica					x				x	xxxx	x	x		xxx	xxx			xxx
Mya arenaria		N							x	x				x	xx			xx
Mytilus edulis									xx	xxxx		xxx		xx	x		xxx	x
Nucula sp.										x								
Petricolaria pholadiformis	Su	N							x					x				1
Pholas dactylus														1				
Potamopyrgus antipodarum		N	B						x	x								x
Pupilla muscorum																		1
Radix ovata						x		x										
Scrobicularia plana	Vu								x	x			x					x
Stagnicola palustris								x										
Succinea putris					x	xx		x										
Tellina tenuis	Vu													x				
Teredo navalis									x									
Tergipes c.f. *tergipes*									x									
Polychaeta																		
Alkmaria romijni			B											x				
Aphelochaeta marioni									x					x				
Arenicola marina									x	xx				x	x			x
Autolytus prolifer														xxx			x	
Boccardiella ligerica	Su		B	xx			xx		x									
Capitella capitata					x									xx	xxx		xx	
Eteone longa					x				x	x				xx	xx		x	xx
Eulalia viridis														xx			x	
Eumida sanguinea														xxx				
Goniadella bobretskii									x					xxx				
Harmothoe imbricata														x				
Harmothoe impar	Su													x				
Harmothoe nodosa														x				
Harmothoe sarsi														x	x			
Hediste diversicolor				xx	x				xxx	xxx	x	x		x	xxx			xxx
Heteromastus filiformis					xx				xxx	xxx	xx	x		xxx	xxx		x	xxx
Lanice conchilega									x					xxx			x	
Lepidonotus squamatus							1					x		xx			xx	
Magelona johnstoni														x				
Magelona mirabilis														xxxx				
Malacoceros tetracerus														x				
Malmgrenia lunulata														1				
Manayunkia aestuarina			B							x								xx
Marenzelleria c.f. *viridis*		N	B	xxx	xxx	x	x	x	xxxx	xxx	x	x		xxx		x		xxx
Marenzelleria c.f. *wireni*		N	B						xx									

Table A-1 (continued)

				Oligohaline zone (km 45-64,9)					Mesohaline zone (km 65-80,9)					Polyhaline zone (km 81-112)				
Taxa	**RL**	**N**	**B**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Microphthalmus aberrans														x				
Microphthalmus listensis														x				
Microphthalmus similis														xxx				
Neanthes succinea							x		xxx	x		xx		x				xx
Nephtys caeca									x					xx				
Nephtys cirrosa														xxx				
Nephtys hombergii									x	x			x	xx	xx			
Nephtys kersivalensis														x				
Nephtys longosetosa									x					xx				
Nereis pelagica	Su													xx			x	
Neanthes virens									x	1			x	xx				xx
Ophelia limacina									x					x				
Ophelia rathkei	Su								x					x				
Ophryotrocha gracilis														1				
Paraonis fulgens														x				
Pectinaria koreni	Su													x				
Pholoe minuta														x				
Phyllodoce maculata														1			x	
Phyllodoce mucosa									x					xxx	x			
Pisione remota														x				
Polydora ciliata									x					x				
Polydora cornuta									xx	xxx		x		x	xx		x	xx
Polydora pulchra										x								
Pygospio elegans									xx	x				x	xxx			xx
Sabellaria spinulosa	Su													1				
Scalibregma inflatum	Su									x								
Scolelepis foliosa														1				
Scolelepis squamata														xx				
Scoloplos armiger										x				xx	x			
Spio filicornis									x					x	xx			
Spio goniocephala														xx				
Spio martinensis														xx				
Spiophanes bombyx														xxx				
Streblospio benedicti	Su		B							x				x				xxx
Tharyx killariensis									x					x				
Aphaelochaeta marioni														x	xxx			
Oligochaeta																		
Enchytraeidae spp.				xx	x	x			x	x	xx	x						xxx
Limnodrilus claparedeanus					x													
Limnodrilus hoffmeisteri				xx	xxx													
Limnodrilus udekemianus					x													
Lumbricillus lineatus					x					x								
Monopylephorus irroratus	Su		B															
Nais elinguis			B	x														xx
Oligochaeta spp.					xxx	x	xx	x		xxx	x	x	x		xxx	x	xx	
Paranais litoralis			B		xxx				x	x								xx
Tubificoides heterochaetus	Su		B	xx	xxx				x	x				1				

Table A-1 (continued)

				Oligohaline zone (km 45-64,9)					Mesohaline zone (km 65-80,9)					Polyhaline zone (km 81-112)				
Taxa	**RL**	**N**	**B**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Psammoryctides barbatus				x														
Tubifex costatus			B	x	xxx				x	xxx				1				1
Tubifex tubifex					x													
Tubificoides benedeni					x				xx	x	x	x		xx			x	1
Nemertini																		
Cephalothrix linearis														x				
Nemertini sp.									x	x				x			x	
Tetrastemma melanocephalum										x								
Crustacea																		
Amphilochoides sp.														xx				
Atylus swammerdami														x				
Balanus crenatus									x			xx		xx			xxx	
Balanus improvisus		N	B	xx	x	x	xxx		xxxx	xxxx	xx	xxxx	x	xx		x	xxx	
Bathyporeia elegans				x					x					xxx				
Bathyporeia guilliamsoniana														xxx				
Bathyporeia pelagica				x					x		x			xxx				
Bathyporeia pilosa			B	x					x	x			x	xx				
Bathyporeia sarsi										x			x	x				
Cancer pagurus	Su																x	
Caprella linearis	Su													x				
Carcinus maenas									xx	xx		xx		x	x		xx	xxx
Corophium arenarium									x									
Corophium lacustre	Vu		B	xx			xx	x	x	xx			x	1		x		
Corophium multisetosum			B	xx	xx	x		x	x									
Corophium volutator				xx	xxx	x	x	x	xxx	xxxx		x	x	x	xxx			xxx
Crangon allmani														x				
Crangon crangon				x	xx			x	x	xx		xx		xxx	xx			xxx
Cumopsis goodsiri														xx				
Diastylis bradyi														x				
Dulichia falcata														1				
Elminius modestus		N									x	x						
Eriocheir sinensis		N	B	x	x	x	x	x	xx	xx	xx	x		x		x		x
Gammarus c.f. *crinicornis*														x				
Gammarus duebeni	Vu		B	xx				x										1
Gammarus locusta											x	x		x				
Gammarus marinus										x	xx	xx						
Gammarus oceanicus														x				
Gammarus salinus			B	xxx				x	xx	xx	x	xx		x		x	x	x
Gammarus tigrinus		N	B		xx	x		x										x
Gammarus zaddachi			B	x	xx	x		x	x			xx	x	x				x
Gastrosaccus spinifer									x					xxx				
Haustorius arenarius														x				
Heterotanais oerstedi	Su		B											1				
Idotea chelipes	Su		B											1				
Idotea linearis	Su			x														
Jaera albifrons				xx					x	x	x	xx		x		x	x	x
Jassa marmorata																		

Table A-1 (continued)

				Oligohaline zone (km 45-64,9)					**Mesohaline zone (km 65-80,9)**					**Polyhaline zone (km 81-112)**				
Taxa	**RL**	**N**	**B**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Lekanesphaera rugicauda			B			x		x			x	x				x		x
Leptocheirus pilosus			B	x					1	x								
Ligia oceanica	Su		B								x	xx	xx					
Liocarcinus holsatus									xx					x				
Melita palmata			B									xx	x					
Mesopodopsis slabberi				xxx					x					xx				x
Microdeutopus gryllotalpa									x									
Microprotopus maculatus														xxx				
Monoculodes carinatus														x				
Neomysis integer			B	xxx	xx			x	xx	x		xx	x	xx				xx
Orchestia cavimana			B			xx					xx	x	x					
Orchestia gammarellus			B								xxx	x	xx					
Ostracoda sp.								x										
Pagurus bernhardus														x				
Palaemon longirostris	Su		B	xxx			1		xx									x
Palaemonetes varians	Su		B					xx				1						xx
Pandalus montagui														x				
Parapleustes sp.																	x	
Pariambus typicus														x				
Perioculodes longimanus														x				
Photis reinhardi														x				
Platorchestia platensis			B			x		x			xx	xx				x		
Pontocrates altamarinus														x				
Praunus flexuosus			B									x		x				x
Praunus inermis									x									
Proasellus coxalis										x			x					
Pseudocuma longicornis														1				
Schistomysis kervillei									x					xx				
Schistomysis ornata									x					x				
Schistomysis spiritus														x				
Semibalanus balanoides											xx	x						
Urothoe poseidonis														x				
Echinodermata																		
Asterias rubens									x					xxx			x	
Marthasterias glacialis														1				
Ophiura albida														x				
Bryozoa																		
Aeta anguina														x				
Conopeum seurati														x				
Electra crustulenta			B	x					xxx			xxx		x				
Electra monostachys				x										1				
Electra pilosa									x					x				
Farella repens									x					x				
Opercularella pumila														1				
Walkeria sp.									xx			xx						

Table A-1 (continued)

				Oligohaline zone (km 45-64,9)					**Mesohaline zone (km 65-80,9)**					**Polyhaline zone (km 81-112)**				
Taxa	**RL**	**N**	**B**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Pantopoda																		
Nymphon brevirostre														1				
Nymphon grossipes														x				
Pycnogonum littorale	Su													x				
Chaetognatha																		
Sagitta sp.																		1
Insecta																		
Ceratopogonidae spp.					xxx	x		x					xx					x
Chironomidae spp.				xx	xx	x		x					xx			x		xxx
Coleoptera spp.						x		x			xx	1	x			x		x
Collembola spp.											xx	xx	xx			x		xx
Diptera spp.L.					xxx	x		x	x		x	1	xx			x		xx
Ephemeroptera spp.L.								x					x					
Heteroptera spp.								x					xx					
Petrobius brevistylus			B								xx							
Trichoptera spp.								x										

Table A-2 Sources of compiled benthic data of Table A-1 (publications are cited in the reference chapter, unpublished studies are listed in Table A-4). Number of data sets represent the intensity of investigation (total number of samples) - reconstructed from number of sites and surveys, as given in the analysed study, number of unpublished study in Table A-4.

Salinity zone	Habitat	Cited studies	No. of unpubl. as listed in Table A-4	Collection	Sampling method	Sites	Surveys	Data sets
Oligohaline (km 45-65)	Subtidal	HAESLOOP 1990		1986, 1987	0.1 m² Van Veen, 1 m frame dredge	4	22	88
		DB Weser (unpubl.)	1	1991-2002	0.1 m² Van Veen, 1 m frame dredge	33	1 to 6	52
	Intertidal	SÖFFKER 1982		1980	Corer, hand collection	45	1	45
		MEYERDIERCKS 2003		1998	Corer (86 cm²)	2	7	14
		NLÖ 2001		1982-1999	Corer (78.5 cm²), hand collection	3	~35	105
	Supratidal	SÖFFKER 1982		1980	Corer, hand collection	45	1	45
		KÜFOG (unpubl.)	2	2000, 2002	Corer (178 cm²), hand collection, net	5	8	40
	Groynes	BFG (1997) (unpubl.)	3	1998	Hand collection	5	1	5
	Ditches, Lagoons	KÜFOG (unpubl.)	4	2000, 2002	Net (20x20 cm, 0.5 mm)	10	8	80
Mesohaline (km 65,1-79,9)	Subtidal	DB Weser (unpubl.)	1	1991-2002	0.1 m² Van Veen, 1 m frame dredge	172	1 to 10	301
		KÜFOG (unpubl.)	5	2001, 2002	0.1 m² Van Veen, 1 m frame dredge	10	2 to 4	32
	Intertidal	NLÖ 2001		1982-1999	Corer, hand collection	4	~35	140
		KÜFOG (unpubl.)	6	1996-1998	Corer, hand collection	9	16	144
	Supratidal	KÜFOG (unpubl.)	5	2000, 2002	Hand collection	4	4	16
	Groynes	KÜFOG (unpubl.)	5	2001, 2002	Hand collection	5	1 to 4	14
		BFG (1997) (unpubl.)	3	1997	Hand collection	5	1	5
	Ditches, Lagoons	KÜFOG (unpubl.)	5	1994, 1996	Net (20x20 cm, 0.5 mm)	2	8	16
Polyhaline (km 80-112)	Subtidal	KÜFOG (unpubl.)	7	1996-1999	0.1 m² Van Veen, 1 m frame dredge	169	1 to 4	299
		DB Weser (unpubl.)	1	1991-2002	0.1 m² Van Veen, 1 m frame dredge	230	1 to10	448
	Intertidal	HEIBER 1988		1983	Corer	8	4	32
	Supratidal	KÜFOG (unpubl.)	8	2000	Hand collection	4	1	4
	Groynes	BFG (1997) (unpubl.)	3	1998	Hand collection	7	1	7
	Ditches, Lagoons	FRÄMBS et al. (2002)		1992-1998	Corer, hand collection, net	14	2 to 4	119

* DB Weser is a data collection of several projects concerning dredging and disposal activities in the Weser estuary since 1991 in behalf of the Harbour Authority of Bremen (bremenports GmbH), the Federal Agency of Water Shipping Administration (WSA Bremerhaven) and the Federal Institute of Hydrology (BFG, Koblenz) since 1995 (estuary monitoring, HABAK). Most of the data collection and further processing was done by IFAÖ, Brodersdorf; Bioconsult, Bremen; WBNL, Bremen; IFAB, Freiburg, Aqua-Marin, Norden and KÜFOG GmbH, Loxstedt (full titles of studies are given in Table A-4).

Table A-3 Compiled benthic data from earlier intertidal surveys in the Weser estuary.
Data from SÖFFKER (1982) were used within the analysis (Table A-1) from brackish habitats only (km 45-65). Data from KOLBE (1995) later than 1980 are similar provided by NLÖ (2001) and added to Table A-1.

Survey	**SÖFFKER 1982**	**KOLBE 1995**	**MICHAELIS & GROTJAHN 1985**		**MICHAELIS 1973**	**MÜLLER 1956**	**MÜLLER 1963**	**MÜLLER 1963**
Section along the estuary (Weser km)	0-70	60-70	60-70		60-80	73-83	73-83	80-90
Time of data collection	1980	1975-1980	1968	1980	1973	1955/56	1961	1962
Taxa								
Cnidaria								
Cordylophora caspia	x		x					
Phaenocora unipuncata	x							
Polychaeta								
Arenicola marina		x	x	x		x	x	x
Capitella capitata		x			x			
Eteone longa		x		x	x	x		x
Hediste diversicolor	x	x	x	x		x	x	x
Heteromastus filiformis		x	x	x		x	x	x
Lanice conchilega							x	x
Marenzelleria c.f. *viridis*		x						
Nephtys hombergii		x			x	x		x
Nereis succinta		x						
Polydora ciliata		x						
Pygospio elegans		x	x	x		x	x	x
Scalibregma inflatum								
Scoloplos armiger		x			x		x	x
Streblospio benedicti	x	x	x	x				
Oligochaeta								
Amphichaeta leydigii	x							
Limnodrilus claparedeanus	x							
Limnodrilus hoffmeisteri	x	x	x	x	x			
Limnodrilus udekemianus	x							

Table A-3 (continued)

Survey	SÖFFKER 1982	KOLBE 1995	MICHAELIS & GROTHJAHN 1985		MICHAELIS 1973	MÜLLER 1956	MÜLLER 1963	MÜLLER 1963
Section along the estuary (km)	0-70	60-70	60-70		60-80	73-83	73-83	80-90
Time of data collection	1980	1975-1980	1968	1980	1973	1955/56	1961	1962
Taxa								
Lumbricillus sp.		x						
Monophylephorus irroratus		x						
Nais elinguis	x	x	x	x				
Paranais litoralis	x	x	x	x				
Potamothrix hammoniensis	x							
Pristina foreli				x				
Pristina sp.	x							
Tubifex costatus	x	x	x	x				
Tubifex tubifex	x							
Tubificoides benedeni		x			x	x		
Tubificoides heterochaetus		x			x			
Mollusco								
Alderia modesta			x	x				
Assiminea grayana	x	x		x				
Cerastoderma edule						x	x	x
Dreissena polymorpha	x							
Hydrobia sp.		x		x				
Hydrobia ulvae								x
Littorina littorea		x						
Macoma baltica	x	x	x	x	x	x		x
Mya arenaria		x		x	x	x	x	x
Mytilus edulis		x			x		x	
Scrobicularia plana						x	x	x
Stagnicola palustris	x			x				
Succinea putris	x			x				

Table A-3 (continued)

Survey	SÖFFKER 1982	KOLBE 1995	MICHAELIS & Grothjahn 1985		MICHAELIS 1973	MÜLLER 1956	MÜLLER 1963	MÜLLER 1963
Section along the estuary (km)	0-70	60-70	60-70		60-80	73-83	73-83	80-90
Time of data collection	1980	1975-1980	1968	1980	1973	1955/56	1961	1962
Taxa								
Crustacea								
Atylus swammerdami				x				
Bathyporeia pilosa		x		x	x			
Bathyporeia sarsi								X
Corophium lacustre	x			x	x			
Corophium sp.							x	
Corophium volutator	x	x	x	x	x	x		x
Crangon crangon	x	x	x	x	x			
Eriocheir sinensis	x			x				
Gammarus duebeni	x		x	x				
Gammarus juv.					x			
Gammarus salinus			x					
Gammarus zaddachi	x	x	x	x	x			
Haustorius arenarius								x
Jaera marina (albifrons)		x						
Lekanesphaera rugicauda	x	x		x				
Ligia oceanica	x			x				
Mysis sp.		x						
Neomysis integer			x					
Diptera								
Diptera L.	x	x	x	x	x			

Table A-4 Unpublished data sources (listed in Table A-2 / Table A-3).

No. in Table A-2	Name in Table A-2	Institution	Year	Title of study	In account of (Agency, Department)
Origin of unpublished data in Table A-1 (data sources listed in Table A-2)					
1	DB Weser	IFAÖ	1991	Faunistische Erhebung des Makrozoobenthos im Weserästuar.	WSA Bremerhaven
		IFAÖ	1992	Erhebung der Makrozoenbestände im Bereich der ehemaligen Verklappstellen. Nachuntersuchung zur „Faunistischen Erhebung des Makrozoobenthos im Weserästuar“.	WSA Bremerhaven
		IFAÖ	1993	Auswertung von drei Untersuchungen zur Entwicklung der benthischen Evertebraten im Sandentnahmebereich zwischen Weser km 68 und 69. Nördliche Erweiterung des Containerterminals Wilhelm Kaisen Bremerhaven (CT III).	bremenports
		IFAÖ	1993	Beweissicherungsuntersuchungen zur Beurteilung der Entwicklung des Sandentnahmebereichs in der Fahrrinne zwischen Weser-km 68 und 69.	bremenports
		IFAÖ	1993	Untersuchungen des Sublitorals im Bereich des geplanten CT III.	bremenports
		IFAÖ	1994	Beweissicherungsuntersuchung am Makrozoobenthos 1994 (Teil I bis III).	bremenports
		IFAÖ	1996	Ökologische Begleituntersuchungen im Bereich der Außenweser - Untersuchungen zum Makrozoobenthos, Beprobung 1995 (Wiederholungserfassung). Teil I-IV	bremenports
		IFAÖ	1997	Ökologische Begleituntersuchungen im Bereich der Außenweser – Untersuchungen zum Makrozoobenthos in den Sandentnahmebereichen und im Verklappgebiet an der Robbenplate. Beprobung 1996 (Wiederholungserfassung).	bremenports
		IFAÖ	1997	Ökologische Begleituntersuchungen im Bereich der Außenweser – Untersuchungen zum Makrozoobenthos in den Sandentnahmebereichen und im Verklappgebiet an der Robbenplate. Beprobung 1997 (Wiederholungserfassung)	bremenports
		BioConsult	1998	Faunistische Erhebungen an WSV Klappstellen im Bereich der Außenweser	BFG
		IFAÖ	1998	Der SKN –14 m Ausbau der Außenweser- Wirkungskontrolle Makrozoobenthos- Bericht zur Beprobung 1998.	WSA Bremerhaven
		IFAÖ	1999	Der SKN –14 m Ausbau der Außenweser- Wirkungskontrolle Makrozoobenthos- Bericht zur Beprobung 1999.	WSA Bremerhaven
		IFAÖ	2000	Der SKN –14 m Ausbau der Außenweser- Wirkungskontrolle Makrozoobenthos- Bericht zur Beprobung 2000.	WSA Bremerhaven
		IFAÖ	2001	Der SKN –14 m Ausbau der Außenweser- Wirkungskontrolle Makrozoobenthos- Bericht zur Beprobung 2001.	WSA Bremerhaven
		BioConsult	2002	Untersuchungen zum Makrozoobenthos im Bereich der WSV-Klappstellen in der Außenweser.	BFG
		BFG	2002	BFG- Ästuarmonitoring 1997-2002.	BFG
2	KÜFOG, unpubl.	KÜFOG	2001	Ökologische Begleituntersuchungen zur Erfolgskontrolle zum Projekt CT III (Erweiterung des Containerterminals Wilhelm Kaisen, Bremerhaven) – 2000. Datenband.	bremenports
		KÜFOG	2003	Ökologische Begleituntersuchungen zur Erfolgskontrolle zum Projekt CT III (Erweiterung des Containerterminals Wilhelm Kaisen, Bremerhaven) – 2002. Datenband.	bremenports
3	BFG, unpubl.	BFG	1997	Buhnenuntersuchung im Weserästuar.	BFG
4	KÜFOG, unpubl.	KÜFOG	2001	Ökologische Begleituntersuchungen zur Erfolgskontrolle zum Projekt CT III (Erweiterung des Containerterminals Wilhelm Kaisen, Bremerhaven) – 2000. Datenband.	bremenports
		KÜFOG	2003	Ökologische Begleituntersuchungen zur Erfolgskontrolle zum Projekt CT III (Erweiterung des Containerterminals Wilhelm Kaisen, Bremerhaven) – 2002. Datenband.	bremenports
5	KÜFOG, unpubl.	KÜFOG	1999	Biologische Bestandsaufnahmen im Wirkungsraum des Baufeldes von CT III nach weitgehendem Abschluss der Infrastrukturmaßnahmen. Datenband.	bremenports
		KÜFOG	2000	Nördliche Ergänzung des Containerterminals in Bremerhaven um einen weiteren Großschiffsliegeplatz. Untersuchungen zur faunistischen Besiedlung von Brackwassertümpeln im Weserästuar.	bremenports
		KÜFOG	2002	Biologische Untersuchungen im Bereich des Plangebietes- Planung CT IV.	bremenports

Table 4 (continued)

No. in Table A-2	Name in Table A-2	Institution	Year	Title of study	In account of (Agency, Department)
6	KÜFOG, unpubl.	KÜFOG	1996	Ökologische Begleituntersuchungen zur Beweissicherung und Erfolgskontrolle zum Projekt CT III (Erweiterung des Containerterminals Wilhelm Kaisen, Bremerhaven) - 1994. Datenband	bremenports
		KÜFOG	1996	Ökologische Begleituntersuchungen zum Projekt CT III - Erfolgskontrolle der Kompensationsmaßnahmen (Erweiterung des Containerterminals Wilhelm Kaisen, Bremerhaven) - 1995. Datenband	bremenports
		KÜFOG	2000	Ökologische Begleituntersuchungen zur Erfolgskontrolle zum Projekt CT III (Erweiterung des Containerterminals Wilhelm Kaisen, Bremerhaven) - 1997. Datenband	bremenports
		KÜFOG	1999	Ökologische Begleituntersuchungen zur Erfolgskontrolle zum Projekt CT III (Erweiterung des Containerterminals Wilhelm Kaisen, Bremerhaven) – 1998. Datenband.	bremenports
7	KÜFOG, unpubl.	KÜFOG	1998	Benthoskundliche Untersuchungen zur Einbringung von Baggergut in den Wurster Arm. Zusammenfassende Darstellung der 1.-3. faunistischen Erhebung.	bremenports
		KÜFOG	1998	Benthoskundliche Unterschungen zur Einbringung von Baggergut in den Wurster Arm - Rasterkartierung und Sonderstationen. Faunistische Erhebungen.	bremenports
		KÜFOG	2000	Benthoskundliche Unterschungen zur Einbringung von Baggergut in den Wurster Arm - Nachuntersuchung	bremenports
8	KÜFOG, unpubl.	KÜFOG	2002	Landespflegerischer Begleitplan zum tidegeregelten Badepolder Burhave- Faunistische Erhebungen	IMP
earlier surveys intertidal (Table A-3)					
		SÖFFKER	1982	Die eulitorale Bodenfauna der Unterweser zwischen Bremerhaven und Bremen.	NLÖ
		KOLBE	1995	Sedimente und Makrozoobenthos der Wesermündung. - Dienstbericht Forschungsstelle Küste. (here only data before 1980)	NLÖ
		GROTJAHN & MICHAELIS	1984	Das Benthos im Einleitungsbereich säure- und eisenhaltiger Abwässer. Vergleich 1968- 1980.	NLÖ
		MICHAELIS	1973	Untersuchungen über das Makrobenthos der Wesermündung.	NLÖ
		MÜLLER	1956	Biologische Untersuchung des Wurster Watts zwischen Weddewarden und Solthörner Buhne.	NLÖ
		MÜLLER	1963	Wattuntersuchungen an der Butjadinger Küste von Langwarden bis Tossens.	NLÖ
		MÜLLER	1963	Fauna im Wurster Watt von Solthörn bis Dorumer Tief und Beeinflussung durch die Februarsturmflut 1962.	NLÖ

7 ACKNOWLEDGEMENTS

I would like to thank all those who supported me during this work in a friendly official or very personal way:

Prof. Dr. Wolf Arntz (AWI) for supervising this work, constructive comments and always fruitful and pragmatic discussions;

Dr. Rainer Knust (AWI) for his support, his friendly welcome as an „external freelancer" to his working group within the section of „Benthic Ecosystems" at the AWI, his increasing interest in estuarine ecology and his short but always honest comments;

Dr. Alexander Schroeder (AWI) for his enduring help, statistical insights, many constructive comments, motivation and good times off the scientific track;

Ina Backhausen (BfN) for careful editing, early comments and patient support;

Dr. Martine Marchand (KÜFOG) for her great support, careful editing and valuable comments;

Dr. Andreas Tesch (WBNL) for early discussions on benthos within spatial planning;

Kerstin Baake and Jutta Kotte (both KÜFOG) for advice and help with always surprising GIS features and sophisticated digital cartography; Pitty, Alex, Inken and Kristina for last minute and late night editing and mental support;

Tony Brunt (Cristchurch, Newzealand) and Peter Brown (Swansea, Wales, UK) for new insights in English grammar and many valuable comments and editing;

bremenports GmbH, namely Uwe von Bargen for the support of this work, the permission to use most of the data and comments on an earlier version of the manuscript,

the crew of the vessel „Hol Deep" for careful navigation and helpful hands during all expeditions into the estuary;

WSA Bremerhaven, namely Volker Steege for the data release, his friendly support and some valuable comments and discussions, Helmut Müller for abiotic data, historical maps and literature of the Weser estuary, Dr. Lange for long-term data of the salinity and Mr. Woldenga (WSD, Aurich) for digital data on the morphology;

BFG Koblenz, namely Dr. Heiko Leuchs for his support and additional benthic data, Dr. Heike Büttner for comments on an earlier draft of the manuscript;

NLÖ Forschungstelle Küste (Wilhelmshaven, Norderney) namely Uda Tuente for information and remarks on the European directives subject, Dr. Meyer for digital sediment data;

Institutes and biologists for data collection and results that were used for interpretation and comparisons which should be represented by the following: Dr. Fritz Gosselck, IFAÖ (Neu Brodersdorf) and Dr. Bastian Schuchardt; BioConsult (Bremen);

KÜFOG GmbH all colleagues for general support, much help during all field works, laboratory and office work, representative to all colleagues and many students I would like to mention Dr. Martine Marchand (head, see above), Arnd Krumwiede, who was with me on the benthic expeditions since my first step into the soft mud of the Weser estuary in 1993 and Silke Allers, who accompanied me during all samplings and benthos related works since then and additionally improved the lay out of this work; Ursula Köhler-Loum replied excellent information on brackish reed beds and Lutz Achilles who was always tolerant on my deficits in house-keeping within our "Hirtenhaus community" during some extreme periods of this work.

I want to thank my parents for their support and patience during the last years and last but by no means least I would like to thank Ina who believed in me and supported me through all ups and downs, travelled hundreds of miles for short weekend visits and who always encouraged me with new spiritual energy…