

Habitat dynamics in response to constructional impacts (JadeWeserPort): a biological approach

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1 General introduction and outline

The North Sea is a semi-enclosed shelf sea in north-west Europe with a surface area of 575,300 km², a volume of 42,294 km³ and a mean depth of 74 m (Otto et al. 1990). This ecosystem is strongly influenced by various human impacts. These include chemical disturbance, such as pollution and eutrophication (e.g. Kröncke and Bergfeld 2001) and physical disturbance due to fisheries, exploitation of energy resources, land reclamation, and extraction of sand and gravel (OSPAR 2000). In addition, the North Sea is highly frequented as a transport route with continuously increasing ship traffic and growing vessel size. As a consequence, an increase in dredging and dumping activities in shipping channels is expected (OSPAR 2009). Furthermore, the demand for marine sand and gravel in coastal protection constructions will also increase as sea level will rise due to human-induced global climate change (OSPAR 2009). Therefore a comprehensive knowledge about the direct and indirect impacts of the extraction of mineral deposits is crucial to conservation management.

1.1 Physical variables structuring spatial macrofauna patterns in the North Sea

Zoobenthos comprise animals, which live *on* (epifauna) and *in* (infauna) the sediments of the seafloor. Animals that also migrate from the sediments into the water column are called hyperbenthos. According to size the zoobenthos is commonly divided into i) meiofauna (>0.063 <0.5 mm), ii) macrofauna (retained in a sieve of 0.5 or 1.0 mm mesh size) and iii) megafauna (> 1cm; Kröncke and Bergfeld 2001). Macrofauna play an important role in nutrient cycling and serve as a food source for higher trophic levels, such as birds or fishes.

One important aim in ecology is identifying patterns of species distributions and their explaining variables (Sokal and Wartenberg 1981). Glémarec (1973) described three different “étages” (open, coastal and littoral) in the North Sea in relation to variations of depth and temperature between bottom and surface. The assemblages of these zones are further structured by sediment composition. According to Künitzer et al. (1992), three main communities are prevalent in the North Sea: a northern community (> 100m) characterised by cold water species; a southern community (< 50m) dominated by warm water species and a transition community in which cold and warm water species overlap along the 70m depth contour in the central North Sea. Beside depth, water temperature and different water masses,

food availability and sediment characteristics belong to the most important structuring variables in the North Sea (Künitzer et al. 1992).

These often reported animal sediment relationships are mediated by hydrodynamic forces which influence the sedimentation and re-suspension of particles (Rhoads 1974; Rhoads and Boyer 1982; Snelgrove and Butman 1994), and thereby also trigger the food availability (Rosenberg 1995; Pearson 2001; Wieking and Kröncke 2005; Kröncke 2006). Areas with strong currents and turbulences are dominated by coarse sediments with low organic content, because the deposition of fine material is inhibited (Pearson and Rosenberg 1978; Rhoads and Boyer 1982). Typical psammophilous species survive tidal scouring events and are adapted to low food concentrations in the sand. They obtain their food mainly from the water column (suspension feeders, filter feeders) or are sand lickers or predators. Under low energetic hydrodynamic conditions fine particles of the water column can settle on the seafloor what leads to an organic enrichment of the sediment. Typical pelophilous species use the settled organic material as food source (deposit feeders). They are usually adapted to oxygen depletion and high hydrogen sulphide concentrations (Forbes et al. 1994; Reiss and Kröncke 2001; Kröncke et al. 2004). However, suspension feeder and deposit feeder do often co-occur in the same sediment type (Snelgrove and Butman 1994) and this strict differentiation between psammophilous and pelophilous species relates only to some taxa.

Kröncke et al. (2011) emphasised the importance of hydrographic variables such as bottom water temperature, bottom water salinity, tidal stress, stratification and food supply (primary production) as the main influential environmental factors for the macrofauna community structure in the North Sea. Epifauna communities and demersal fish showed similar large-scale distribution patterns as the macrofauna in the North Sea (southern, central and northern community) and were attributed to similar structuring factors (Reiss et al. 2009).

1.2 Benthic habitat mapping with hydroacoustic tools

Strong links exist between hydroacoustic signals and sediment composition (Collier and Brown 2005). As described in chapter 1.1 the composition of macrofauna communities is related to sediment distribution patterns. These interrelationships are used by interdisciplinary working groups when mapping benthic habitats with hydroacoustic tools.

The most commonly used hydroacoustic tools are single beam echosounder, multi beam echosounder and side scan sonar. While single beam and multi beam echosounder are mounted on the ship, side scan sonar systems are towed behind the ship. Each device has a

transducer unit, which sends an acoustic signal through the water column to the sea bottom. This acoustic signal is reflected by the sea bottom and is sent back to the transducer unit, which also works as a receiver. The time, which the acoustic signal needs from the transducer and back, allows conclusions about the water depths beneath the ship that operates the hydroacoustic tool. The reflected acoustic signal is influenced by geological seafloor properties such as sediment density, surface roughness, sedimentary structures and grain size (Collins and Galloway 1998; Bornhold et al. 1999; Preston et al. 2004; Markert et al. 2013), but also by living or dead epibenthic faunal structures such as blue mussel or oyster beds and shell debris, (Quester Tangent Corporation 2003; Wienberg and Bartholomä 2005; Van Overmeeren et al. 2009), biogenic reefs of the tube building worm *Lanice conchilega* (Degraer et al. 2008), coral reefs (Gleason et al. 2006; Gleason 2009) or seaweed (Preston 2006; Hass and Bartsch 2008). However, despite high resolution, especially benthic biotopes without a prominent superficial structure cannot be directly detected using hydroacoustic tools (Brown et al. 2011). In such cases, benthic habitat mapping is based on the links between the measurable sediment characteristics and the corresponding macrofauna.

Single beam and multibeam echosounder devices differ in the amount of emitted acoustic signals (beams) and in their range of seafloor coverage (Holler 1995). While single beam echosounder deliver only single line profiles, multibeam echosounder continuously cover a larger area. In contrast to traditional point sampling via grabs, cores and dredges, spatially continuous mapping by hydroacoustic mapping is a great advantage. Nevertheless, point sampling is still necessary for the groundtruthing of the hydroacoustic information (Brown et al. 2011; Markert et al. 2013).

In homogeneous habitats with sharp boundaries, hydroacoustic mapping is an efficient, low cost and easily repeatable method for monitoring the seafloor of large areas (Anderson et al. 2008; Van Rein et al. 2011). In contrast, in heterogeneous habitats with gradational boundaries, hydroacoustic mapping is more complicated (Brown et al. 2004a). In heterogeneous habitats problems in the acoustic classification arises, because one has to decide between lumping and splitting of classes (Brown et al. 2004a). Therefore, automated classification approaches fail in such habitats and manual expert classification is needed. Additional complications occur when species without strict sediment preferences dominate in the investigated area. This is often the case in disturbed habitats.

1.3 Study area: The Inner Jade

The Jade is a tidal channel in the German Bight of the southern North Sea, which comprises 554.5 km² (Dörjes 1969). The name “Jade” originates from the 22 km long river Jade, which flows into the Jade Bay eastern of Varel. However, in contrast to estuaries such as Ems, Weser, Elbe or Eider, the Jade has no significant freshwater discharge and the salinity of the Jade varies between 29 and 32 (Götschenberg and Kahlfeld 2008). This is slightly less than the average salinity in the central North Sea (32-35, OSPAR 2000). Semi-diurnal tides range from 2.8 m in the north of the Jade channel to 3.8 m in the south at Jade Bay. Thus, the Jade is classified as upper mesotidal regime (Kubicki and Bartholomä 2011). Thermal stratification is prevented by strong ebb and flood currents (OSPAR 2000), which reach maximum velocities of 2.5 m/sec in the main Jade channel and can lead to considerable sediment reworking (Hertweck 1994).

The Jade consists of three parts: the Jade Bay (162 km²) in the south, the Inner Jade (218.5 km²) in the centre and the Outer Jade (174 km²) in the north (Dörjes 1969) (Fig. 1.1). The southern border of the Inner Jade lies at the bearing line between Wilhelmshaven and Eckwarderhörne at km 2 of the navigation channel. The northern border is situated at the line between Schillig and Mellum at km 25 of the navigation channel. The eastern margin of the Inner Jade consists of the peninsula Butjadingen in the south and the tidal flat area “Der Hohe Weg” in the north. “Der Hohe Weg” comprises 24 700 ha and is subordinated to nature conservation. Both, the eastern and the western margin of the Inner Jade belong to the Lower Saxon Wadden Sea National Park. At the western border lie the nature conservation areas “Voslapper Groden Süd” and “Voslapper Groden Nord”.

The Jade navigation channel runs in the centre of the Inner Jade, which borders on the western mainland at Germany’s only deepwater port, the Jade Weser Port (JWP). 360 ha land was reclaimed to create the JWP container terminal. North and south of the JWP two sand extraction sites exhibit depths of up to 50 m (referred to normal height null (NHN); Gutperlet et al. 2015). The depth of the navigation channel is maintained at 20.1 m (referred to NHN) by regular dredging of the harbour authorities (Wasser- und Schifffahrtsamt Wilhelmshaven (WSA)). This enables access of very large container vessels with draught up to 16.5 m regardless of the tides (Götschenberg and Kahlfeld 2008). The study area of chapters 2 and 3 comprised an approximately 10.2 km² subtidal area in front of the JWP.

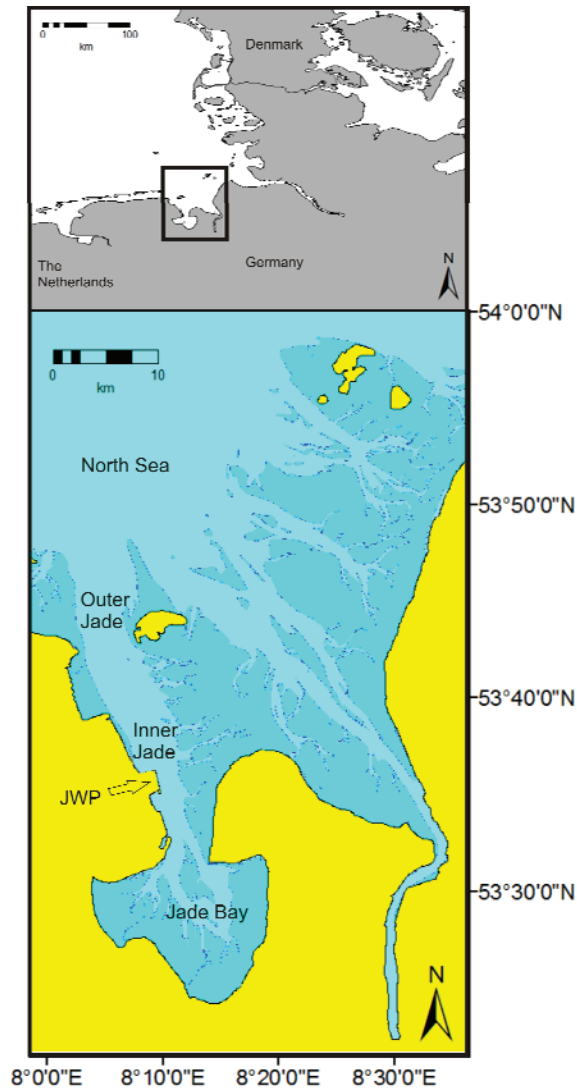


Figure 1.1 Location of the Inner Jade and the Jade Weser Port (JWP) in the German Bight of the southern North Sea

1.4 Human impacts in the Jade

The Jade developed at the Frisian marsh coast in the North Sea between the 11th and 15th century. Over the years, storm tides and several dyking activities gave the Jade its present shape (Götschenberg and Kahlfeld 2008). Since the relocation of the navigation channel near Hooksiel in 1987, no major construction works have been taken place in the Jade, before the construction of the JWP started in 2008 (Götschenberg and Kahlfeld 2008). However, already in 2007 the western Inner Jade was classified as “heavily modified water body” (Schuchardt et al. 2007) due to the hydro-engineering activities completed by then (Table 1.1).

The navigation channel, which was formerly characterised by river bifurcations, was successively deepened until a depth of 20.1 m (referred to NHN) was reached (Kubicki and Bartholomä 2011). Regular dredging is necessary for the maintenance of the navigation channel. In total, about 500 million m³ of sediment were either moved sideways or completely removed from the Jade channel (Kubicki and Bartholomä 2011). To date, several dumping areas are located in the southern Inner Jade and the Outer Jade (BfG and WSA 2003). Moreover, the Jade is affected by several additional human impacts, e.g. fishery, mussel farming and to a certain extent to tourism.

Table 1.1 Hydro engineering in the Jade

date	intervention
1893-1897	construction of the training wall on the "Schweinsrücken" in the Jade Bay
1908-1910	southextension of Wilhelmshaven with 7.4 km ² land reclamation in the Jade Bay
1909-1931	"Jade correction": improvement and deepening of the navigation channel to SKN -10.0 m
1909	implementing of the III. port entrance (detonation in 1949)
1909-1913	completion of the main dam and of the groynes A and C at Minsener Oog
1926-1936	further mountings at Minsener Oog (groyne B)
1940	land reclamation in the western Inner Jade: "Heppenser Groden" (6.0 km ²)
1942	implementing of the IV. port entrance (detonation in 1949)
1942-1956	no maintenance dredging (depths of SKN -12 m were partly measured in 1952)
1945	partly detonation of the protection system at Minsener Oog
1957-1964	reconstruction of the IV. port entrance, implementing in 1964
1958	completion of the transshipment pier of the Northwest-Ölleitung GmbH (site A)
1960	land reclamation in the western Inner Jade: "Rüstersieler Groden" (4.0 km ²)
1953-1963	deepening of the navigation channel to SKN -12.0 m (dredge amount: 21.5 million m ³)
1964-1967	deepening of the navigation channel to SKN -13.0 m (dredge amount: 22.6 million m ³)
1967-1969	deepening of the navigation channel to SKN -15.0 m (dredge amount: 37.7 million m ³)
1970	land reclamation in the western Inner Jade: "Voslapper Groden" (16.7 m ²)
1969-1971	deepening of the navigation channel to SKN -17.0 m (dredge amount: 41.6 million m ³)
1971-1976	deepening of the navigation channel to SKN -18.5 m (dredge amount: 91.0 million m ³)
1972	completion of the transshipment pier "Niedersachsenbrücke" (site B)
1975	completion of the transshipment pier for the refinery (site C)
1975-1979	hydraulic filling at Minsener Oog
1980	completion of the transshipment pier "Voslapper Groden" (site D)
1985-1987	drop of the wreck "Yorck" and following relocation of the navigation channel near Hooksiel
2008-2012	construction works for the Jade Weser Port: land reclamation and relocation of the navigation channel

translated from Schuchardt et al. (2007)

1.5 Macrofauna in the Jade

The macrofauna in the Jade belongs to the *Macoma balthica* community (Dörjes et al. 1969), which occurs also near the coasts of the North Sea (Rachor and Nehmer 2003). In the 1960s, Dörjes et al. (1969) found 8 major subgroups of the *Macoma balthica* community in the Jade of which three occurred in the sublittoral area of the Inner Jade. The *Ophelia limacina*

community prevailed on gravel and coarse sand in the centre of the Jade channel. At the littoral zones, and in the southern centre of the Inner Jade, a *Magelona papillicornis* dominated community was found in fine and medium sized sand. At the clay ridges, and at solid mud and muddy sand, a *Petricola pholadiformis* dominated community appeared in the Inner Jade. Thus, in the 1960s a strong link between the sediment distribution and the community structure was detected (Dörjes et al. 1969).

In comparison to the 1960s, the sediment distribution in the Inner Jade had changed markedly in 2002 and the altered macrofauna community structure was described by Schuchardt et al. (2003). The authors investigated sublittoral sediments of the Inner Jade in spring, summer and autumn 2002, in order to write a report for the Jade Weser Port Realisation Company. Despite strong inter-annual variability, three main communities were found in 2002 (Schuchardt et al. 2003). The western Inner Jade was dominated by pelophilous species, whereas in the navigation channel psammophilous species were prevalent. The eastern tidal creeks were inhabited by species with heterogeneous sediment preferences. Thus, the heterogeneity of sediments and hydrodynamic forces affected the macrofauna composition in 2002 (Schuchardt et al. 2003). The formerly described *Ophelia limacina* community and the *Petricola pholadiformis* community (Dörjes et al. 1969) had changed in their spatial distribution. The *Magelona papillicornis* community was missing in 2002, in particular the formerly dominant species was found in very low numbers (Schuchardt et al. 2003). Due to the high amount of samples, the total taxa number was higher than in the 1960s, but the mean taxa number per station was lower in 2002 (Schuchardt et al. 2003). Schuchardt et al. (2003) stated that the low mean taxa number is typical for muddy habitats and mobile sands.

Alterations of sediment characteristics, e.g. due to dredging and dumping activities, affect the species composition and the community structure of the respective area. These changes may lead to cascading effects on animals of higher trophic levels with serious consequences for the entire ecosystem.

1.6 Macrofauna as an indicator of disturbance

Macrofauna species are sensitive indicators of changes in the marine environment (e.g. Kröncke and Reiss 2010). Therefore, macrofauna community structure is often used as quality indices in environmental impact assessments for the evaluation of the *status quo* of an ecosystem (Warwick 1993; Borja et al. 2013). The macrofauna community structure is a

result of spatial and temporal changes in the marine ecosystem and therefore a mosaic of different succession stages developed (Johnson 1972).

Re-colonisation after disturbance begins with opportunistic species, so called r-selected strategists. Characteristic r-selected species are small polychaete worms such as capitellids and spionids, which have short live cycles and reproduce many times a year. They have high recruitment (r-selected), turnover, and death rates (Gray and Elliott 2009). Over time, these pioneer species are replaced by K-selected strategists, whose populations fluctuate at the carrying capacity (K). These species are larger and long-lived, with few reproductions per year. They are slow developers with low death rate (Gray and Elliott 2009). They are deeper bioturbators and stronger competitors, such as bivalves and echinoderms.

For example, Kröncke and Bergfeld (2001) detected a regime shift from K-selected strategists to r-selected opportunists in the North Sea what the authors also related to the physical disturbance of fishing (Kröncke and Bergfeld 2001). Such regularly disturbed habitats remain in an early succession stage, where r-strategists and stress tolerant species dominate. Recovery after cessation of the disturbance has occurred only when the formerly prevailing *status quo* of the ecosystem has re-established. If dredging activities uncovered a certain substratum type, another community than the original one will develop (Kenny and Rees 1996; Boyd et al. 2005).

1.7 Post-settlement dispersal of macrofauna

The fact that macrofauna species are sensitive indicators for changes in the marine environment, is often explained by their relatively sessile lifestyle with only a small scale mobility and thus their incapability to avoid unfavourable conditions (Clark and Frid 2001; Reiss et al. 2006). However, to a certain extent most macrofauna species have the ability to move over larger distances. Not only do their planktonic larvae drift in the water column, but juveniles and adults migrate by crawling, rolling along the sediment surface as bedload or by drifting in the water column. Post-settlement dispersal describes the spatial redistribution of individuals which have completed their larval metamorphosis and undertaken a benthic existence (Stocks 2002). Many taxa use post-settlement dispersal for their redistribution after their initial settlement, including polychaetes (Tamaki 1987; Shull 1997; Stocks 2002), crustaceans (Grant 1980; Hedvall et al. 1998; Blackmon and Eggleston 2001; Moksnes 2002), gastropods (Levinton 1979; Levinton et al. 1995) and bivalves (Sirgurdsson et al. 1976; Beukema and de Vlas 1989; Armonies 1992, 1996; Commito et al. 1995; Cummings et al.

1995; Hewitt et al. 1997; Turner et al. 1997; Hunt and Scheibling 1998; Hunt et al. 2003). Post-settlement dispersal is not only a passive mechanism, but can also be actively triggered by behaviour (Günther 1992; Lundquist et al. 2004). For example, bivalves burying deeper into the sediment avoid dispersal, whereas emergence increases the likelihood of dispersal (Lundquist et al. 2004). Thus, both juveniles and adults are able to leave unfavourable conditions and contribute to the re-colonization and recovery of disturbed habitats.

1.8 Adult-juvenile interactions

In undisturbed homogenous habitats, intra- and inter-specific interactions will influence macrofauna community structure. The presence of predators or the competition for space and food between adults and juveniles are possible motivations for the post-dispersal of juveniles. Physical disturbance due to bioturbation activities by adult deposit feeders (Woodin 1976) or highly mobile suspension feeders is another reason why juveniles actively leave the habitat of the adults. In contrast, settlement in the vicinity of adult con-specifics promises a suitable habitat.

Field studies of adult-juvenile interactions of the bivalves *Macomona liliana* (mainly deposit feeder) and *Austrovenus stutchburyi* (suspension feeder) led to contrasting interpretations. Legendre et al. (1997) found no support for adult-juvenile interactions for both bivalves *Macomona liliana* and *Austrovenus stutchburyi*. In contrast, Thrush et al. (1992) reported facilitation of the colonisation of juvenile *Macomona liliana* in the vicinity of adult con-specifics. In other studies, high densities of *Macomona liliana* had negative impacts on juvenile con-specifics and also on other taxa (Thrush et al. 1994, 2000; Turner et al. 1997). These outcomes can be easily misinterpreted due to high levels of natural variability, or by failing to take into account the effects of factors that were not investigated (Pillay et al. 2007). Laboratory experiments on the other hand have the advantage of controlled conditions. The difference in the feeding modes of the two study species made it possible to compare the effects on juvenile settlement of a deposit feeder, *Macomona liliana* with a suspension feeder, *Austrovenus stutchburyi*.

1.9 Objectives of the present study

While benthic habitat mapping with hydroacoustic tools was often successfully applied in homogenous areas with sharp boundaries (Brown et al. 2002, Brown et al. 2004b, Freitas et al. 2003; Freitas et al. 2005; Markert et al. 2013), the application of this method has been a challenge in heterogeneous study areas, such as the Inner Jade. Various anthropogenic impacts, in particular the dumping and dredging activities for the construction of the JWP, have contributed to the sediments heterogeneity in the Inner Jade. Subsequent changes of the benthic macrofauna composition had to be expected. Often, the intermediate state is missing in the standard before/after disturbance analyses and the improvement of succession models throughout the ongoing disturbance is crucial to understanding of the processes that occur (Vöge et al. 2008). Post-settlement dispersal plays a key role in the re-colonisation of disturbed habitats. In undisturbed areas post-settlement dispersal might contribute to the maintenance of certain macrofauna distribution patterns, e.g. due to adult-juvenile interactions.

The specific objectives of this thesis were to:

- I) compare patterns of hydroacoustics, sediments and macrofauna in the Inner Jade, a heterogeneous study area, which is naturally highly dynamic and influenced by various anthropogenic stressors.
- II) study the direct and indirect effects of ongoing dredging activities on the spatial distribution of sediments and macrofauna in the Inner Jade.
- III) assess the impact of the presence of two adult bivalve species (*Austrovenus stutchburyi* and *Macomona liliana*) on the post-settlement dispersal behaviour of juveniles in a flume.

1.10 Outline of this study

Chapter 2 describes a methodological approach of benthic habitat mapping in the Inner Jade in May 2010 using a Benthos 1624TM side scan sonar. Manual expert classification was applied in this heterogeneous study area. For the ground-truthing of the hydroacoustic data 55 stations were sampled along eight west-east transects. A 0.1 m² Van Veen grab was used for sediment and macrofauna sampling. Macrofauna was retained in a 1 mm mesh. The abundance data of the two macrofauna samples per station were averaged. After fourth root

transformation, similarities between sampling stations were calculated with the Bray-Curtis coefficient (Bray and Curtis 1957) and interpreted by means of the similarity profile test SIMPROF, which tests the null hypothesis that a specific set of samples, which are not a priori divided into groups, do not differ from each other (Clarke and Gorley 2006). The cluster analysis of the abundance data determined the macrofauna community structure of the study area. Ordination of the macrofauna data was done by non-metric multidimensional scaling (MDS; Shepard 1962; Kruskal 1964). The significance of differences between communities (clusters) was determined with the one-way PERMANOVA (Anderson et al. 2008). Characteristic taxa were identified with the similarity percentage routine SIMPER. GIS (Geographic Information System) maps visualized the patterns of macrofauna communities, sediment composition, and hydroacoustic classes. The routine RELATE tested for significant correlations between the hydroacoustic classification, the sediment classification and the macrofauna community structure. To assess the contribution of the environmental variables to the variability observed in the macrofauna community structure, distance-based linear models (DISTLM) were carried out. DISTLM is a multivariate multiple regression routine in which a resemblance matrix of multivariate species abundance data is regressed against a set of explanatory (environmental) variables (Anderson et al. 2008). The environmental variables were analysed individually (marginal tests), ignoring all other variables, and sequentially using a stepwise selection procedure based on the R^2 criterion. The model results were visualised through the use of a distance-based redundancy analysis routine (db-RDA; Legendre and Anderson 1999; McArdle and Anderson 2001; Anderson et al. 2004).

In **chapter 3** a subset (30 stations) of the data which was collected in May 2010 was analysed. In April 2002, the consultant office BIOCONSULT sampled the same 30 stations with a 0.1 m² Van Veen grab and the macrofauna was retained by using also a 1-mm mesh. For comparison with 2010, BIOCONSULT made the raw data of sediments and macrofauna available, in order to evaluate the effects of the ongoing dredging activities for the JWP. The JadeWeserPort Realisation Company and the local harbour authority WSA (Wasser- und Schifffahrtsamt Wilhelmshaven) provided data on their dredging and dumping activities. The federal maritime and hydrographic agency BSH (Bundesamt für Seeschifffahrt und Hydrographie) and the WSA provided singlebeam echosounder (SBES) data of the study area in 2002. In order to show the changes in seafloor topography between 2002 and 2010, two bathymetry maps were generated. The digital terrain model of 2010 was based on

measurements on board of the RV “Senckenberg” with a Reson 8125 multibeam 455 kHz echosounder (MBES) in May 2010 and was complemented with MBES data collected on behalf of the JadeWeserPort Realisation Company in April 2010. The changes in sand and mud content between 2002 and 2010 were analysed. One-way ANOVA tested for the significance in changes of taxa number, abundance, and effective number of species. The macrofauna community structure was determined by cluster analyses and interpreted by means of the similarity profile test SIMPROF. Characteristic taxa were identified by the similarity percentage routine SIMPER. All taxa were divided into their most common feeding type (omnivores/predators, deposit feeders, and suspension feeders). The routine BIOENV tested for the significant Spearman rank correlations between the community structure in 2010 and the dredging activities for the JWP, depth or the sediment composition. The routine RELATE matched the resemblance matrices of macrofauna abundance data of 2002 and 2010, in order to compare the similarity of patterns. One-way PERMANOVA tested for the significance of differences between macrofauna clusters. The routine PERMDISP was used for testing the homogeneity of multivariate dispersions from group centroids on basis of the resemblance measure. Furthermore, the datasets of 2002 and 2010 were combined in one cluster analyses and the similarity of the two corresponding stations was categorised in high, medium, and low. Finally, GIS (Geographic Information System) maps were generated to visualize the changes in patterns of macrofauna communities (clusters), taxa number, abundance, biomass, and selected taxa in relation to dredging and dumping activities.

Chapter 4 describes an adult-juvenile interaction experiment which was conducted in the flume laboratory of the Waikato University in Hamilton, New Zealand. Aim of the investigation was to test, if the presence of adults has an impact on the post-settlement dispersal of juveniles. Therefore, sediments, adult and juvenile bivalves of the species *Austrovenus stutchburyi* and *Macomona liliana* were collected at Taupiro Point, a sheltered sand flat in the Bay of Plenty. For each experimental run two cores were filled with sediment and adult bivalves. A core without adult bivalves served as control. Juvenile bivalves of both species were added to the cores which were inserted in a flume. At a flow speed which was low enough to avoid erosion and high enough to allow active dispersal, the juveniles had 48 hours for post-settlement dispersal. Afterwards the juveniles were recovered from the acrylic flume floors, the bedload traps, the plankton net and the cores with the adult treatments. Thus, the different dispersal modes (crawling, rolling as bedload and drifting into the plankton net) could be differentiated. For the reconstruction from which core the juvenile bivalves

originated from, one half of the juveniles were stained with fluorescein before the experiment was started. At the end of each experimental run the recovered juveniles were sorted under blue light excitation, in order to determine if they were fluorescent. Additionally, the shell length of each bivalve was measured for the validation that juveniles of a similar size were used in the experiment. For the fourfold replication six experimental runs were necessary. The exact flow speed which was used for each run was measured with an Acoustic Doppler Velocity meter (ADV). One way ANOVA determined the significance of differences in juvenile dispersal between the two adult treatments and the control without bivalves. A two way ANOVA was performed, in order to test for significant differences between the two factors “treatment” and “dispersal mode”. In case of a significant interaction between these two factors, a separate ANOVA/Welch test was calculated per treatment. A post hoc test (Turkey’s Honestly Significant Difference) was used to identify the significant differences of dispersal mode per treatment. The significance of differences in size per capture position in the flume (acrylic floor, bedload traps, plankton net) was determined by Kruskal Wallis tests. A post hoc test (Mann-Whitney test) was used to detect significant differences in size of the juveniles between the different capture positions.

1.11 Manuscripts

Chapter 2:

Gutperlet, R., Capperucci, R.M., Bartholomä, A. Kröncke, I. (submitted) Relationships between spatial patterns of macrofauna communities, sediments and hydroacoustic backscatter images in a highly heterogeneous und human disturbed environment. *Journal of Sea Research*

The conception, the macrofauna sampling, the macrofauna sample processing, data analyses and writing were done by Ruth Gutperlet. The co-author Ruggero M. Capperucci did the sediment sampling and the acoustic measurement, provided acoustic data and sediment data and helped to write the correspondent parts of the manuscript. Ingrid Kröncke and Alexander Bartholomä supervised the work and reviewed the manuscript.

Chapter 3:

Gutperlet, R., Capperucci, R.M., Bartholomä, A. Kröncke, I. (2015) Benthic biodiversity changes in response to dredging activities during the construction of a deep-water port. *Marine Biodiversity* 45:819-839

The conception, the macrofauna sampling, the macrofauna sample processing, data analyses and writing were done by Ruth Gutperlet. The co-author Ruggero M. Capperucci did the sediment sampling and the acoustic measurements, provided acoustic data and sediment data and wrote the correspondent parts of the manuscript. Ingrid Kröncke and Alexander Bartholomä supervised the work and reviewed the manuscript.

Chapter 4:

Gutperlet, R., Pilditch, C.

Comparison of adult-juvenile interactions of a deposit-feeding and a suspension-feeding bivalve under controlled conditions

The conception, the macrofauna and sediment collection, the experimental procedure, data analyses and writing were done by Ruth Gutperlet. Conrad Pilditch supervised the work and reviewed the manuscript.

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2 Relationships between spatial patterns of macrofauna communities, sediments and hydroacoustic backscatter images in a highly heterogeneous and human disturbed environment

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2.1 Abstract

A survey was conducted in the Inner Jade, a tidal channel in the southern North Sea, to investigate the relationships between macrofauna community structure and natural as well as anthropogenic environmental variables in a very heterogeneous and human disturbed environment. The manual expert hydroacoustic classification of the backscatter image derived by sidescan sonar was successful to detect the different dredging activities and the natural bedforms in the undisturbed areas. The sediment distribution was very patchy and no significant congruence with the hydroacoustic classification could be detected. In contrast, low, but significant relationships between the hydroacoustic classification and the macrofauna community structure as well as the sediment distribution and the macrofauna communities were found. The most important impact on the spatial community structure was the number of days after the last dredging/dumping activity for the JadeWeserPort (JWP), followed by sediment characteristics explained by the grey values of the backscatter image. Sand dominated the western stations, which were dredged for the JWP and were inhabited by a characteristic macrofauna community. Another community occurred mainly on stations with elevated mud content in the regularly dredged old navigation channel and the undisturbed south eastern area. The communities in the north eastern undisturbed area coincided with elevated contents of gravel and shells. This study stresses the problems of benthic habitat mapping in such a heterogeneous area.

2.2 Key words

JadeWeserPort, macrofauna, spatial variability, sediment heterogeneity, hydroacoustics, dredging activities

2.3 Introduction

In environmental impact assessments, macrofauna community structure is used as an essential tool for the evaluation of the status quo of the ecosystem (Warwick 1993; Borja et al. 2013), because the macrofaunal patterns integrate temporal and spatial changes in the marine habitat (Johnson 1972). Biodiversity in a benthic habitat is influenced by water mass and current related factors such as oxygen, temperature, salinity and load of organic material (Robert et al 2014). Furthermore, benthic community structure depends on hydrodynamically mediated food resources (Wieking and Kröncke 2005; Kröncke 2006) and at least to some degree on substrate type (Gray 1974; Rhoads 1974; Snelgrove and Butman 1994). Anthropogenic physical disturbance, e.g. fishing (Auster and Langton 1998) and dredging (Newell et al. 1998; van Dalssen et al. 2000; Simonini et al. 2007) has also a strong impact on taxa composition and abundance.

The influences of sediment extraction on the seabed and the associated macrofauna have been widely reviewed (Boyd et al. 2003; ICES 1992, 2001; Newell et al. 1998). Initial effects of dredging involve a 30-70% reduction of species diversity and a 40-90% reduction in population density within the boundaries of the dredged areas (Newell et al. 1998). Adjacent areas can be also affected by the deposition of material mobilised by dredging and transported outside the boundaries of the dredge site (Newell et al. 2002; Hitchcock and Bell 2004). Recovery rates are highly site specific (Boyd et al. 2004; Cooper et al. 2005; Kenny and Rees 1994, 1996; Kenny et al. 1998) and vary between 2 and 10 years (Newell et al. 1998). When dredging activities remove the surface layers of sediments, the remaining substratum may be a totally different sediment type than the original one and might be unsuitable for re-colonisation by the species that previously inhabited the area (Kenny and Rees 1996; Boyd et al. 2005).

In the past decades technological advance in hydroacoustic tools (single-beam echo sounder, side-scan sonar (SSS), multi-beam echo sounder) went hand in hand with highly resolution backscatter images (Brown et al 2002), which detect seafloor characteristics and benthic community patterns. Many studies in homogenous areas showed the utility of hydroacoustic tools for successful benthic habitat mapping (e.g. Brown et al. 2002, Brown et al. 2004b,

Freitas et al. 2003, Freitas et al. 2005). Recent studies in undisturbed homogeneous environments focus on spatial continuous hydroacoustic sampling, since this low cost, efficient, and easily repeatable method allows 100% coverage of the seafloor (Brown et al. 2004). Acoustic backscatter is strongly linked to surficial seabed characteristics (Collier and Brown 2005, Markert et al. 2013), such as seafloor topography, sediment grain size and roughness. Some biogenic aggregation structures, such as sea weed meadows (Preston 2006), blue mussel beds (Van Overmeeren et al 2009), coral reefs (Gleason et al 2006; Gleason 2009), oyster beds (Quester Tangent Corporation 2003) or aggregations of tube building worms like *Lanice conchilega* (Degraer et al 2008) and brittle star arms (Markert et al. 2015a) can also be successfully detected and mapped. However, although high-resolution SSS are able to show decimetre-size features (Kenny et al. 2003), individual macrofauna organisms without a prominent superficial structure cannot be detected. For a reliable ground-truthing of the backscatter data, traditional point sampling with e.g. grabs or corers is needed to achieve a comprehensive data acquisition (Kenny et al. 2003). Many field studies first map the seabed with hydroacoustic tools and then take only a few samples in the so defined habitats (Eastwood et al. 2006). Such a low data density leads to interpolations, which might give a wrong image of the current habitat stage (Diaz et al. 2004). Despite a dense ground-truth sampling grid, uncertainties occurred in some study areas, e.g. Markert et al. (2013) found sharp boundaries between habitats of sorted bedforms, but their hydroacoustic classification failed to detect a transition macrofauna community. Similarly, Freitas et al. (2006) described three acoustic classes, but four biological affinity groups were found along the acoustic gradient. In contrast, also one community that occurred in more than one habitats was reported (Kostylev et al. 2001, Freitas et al. 2003). In general, soft-sediment habitats are difficult to map, because macrofauna communities frequently overlap substrate boundaries (Shumchenia and King 2010).

Heterogeneous habitats with a patchy distribution of sediment types and/or biological communities are even more difficult to map than homogenous substrates with clearly definable boundaries (Brown et al 2004a) or a distinct gradient. One example for a heterogeneous study area is the Inner Jade, a tidal channel in the German Bight of the southern North Sea. Naturally mobile bedforms (Kubicki and Bartholomä 2011) and dredging activities for the maintenance of the navigation channel coupled with construction works for a deep-water port, including the introduction of new sources of different sediments, e.g. the clay formation “Lauenburger Ton”, whose outcrops were extremely rare in the Jade system, before the construction works had begun, formed a dynamic mosaic of microhabitats in that area.

While Gutperlet et al. (2015) compared the impacts on the macrofauna before and after dredging activities in the Inner Jade, the objectives of this study were i) to characterise the habitats in this heterogeneous study area based on manual expert interpretation of the SSS data, the sediment distribution and macrofauna community structure, ii) to compare the spatial patterns of the hydroacoustic classification, sediment composition and macrofauna communities and to test for significant congruence of these patterns, and iii) to investigate the relationships between macrofauna community structure and natural and anthropogenic environmental factors (including dredging activities and grey values of the backscatter image derived by side scan sonar) using multivariate statistical approaches.

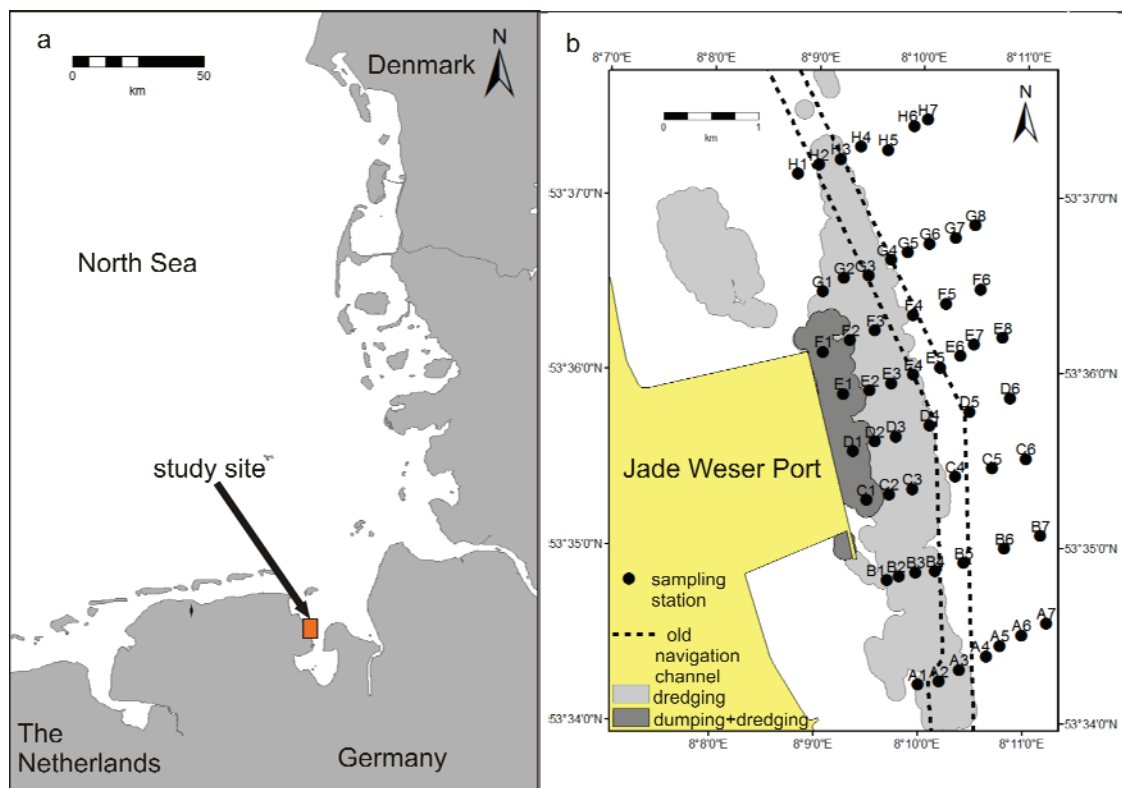


Figure 2.1 Location of a) the study area in the German Bight of the southern North Sea and b) the main features related to the new coastline (yellow land), the dredging and dumping activities for the “JadeWeserPort” (JWP), the regularly dredged old navigation channel (pointed lines), and the sampling stations (black dots).

2.4 Material and methods

2.4.1 Study area

In the German Bight (southern North Sea), the study area was located in the Inner Jade (Fig. 2.1a), a tidal channel with the deepwater port of the German city Wilhelmshaven, the JadeWeserPort (JWP). The subtidal study area in front of the JWP is characterised by an upper mesotidal regime. Semi-diurnal tides range from 2.8 m at the northern entrance to 3.8 m at the Jade Bay in the south (Kubicki and Bartholomä 2011). The tidal flat area “Der Hohe Weg” borders the eastern channel margin.

The study area was located between km 7.1 and km 14.5 of the old navigation channel, which is situated in the centre of the Inner Jade (Fig. 2.1b). Regular dredging of the old navigation channel by the local harbour authority WSA (Wasser- und Schifffahrtsamt Wilhelmshaven) guarantees a width of 300 m and a depth of 20.1 m (referred to the local chart datum, Normalhöhennull (NHN); Kubicki and Bartholomä 2011).

Since March 2008, 46 million m³ sand was used by the JWP Realization Company to build the 360 ha terminal area. Before piling, fine soft sediment had to be replaced by coarser material. Thus, sand was dumped not only in the terminal area, but also in front of the bulkhead (Fig. 2.1b). The deepest parts of the study area were two sand extraction pits, north and south of the JWP (approx. 50 m; Fig. 2.2). In 2012, land reclamation and the redirection of the navigation channel for access to the JWP were completed. In May 2010, a survey was carried out aboard the RV “Senckenberg”.

2.4.2 Acoustic seafloor classification

A dual frequency BenthosTM 1624 SSS was deployed for covering an area of approx. 10.2 km² in front of the JWP construction site (6.1 km in north-south direction and 1.5 km in east-west direction). The Benthos 1624 SSS operates at two different frequency ranges: 110-130 kHz (low frequency, beam size 0.5° horizontal and 55° vertical) and 370-390 kHz (high frequency, beam size 0.5° horizontal and 35° vertical). A 200 m swath width was used for data coverage. Based on the previous knowledge of the area and on the expected enhanced disturbance due to the constructional works, for the present study only the high frequency was processed and analysed. The recording and processing were carried out by means of the SonarWizTM software. Processing steps included both geometric and radiometric corrections.

A final mosaic of the study area was exported (at 0.5 m resolution) and loaded into a GIS software (Global Mapper™ 13) for data analysis, mapping and interpretation.

The analysis and subdivision of the mosaic in regions (classification) was done manually, based on backscatter values (i.e. grey scale values) and seabed texture. The mapping took into account both the intensity of the backscatter, the presence/absence of seabed features, and the characteristics of such features (e.g. size, distribution, regularity, etc.). The attempt to use automated or semi-automated classification tools for the side scan sonar data of the Inner Jade was not successful, due to the high variability of both, sediment types and morphologies. In addition, specific features (e.g. different generations of dredging marks, in some cases partially reworked by the highly dynamic sediments). generated patterns, which led to misclassifications. Therefore manual expert classification was applied.

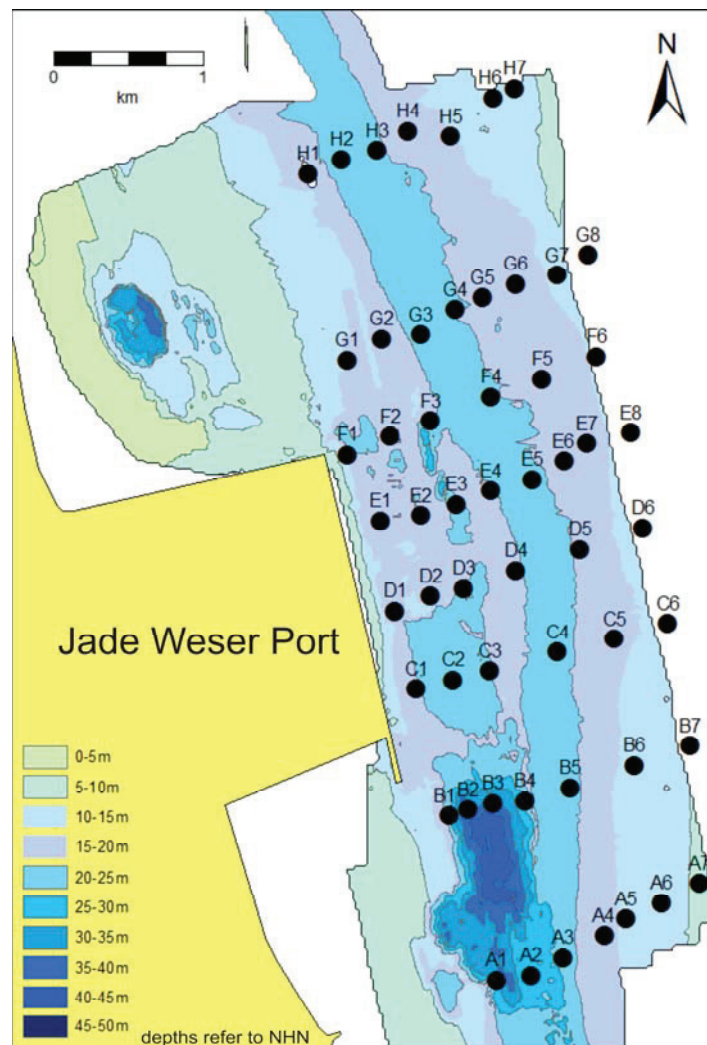


Figure 2.2 Bathymetry of the study area, depths in meter refer to Normalhöhenull (NHN)

2.4.3 Sampling

Directly after the SSS data collection, 55 stations were sampled along 8 west–east transects A-H (Fig. 2.1b) with an average distance between the stations of approx. 250 m. Around each JWP dredging and dumping position (midpoint coordinates were provided by the JWP Realization Company) a buffer of 100 m was created. Within the 100 m radius around each sampling station, all dredging and dumping activities before and during the sampling were summed. The sampling transects were designed in order to include 25 stations in the area, which was directly affected by construction works for the JWP (Table 2.1).

Table 2.1 Number of dredging days for the JWP and number of days between the last dredging/dumping activity for the JWP and the sampling date for the JWP dredged stations (The regular dredging activities in the old navigation channel are not included here.)

dredged stations	dredging days	days after
A2	25	263
A3	12	277
B1	4	342
B2	10	247
B3	30	139
B4	3	221
C1	3	382
C2	9	302
C3	19	341
D1	4	230
D2	3	387
D3	56	425
D4	2	322
E1	17	276
E2	26	375
E3	45	470
E4	5	274
F1	4	617
F2	11	381
F3	100	415
G1	3	56
G2	46	4
G3	22	259
H2	4	283
H3	2	252

The local harbour authority WSA provided data on the yearly total sediment volumes, which were dredged in the old navigation channel (between km 8 and km 12) in the years 2008-2010. 11 stations were placed in the regularly dredged old navigation channel.

Sampling was carried out with a 0.1 m² Van Veen grab. At each station three samples were taken: two replicates for macrofauna and one sample for sediment analyses. At one station (G5) no sediment sample could be collected.

2.4.4 Sediment sample procedure

After a macroscopic description of the recovered sediment sample, a subsample (approx. 200 ml) was taken for grain size analysis. In the laboratory the sediments were split into mud fraction (< 0.063 mm) and sand/gravel fraction by wet sieving over a 63 µm mesh. The sand and gravel fractions were separated by dry sieving over a 2 mm mesh. The sand content (0.063 – 2 mm) was weighed, treated with hydrochloric acid, and weighed again, in order to determine the content of sand sized shell debris. The gravel content (> 2 mm) was determined by dry sieving over a 2 mm mesh and then sorted into gravel and shell debris. For the total amount of shell debris in a sample, the shell debris of the sand sized and the gravel sized fraction were summed up.

2.4.5 Macrofauna sample procedure

The samples were sieved onboard over a 1 mm mesh. The retained material was fixed with 4 % buffered formaldehyde. In the laboratory, the samples were sieved again over 1 mm mesh and the organisms were stained with Rose Bengal. After sorting, the organisms were counted and identified to the lowest taxonomic level possible.

2.4.6 Data analysis

The PRIMERTM v6 program package (Plymouth Marine Laboratory) was used for the multivariate statistical analyses (Anderson et al. 2008a) of the macrofauna community structure. Taxa, which were not sampled quantitatively by the van Veen grab (Hydrozoa, Bryozoa, Balanidae, Mysidacea, and large, mobile epifauna) were excluded from the analyses. The abundance data of the two macrofauna samples per station were averaged. After fourth root transformation, similarities between sampling stations were calculated with the Bray-Curtis coefficient (Bray and Curtis 1957) and interpreted by means of the similarity profile test SIMPROF, which tests the null hypothesis that a specific set of samples, which are not a priori divided into groups, do not differ from each other (Clarke and Gorley 2006). The cluster analysis of the abundance data determined the macrofauna community structure of the study area. Ordination was done by MDS (non-metric multidimensional scaling) (Shepard

1962; Kruskal 1964). The significance of differences between communities (clusters) was tested with the one-way PERMANOVA (Anderson et al. 2008a). The similarity percentage routine SIMPER, compares the taxa abundance between the clusters and was used to identify the characteristic taxa of the different macrofauna communities (Clarke and Warwick 2001). Using ArcMap 10TM, GIS maps were generated to visualize the patterns of hydroacoustic classes, sediment composition, and macrofauna communities. The routine RELATE was used to match the resemblance matrices of the macrofauna abundance, hydroacoustic classification and sediment classes, in order to compare the similarity of the spatial patterns.

To assess the contribution of the environmental variables to the variability observed in the macrofauna community structure, distance-based linear models (DISTLM) were carried out. DISTLM is a multivariate multiple regression routine, in which a resemblance matrix of multivariate species abundance data is regressed against a set of explanatory (environmental) variables (Anderson et al. 2008a). Prior to analysis, environmental variables were normalized to eliminate their physical units (Legendre and Birks 2012). Skewness of the environmental variables was inspected using draftsman plots (Anderson et al. 2008a). The environmental variables were analysed individually (marginal tests), ignoring all other variables, and sequentially using a stepwise selection procedure based on the R² criterion. The model results were visualised through the use of a distance-based redundancy analysis routine (db-RDA; Legendre and Anderson 1999; McArdle and Anderson 2001; Anderson et al. 2004).

For the variable “days after” (Table 2.1) a dummy variable (10 000) was used for all stations, which were not dredged or for which the date of the last dredging activity is unknown. The “grey values” were extracted from the backscatter image derived by side scan sonar (Fig. 2.3).

2.5 Results

2.5.1 Hydroacoustic classification

The backscatter data were divided into 10 classes (A-J) by manual expert interpretation (Fig. 2.3). The features characterising each hydroacoustic class are summarised in Table 2.2.

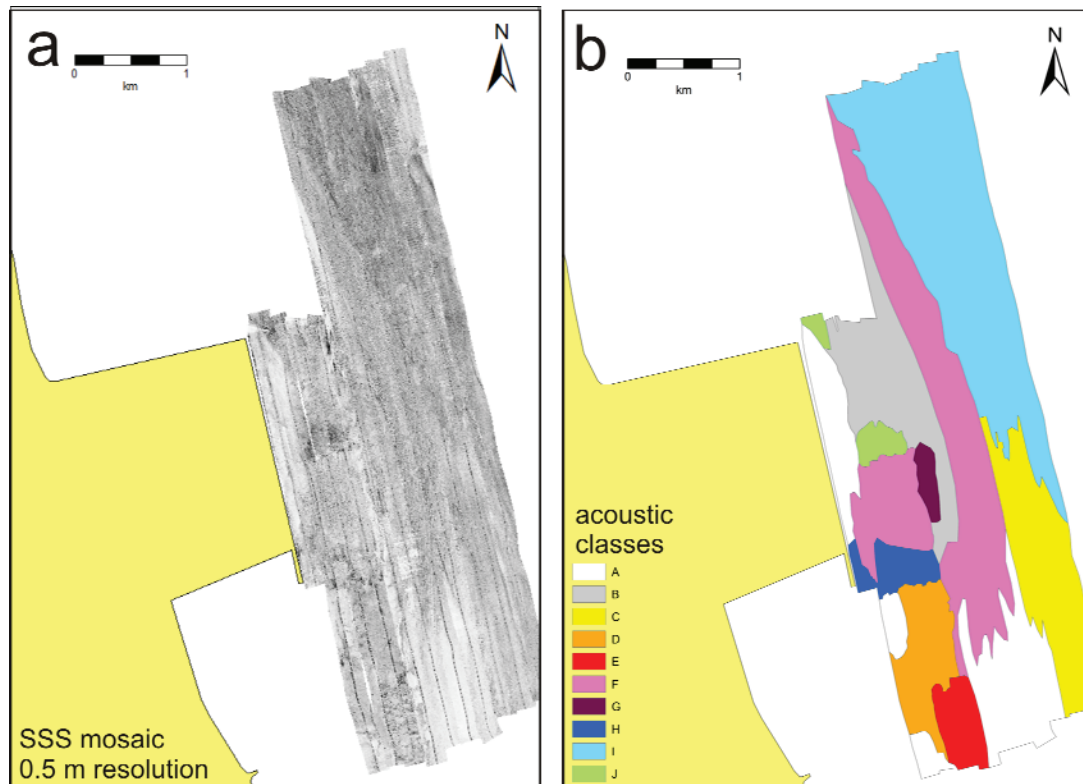


Figure 2.3 a) Side-scan sonar (SSS) mosaic in 0.5 m resolution and b) manual expert classification

Table 2.2 Characteristics for the hydroacoustic classes derived by manual expert classification

backscatter	mean greyscale	acoustic class	features of acoustic class
LB	216	A	Low backscatter. Absence of relevant seabed features.
MB	195	B	Dredged area (JWP; backhoe dredger), with remobilised and reworked material (bedforms) partially superimposing the dredging marks
	194	C	Relatively "undisturbed" area, scarce seabed features, few elongated marks (sand ribbons?).
	193	D	Absence of relevant seabed features.
	193	E	Dredging and dumping area. Patchy-bumpy texture.
	191	F	Dredged areas (old navigation channel and JWP area) with regularly shaped dredging marks (forming characteristic textures)
	191	G	Dredged area (JWP). Bedforms (likely superimposing the dredging marks).
	189	H	Dredged area (JWP). Irregular seabed features (dips and bumps).
HB	170	I	Relatively "undisturbed" area (though a part includes the Voslapp Reede site). Irregular morphologies, bedforms and elongated features (sand ribbons?).
	162	J	Dredged areas.

2.5.2 Sediment distribution

The sediment distribution was heterogeneous in the study area around the JWP (Table 2.3). sand dominated most of the pie charts in Fig. 2.4a. Elevated mud contents were determined in the old navigation channel (A2, A3, B5, C4, E5, F4, G3, G4, H2, H3), at some undisturbed eastern stations (A7, B6, B7, C5, C6, D5, E6, E7) and at a few western, dredged stations (B1-B4, C2, D2). Elevated contents of gravel and shells were mainly found in the undisturbed north eastern area (D6, F6, G6-G8, H5-H7) and at one station in the old navigation channel (C4).

Table 2.3 Sediment characteristics per station in the Inner Jade

station	mud	sand	gravel	gravelly shells	sandy shells	total shell debris	textural group (Folk 1954)	symbol
	<0.063mm	0.063-2mm	>2mm					
	%	%	%	ca. %	ca. %	ca. %		
A1	17.96	79.16	0.00	0.00	2.87	2.87	muddy sand	mS
A2	34.69	61.94	0.58	0.01	2.79	2.79	slightly gravelly muddy sand	Sl_gmS
A3	80.41	19.09	0.12	0.02	0.35	0.37	slightly gravelly sandy mud	Sl_gsM
A4	12.34	83.20	0.00	0.00	4.46	4.46	muddy sand	mS
A5	15.27	81.11	0.00	0.00	3.61	3.61	muddy sand	mS
A6	4.03	93.03	0.08	0.77	2.10	2.86	slightly gravelly sand	Sl_gS
A7	59.28	36.44	0.42	2.23	1.63	3.86	slightly gravelly sandy mud	Sl_gsM
B1	46.11	51.51	0.00	0.00	2.38	2.38	muddy sand	mS
B2	37.34	56.58	1.95	0.00	4.12	4.12	slightly gravelly muddy sand	Sl_gmS
B3	34.52	62.42	0.00	0.00	3.06	3.06	muddy sand	mS
B4	35.13	61.95	0.00	0.00	2.93	2.93	muddy sand	mS
B5	20.40	77.95	0.00	0.00	1.64	1.64	muddy sand	mS
B6	27.44	65.25	2.06	0.70	4.55	5.25	slightly gravelly muddy sand	Sl_gmS
B7	65.83	32.21	0.00	0.00	1.96	1.96	sandy mud	sM
C1	10.57	82.09	5.12	1.42	0.81	2.23	gravelly muddy sand	gmS
C2	70.21	27.16	2.47	0.00	0.16	0.16	slightly gravelly sandy mud	Sl_gsM
C3	14.65	85.27	0.08	0.00	0.00	0.00	slightly gravelly muddy sand	Sl_gmS
C4	38.97	35.37	25.60	0.07	0.00	0.07	gravelly mud	gM
C5	86.49	12.85	0.00	0.00	0.66	0.66	sandy mud	sM
C6	26.44	65.71	1.42	3.96	2.47	6.44	slightly gravelly muddy sand	Sl_gmS
D1	10.66	88.28	0.00	0.01	1.05	1.06	muddy sand	mS
D2	43.34	55.35	0.29	0.20	0.83	1.03	slightly gravelly muddy sand	Sl_gmS
D3	14.16	84.79	0.05	0.00	1.00	1.00	slightly gravelly muddy sand	Sl_gmS
D4	3.18	89.80	0.82	3.42	2.77	6.19	slightly gravelly sand	Sl_gS
D5	50.54	46.73	0.07	0.05	2.61	2.67	slightly gravelly sandy mud	Sl_gsM
D6	0.89	69.69	2.40	22.37	4.65	27.01	slightly gravelly sand	Sl_gS
E1	1.61	97.59	0.01	0.00	0.78	0.78	slightly gravelly sand	Sl_gS
E2	0.70	94.57	3.22	1.09	0.42	1.51	slightly gravelly sand	Sl_gS
E3	21.45	76.95	0.77	0.32	0.51	0.83	slightly gravelly muddy sand	Sl_gmS
E4	4.05	90.41	2.48	1.79	1.26	3.06	slightly gravelly sand	Sl_gS
E5	68.56	28.87	0.00	0.00	2.57	2.57	sandy mud	sM
E6	83.07	15.17	1.03	0.26	0.47	0.73	slightly gravelly sandy mud	Sl_gsM
E7	62.76	34.48	0.04	0.08	2.64	2.72	slightly gravelly sandy mud	Sl_gsM
E8	7.22	86.26	0.01	3.22	3.29	6.51	slightly gravelly sand	Sl_gS
F1	3.35	92.33	3.46	0.55	0.31	0.86	slightly gravelly sand	Sl_gS
F2	1.29	97.75	0.29	0.21	0.45	0.66	slightly gravelly sand	Sl_gS
F3	9.08	90.44	0.14	0.01	0.32	0.34	slightly gravelly sand	Sl_gS
F4	36.00	60.39	0.00	0.05	3.57	3.62	muddy sand	mS
F5	3.06	88.88	2.16	4.68	1.21	5.90	slightly gravelly sand	Sl_gS
F6	4.89	63.53	0.01	26.38	5.19	31.57	slightly gravelly sand	Sl_gS
G1	2.48	94.78	2.21	0.06	0.46	0.52	slightly gravelly sand	Sl_gS
G2	7.20	90.87	1.38	0.03	0.53	0.56	slightly gravelly sand	Sl_gS
G3	44.50	52.37	0.21	0.20	2.73	2.93	slightly gravelly muddy sand	Sl_gmS
G4	45.37	52.15	0.00	0.03	2.45	2.48	muddy sand	mS
G5	no data	no data	no data	no data	no data	no data	no data	no data
G6	3.39	77.52	2.80	13.54	2.75	16.29	slightly gravelly sand	Sl_gS
G7	5.00	55.21	25.54	11.44	2.81	14.24	gravelly sand	gS
G8	14.82	62.42	4.19	15.85	2.72	18.57	gravelly muddy sand	gmS
H1	0.26	99.32	0.00	0.00	0.42	0.42	sand	S
H2	34.73	63.82	0.00	0.00	1.45	1.45	muddy sand	mS
H3	50.35	45.99	0.30	0.58	2.78	3.36	slightly gravelly sandy mud	Sl_gsM
H4	4.27	90.66	0.73	2.19	2.15	4.34	slightly gravelly sand	Sl_gS
H5	0.37	84.78	3.95	7.46	3.44	10.90	slightly gravelly sand	Sl_gS
H6	6.84	50.80	35.10	5.57	1.69	7.25	muddy sandy gravel	msG
H7	10.68	70.79	4.88	11.49	2.16	13.65	gravelly muddy sand	gmS

According to Folk (1954) 10 sediment classes were present in the study area (sandy mud, slightly gravelly sandy mud, gravelly mud, muddy sand, slightly gravelly muddy sand, gravelly muddy sand, sand, slightly gravelly sand, gravelly sand, and muddy sandy gravel). Slightly gravelly sand (17 of 54 stations) dominated the north-western dredged stations (D4, E1, E2, E4, F1-F3, G1, G2) and appeared at 7 undisturbed north-eastern stations (D6, E8, F5, F6, G6, H4, H5) and at 1 station in the south-eastern area (A6). The south-western dredged

stations were dominated by muddy sand (A1, B1, B3-B5, D1), which occurred also at 2 stations in the old navigation channel (F4, G4), at 1 station in the north-western area (H2) and at 2 stations in the undisturbed south-eastern area (A4, A5). Slightly gravelly muddy sand was mainly found in the western dredged area (A2, B2, C3, D2, D3, E3, G3) and at 2 stations in the undisturbed eastern area (B6, C6). Slightly gravelly sandy mud appeared at 4 stations in the eastern area (A7, D5, E6, E7), at 2 stations in the old navigation channel (A3, H3), and at 1 western dredged station (C2). Sandy mud occurred at 2 south-eastern stations (B7, C5) and at 1 station in the old navigation channel (E5). Gravelly mud was found at only 1 station in the old navigation channel (C4). Gravelly muddy sand was located at 2 stations in the undisturbed north-eastern area (G8, H7) and in front of the JWP bulkhead (C1). Pure sand occurred only at 1 north-western station (H1). Gravelly sand was found at 1 station in the north-eastern area (G7). Muddy sandy gravel appeared also at only 1 north-eastern station (H6).

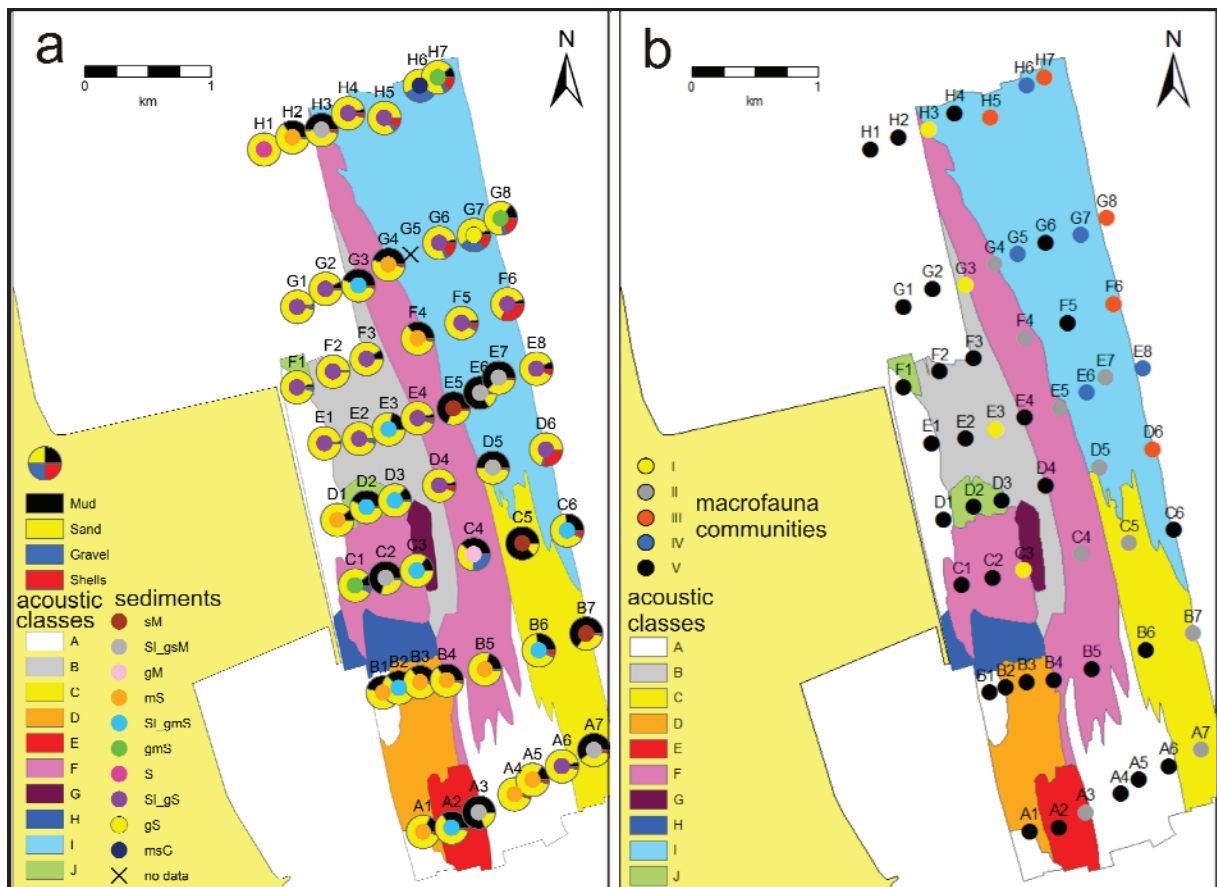


Figure 2.4 Spatial alignment of a) the sediment classes and b) the macrofauna communities in relation to the hydroacoustic classification

2.5.3 Macrofauna

In total, 71 macrofauna taxa were identified. 50.7% of the organisms were polychaetes, 19.7% crustaceans, and 14.1% molluscs (15.5% belonged to Anthozoa and other groups). The SIMPROF test of the cluster analyses (Fig. 2.5) revealed an “outlier” group (community I) and 4 communities (II-V). All communities were significantly different according to the PERMANOVA (Table 2.4).

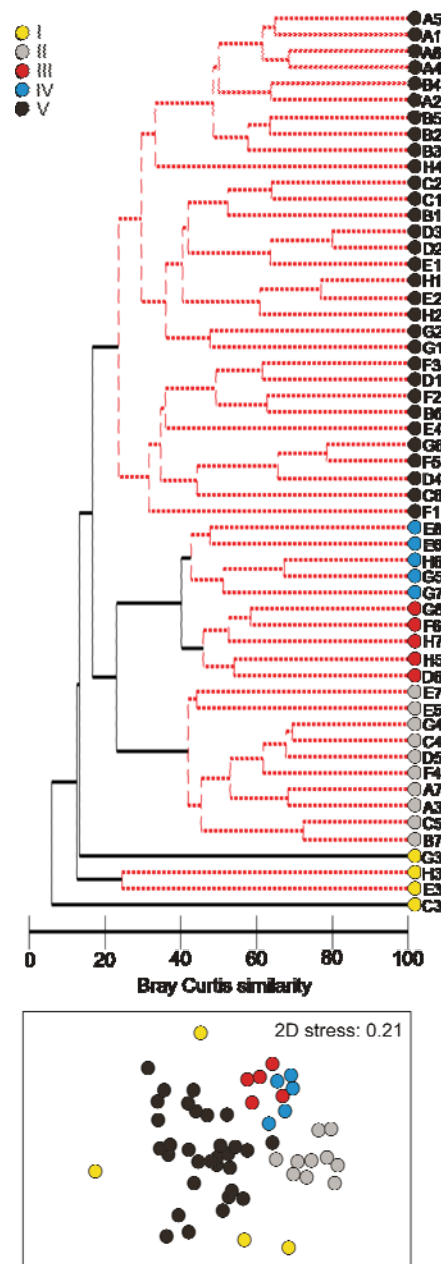


Figure 2.5 a) Cluster analysis and b) MDS of macrofauna data, based on Bray Curtis similarity, using fourth-root transformed data; black lines indicate the significantly different cluster according to the SIMPOROF test ($p < 0.05$)

Table 2.4 Results of the PERMANOVA and PERMDISP pairwise test of all macrofauna communities, statistically significant ($p < 0.05$) are marked in bold

macrofauna communities	df	PERMANOVA		PERMDISP	
		t	p	t	p
I, II	12	2.1574	0.002	6.9123	0.001
I, III	7	1.8193	0.009	7.409	0.006
I, IV	7	1.7360	0.010	8.3622	0.004
I, V	33	1.5727	0.013	2.1731	0.208
II, III	13	3.1765	0.001	0.6723	0.566
II, IV	13	2.8661	0.002	0.27047	0.861
II, V	13	3.5894	0.001	4.3614	0.003
III, IV	8	1.6412	0.013	0.46037	0.643
III, V	34	2.3925	0.001	3.702	0.005
IV, V	34	2.4478	0.001	3.4231	0.012

The four stations belonging to **community I** showed the lowest mean taxa number, the lowest mean abundance, and the lowest biodiversity in the study area (Table 2.5). Community I was located within the old navigation channel and in the area, which was dredged for the JWP (Fig. 2.4b), associated with slightly gravelly muddy sand (75%) and slightly gravelly sandy mud (25%). The bivalve *Petricolaria pholadiformis*, which prefers fine sediments, resulted to be the characteristic species (Table 2.6).

Table 2.5 Taxa number per station (0.1m^2), abundance (individuals/ m^2) and effective species number of all macrofauna communities are given as mean with standard deviation (sd) with sediment categories (%), depth and number of dredging days for the JWP at the concerning stations

macrofauna community	I		II		III		IV		V	
	mean	(sd)	mean	(sd)	mean	(sd)	mean	(sd)	mean	(sd)
taxa number	3.5	(1.7)	7.3	(3.9)	11.2	(3.6)	17.6	(4.6)	4.8	(2.5)
abundance [ind./ m^2]	25.0	(12.9)	655.0	(855.9)	474.0	(271.5)	1682.0	(1499.5)	123.2	(135.8)
effective number of taxa (Jost 2006)	3.197	(1.468)	3.372	(1.502)	4.914	(2.711)	6.055	(1.473)	3.359	(1.518)
mud content [%]	32.74	(17.35)	59.42	(16.84)	6.33	(6.29)	25.53	(38.37)	17.40	(17.34)
sand content [%]	65.15	(18.92)	35.86	(14.38)	70.24	(8.92)	51.86	(29.11)	78.59	(17.16)
gravel content [%]	0.34	(0.30)	2.62	(8.07)	3.09	(1.94)	15.42	(17.65)	1.09	(1.36)
shell debris content [%]	1.78	(1.62)	2.10	(1.32)	20.34	(8.77)	7.18	(5.54)	2.93	(3.09)
depth [m]	25.0	(0)	20.5	(6.0)	13.0	(4.5)	15.0	(4.1)	21.5	(5.2)
dredging days	22.0	(17.7)	1.2	(3.8)	0	(0)	0	(0)	11.8	(21.6)

Community II appeared at stations with high mud content (40% of stations on slightly gravelly sandy mud, 30% on sandy mud, 20% on muddy sand, and 10% on gravelly mud) and was located in the regularly dredged old navigation channel, the south eastern area and at one station (A3) in the south western dredged area (Fig. 2.4b). Beside the mudphil amphipod *Corophium volutator*, the opportunistic spionids *Pygospio elegans* and *Polydora cornuta*, the bivalve *Petricolaria pholadiformis*, and juvenile mussels of the family Mytilidae characterised this community (Table 2.6).

Community III occurred in the north eastern area on elevated contents of shell debris at slightly gravelly sand (60%) and at gravelly muddy sand (40%; Fig. 2.4b, Table 2.5). The polychaetes *Scoloplos (Scoloplos) armiger*, *Pygospio elegans*, *Nephtys caeca*, *Gattyana* cf. *cirrrosa*, *Nephtys* spp. juv., and *Eteone longa* were characteristic taxa of this community, as well as Anthozoa (Table 2.6).

Community IV showed the highest mean taxa number, mean abundance, and biodiversity in the study area (Table 2.5). Similarly to community III, community IV was situated in the north eastern area (Fig. 2.4b). It appeared associated with mixed sediments (sand with high gravel or high mud content; Table 2.5) at slightly gravelly sandy mud (E6), slightly gravelly sand (E8), gravelly sand (G7) and muddy sandy gravel (H6; Fig. 2.4). Community IV was characterised by Anthozoa, the polychaetes *Pygospio elegans*, *Scoloplos (Scoloplos) armiger*, *Nephtys caeca*, *Gattyana* cf. *cirrrosa*, the bivalves Mytilidae spp. juv. and *Bivalvia* spp. juv., the amphipods *Caprella* sp., and *Dyopedos monacanthus* and the oligochaete *Tubificoides benedii* (Table 2.6).

Community V was also found on mixed sediments (41.9% on slightly gravelly sand, 29.0% on muddy sand, 19.4% on slightly gravelly muddy sand, 3.2% on gravelly muddy sand, 3.2% on slightly gravelly sandy mud, and 3.2% on sand) mainly in the western area, which was dredged for the JWP, and in the southern transects A and B (Fig. 2.4b). In contrast to community IV, mean taxa number, mean abundance, and biodiversity were low in community V (Table 2.5). *Scoloplos (Scoloplos) armiger* and the bivalve *Macoma balthica* dominated community V, which was also characterised by juvenile Mytilidae, the mud snail *Peringia ulvae*, and the polychaetes *Pygospio elegans* and *Nephtys hombergii* (Table 2.6).

Table 2.6 Characteristic macrofauna taxa with mean abundance of not transformed data and mean similarity and percentage of their contribution to the community, based on Bray-Curtis similarity, using fourth-root-transformed taxa abundance data

	mean abundance	mean similarity	contribution %
community I		4.07	
<i>Petricolaria pholadiformis</i>	0.3	4.07	100
community II		49.19	
<i>Corophium volutator</i>	26.6	19.94	40.53
<i>Pygospio elegans</i>	8.2	14.88	30.25
Mytilidae sp. juv.	1.1	5.8	11.79
<i>Petricolaria pholadiformis</i>	1.1	3.25	6.6
<i>Polydora cornuta</i>	24.7	2.54	5.15
community III		49.36	
<i>Scoloplos (Scoloplos) armiger</i>	6.8	11.00	22.28
<i>Pygospio elegans</i>	23.7	9.89	20.03
<i>Nephtys caeca</i>	2.3	8.06	16.33
<i>Gattyana cf. cirrhosa</i>	1.1	6.92	14.02
Anthozoa	5.7	6.54	13.25
<i>Nephtys spp. juv.</i>	0.5	1.88	3.82
<i>Eteone longa</i>	0.5	1.67	3.39
community IV		47.4	
Anthozoa	32.3	7.47	15.77
<i>Pygospio elegans</i>	12.5	5.97	12.6
Mytilidae sp. juv.	45.9	5.96	12.58
<i>Scoloplos (Scoloplos) armiger</i>	5.1	5.35	11.3
<i>Caprella sp.</i>	36.0	4.46	9.41
<i>Nephtys caeca</i>	0.8	3.8	8.01
<i>Gattyana cf. cirrhosa</i>	8.3	3.1	6.55
<i>Bivalvia spp. juv.</i>	1.1	2.76	5.82
<i>Tubificoides benedii</i>	3.5	1.31	2.77
<i>Dyopededos monacanthus</i>	2.2	1.12	2.35
community V		31.32	
<i>Scoloplos (Scoloplos) armiger</i>	2.0	13.01	41.52
<i>Macoma balthica</i>	3.3	9.38	29.95
Mytilidae sp. juv.	1.4	2.24	7.16
<i>Peringia ulvae</i>	2.9	2.06	6.58
<i>Pygospio elegans</i>	0.3	1.24	3.97
<i>Nephtys hombergii</i>	0.3	0.95	3.02

2.5.4 Comparison of spatial patterns

The RELATE routine determined a low, but significant similarity between the macrofauna abundance and the 10 acoustic classes (Rho = 0.093; $p = 0.008$). The similarity between macrofauna abundance and the sediment classes was higher and also significant (Rho = 0.211; $p = 0.001$). In contrast, RELATE revealed no significant similarity between the patterns of sediments and the acoustic classification (Rho = -0.007; $p = 0.496$). Nevertheless Fig. 2.6 shows some trends in the sediment distribution per acoustic class. In the area, which was dredged for the JWP, classes A and B were mainly characterised by sand. In class D, muddy sand prevailed. Sandy mud characterised class E. Class F comprised an area in front of the JWP bulkhead and the old navigation channel and the sediments in the diagram aligned mainly on the sand-mud axis, only at one station (C4) gravelly mud was detected. In contrast, the sediments in the undisturbed north-eastern area (class I) aligned mainly along the sand-gravel axis. The undisturbed south-eastern area (class C) contained muddy sand and sandy mud.

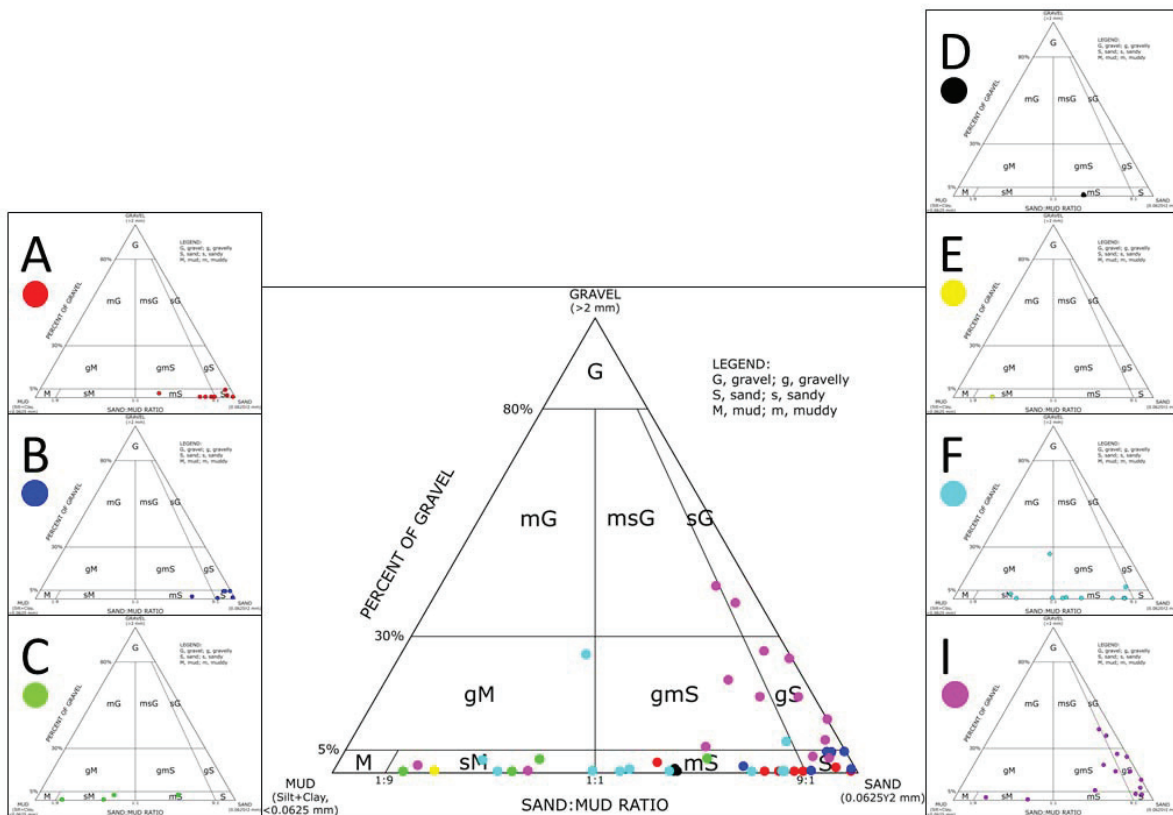


Figure 2.6 Sediment distribution per hydroacoustic class in triangles according to Folk 1954

2.5.5 Relationship between environmental variables and macrofauna community structure

Differences in the spatial distribution of macrofauna communities were best explained by the correlation with the number of days after the last dredging/dumping activity for the JWP (Table 2.7), followed by sediment characteristics (content of sand, mud and shell debris). High backscatter, depth, low backscatter, and the number of dredging days for the JWP played also a significant role in structuring the macrofauna communities. Medium backscatter and gravel content was less important.

Table 2.7 Results of the multivariate regression analysis (DistLM), environmental variables were analysed individually (marginal test) and sequentially using a stepwise forward selection procedure (R^2 criterion). % Prop. is the proportion of variance in macrofauna taxa explained by that variable. Significant (<0.05) values are indicated in bold (“days after” means the number of days after the last dredging/dumping activity for the JWP)

Environmental variables	Marginal tests			Environmental variables	Sequential tests			
	Pseudo-F	p	% Prop.		R^2	Pseudo-F	p	% Prop.
days after	6.2089	0.001	10.49	sand content	0.13	5.8128	0.001	9.76
sand content	6.0364	0.001	10.23	days after	0.30	3.5284	0.002	5.18
mud content	5.3962	0.001	9.24	shell debris content	0.23	3.3427	0.001	5.15
shell debris content	4.3442	0.001	7.58	mud content	0.18	3.1893	0.001	5.14
high backscatter	4.2593	0.001	7.44	depth	0.33	2.4501	0.006	3.49
depth	3.5748	0.001	6.32	gravel content	0.03	1.6134	0.113	2.95
low backscatter	2.5586	0.011	4.61	low backscatter	0.36	1.9950	0.030	2.78
dredging days	2.0404	0.027	3.71	high backscatter	0.40	1.5750	0.109	2.15
medium backscatter	1.6726	0.106	3.06	medium backscatter	0.38	1.3236	0.202	1.83
gravel content	1.6134	0.095	2.95	dredging days	0.24	0.9233	0.531	1.42

The db-RDA-plot (Fig. 2.7) confirms these results on community scale and shows that communities I and V align at the axes of sand, dredging days and depth. In contrast, mud content was the most important structuring factor for community II. Communities III and IV coincided with elevated contents of gravel and shells and high backscatter. In total, the degree of variation explained by these environmental variables was rather low, at 40% ($R^2 = 0.39853$).

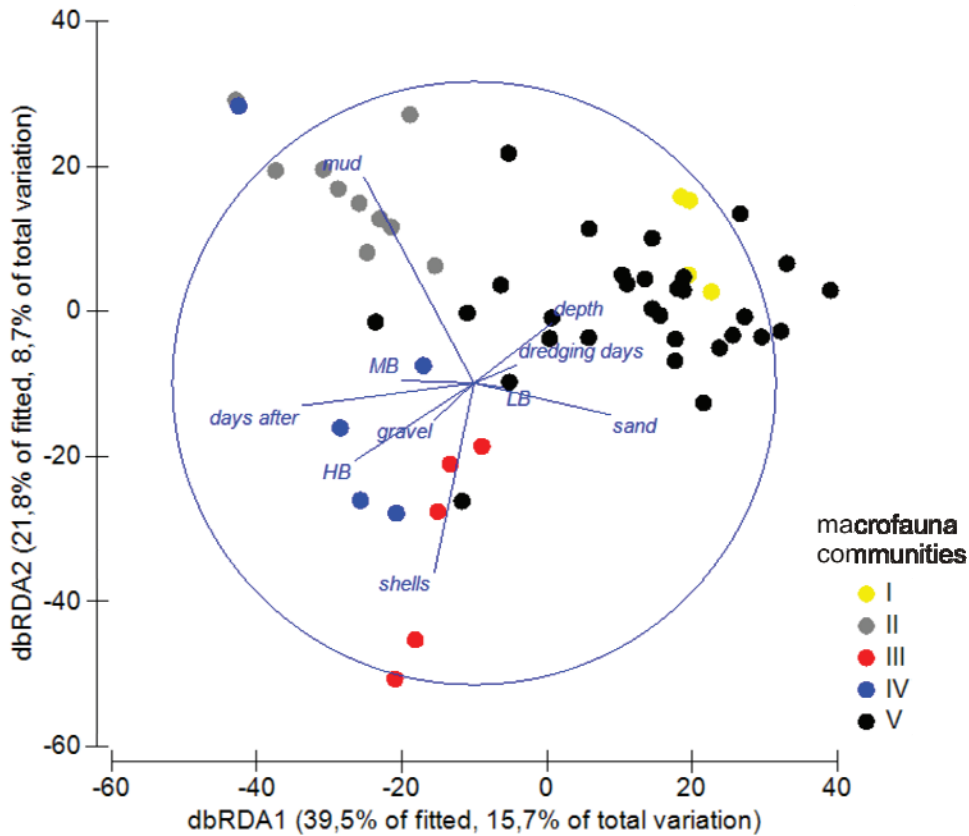


Figure 2.7 dbRDA plot representing the model of spatial variation in macrofauna community structure and its relationship to environmental parameters (“days after” means the number of days after the last dredging/dumping activity for the JWP; HB = high backscatter, MB = medium backscatter, LB = low backscatter)

2.6 Discussion

The study area in the Inner Jade is a very heterogeneous environment. The western part and the old navigation channel are anthropogenic disturbed areas due to the conducted dredging activities, while the eastern part is relatively undisturbed. Many studies demonstrated that acoustic seabed classification using SSS is a suitable tool for the detection of benthic habitats in various environments (Brown et al. 2004b, Ehrhold et al. 2006, Zajac et al. 2003, Franklin et al. 2003, Brown and Collier 2008). However, in such a heterogeneous area as the Inner Jade benthic habitat mapping is a challenge.

Brown et al. 2004a described the problem of generalization (lumping) versus separation (splitting) of acoustic classes in a heterogeneous study area. The high degree of sediment heterogeneity was problematic for the identification of discrete boundaries between the physical habitats (Brown et al. 2004a). The acoustic classification reflected various dredge marks in the western area, which was dredged for the JWP (classes B, E, F, G, H, J) and in the regularly dredged old navigation channel (class F). Only in the western classes A and D

relevant seabed features were absent. In contrast, in the undisturbed eastern area (classes C and I) natural bedforms dominated, which were already reported by Capperucci and Bartholomä (2012) and Kubicki and Bartholomä (2011). Thus, the split classification represented the dredge marks and natural bedforms, but not the full heterogeneity of sediments in the Inner Jade.

2.6.1 Hydroacoustic classification versus sediment distribution

Strong links between sediments and acoustics have been demonstrated, but the relationship between sediment and backscatter is not always clear (Ehrhold et al. 2006). Sedimentological factors (e.g. grain size, volumetric heterogeneity, fine-scale roughness or surface sediment) and significant slope variation may play an important role in the acoustic response (Urick 1983). In this study, low backscatter intensities (class A) were detected in areas, where muddy sand and slightly gravelly sand dominated in front of the bulkhead and in the southern area. In contrast, shells are known as strong and characteristic acoustic reflectors (Wienberg and Bartholomä 2005), therefore the north eastern area was clearly identifiable as high backscatter region (class I). The medium backscatter classes (B-H) were dominated by various sediments (slightly gravelly sand, sandy mud, muddy sand, slightly gravelly sandy mud). Thus, no significant relationship between the acoustic classification and the sediment classes could be expected in this heterogeneous study area. Brown and Collier (2008) concluded that in special environments it will not be possible to extrapolate substrate maps into habitat maps based on acoustic signatures. Due to the high anthropogenic impact in combination with natural variability the Inner Jade seemed to be an example for such a certain environment.

2.6.2 Hydroacoustic classification and sediments versus macrofauna community structure

The low, but significant correlation between the resemblance matrices of the acoustic classification and the macrofauna community structure stressed the heterogeneity in the Inner Jade. In this study, the low average similarity of macrofauna communities (4-49%, Table 2.6) indicated a high level of spatial heterogeneity also within the species distribution. This spatial heterogeneity of species was probably linked to the high heterogeneity of sediments (Brown et al. 2004a) as indicated by the low, but significant relationship between the macrofauna community structure and the 10 sediment classes. Markert et al. (2015b) found also a high

heterogeneity in the sediment composition and macrofauna community structure in the shore-face connected ridges north of the island Spiekeroog in the German Bight of the southern North Sea. The authors could explain the small scale spatial distribution of the macrofaunal affinity groups by a heterogeneous surface sediment pattern resulting from local hydrodynamics, which also influences the food availability. However, only few taxa with known sediment preferences were characteristic taxa in the Inner Jade. These were Anthozoa which settle on gravel and shells in the undisturbed north-eastern area (communities III and IV). In contrast, *Corophium volutator* and *Petricolaria pholadiformis* prefer fine sediments (Fenchel et al. 1975; Tebble 1976) and were found in the regularly dredged old navigation channel and at some stations in the undisturbed south-eastern area (communities I and II). *Scoloplos (Scoloplos) armiger* (communities III, IV, V) is more cosmopolitan without a real sediment preference (Coosen et al. 1994) and the opportunist *Pygospio elegans* (communities II, III, IV, V) has also a wide habitat tolerance (Bolam and Fernandes 2003). Therefore, these taxa cannot be used as indicators for a particular sediment type, but probably for tolerance of disturbance. The impoverished macrofauna abundance in the areas, which were dredged for the JWP, was most likely a result of the physical disturbance by the conducted dredging activities and not on sedimentary characteristics of the bottom. In general, the macrofauna data proofed that quick re-colonisation after the cessation of dredging activities is possible in highly dynamic areas (Borja et al. 2010), such as the Inner Jade. Nevertheless, community V showed still the characteristics of an early succession state (low taxa number, low abundance and dominance of cosmopolitan and opportunistic taxa).

2.6.3 Environmental factors structuring the macrofauna communities

The number of days after the last dredging/dumping activities for the JWP was the most important parameter structuring the variability of macrofauna communities in the Inner Jade, followed by sediment characteristics (content of sand, mud and shell debris). Depth, high and low backscatter grey values, and dredging intensity (expressed as the number of dredging days for the JWP) played also a significant role. Gravel content was less important, because only community IV appeared on undisturbed stations with elevated gravel content. Community V was the biggest group and occurred mainly in the area, which was dredged for the JWP, and which was also the deepest site of the study area and was dominated by sand. Community II showed an affinity to elevated mud contents, which mainly prevailed in and close to the old navigation channel. In contrast, the spatial distribution of community III was

best explained by the presence of shell debris in the undisturbed north-eastern area. However, the total degree of variation explained by all these variables was rather low, at 40%, indicating that there were additional forces active in the study area.

In the adjacent Jade Bay, Schückel et al. (2015) found that the species composition was best explained by the variability of tidal current velocity and depth, followed by sediment characteristics (mud, total organic carbon, gravel and median grain size). Schückel et al. (2015) could also only explain 30% of the total variability in the macrofauna community structure by using these natural parameters. Therefore the authors suggested that variables related to food availability (chlorophyll a content), predation or topographical characteristics could be responsible for the unexplained variability. Additionally, the unknown dredging intensity in the old navigation channel in the Inner Jade could be helpful information to explain the re-colonisation in that area.

2.7 Summary

The acoustic classification reflected the dredge marks and natural bedforms, but not the full heterogeneity of sediments in the Inner Jade. Thus, this detailed classification approach was successful in identifying anthropogenic disturbance at the seabed and the mapping of natural bedforms. The acoustic classification failed to distinguish two communities in the undisturbed area. According to the different dredge marks, more acoustic classes in the disturbed area were generated than macrofauna communities were present. Thus, there were no strong links between the geological, biological and hydroacoustic patterns. Differences in the spatial distribution of macrofauna communities were best explained by the number of days after the last dredging/dumping activity, followed by sediment characteristics. Depth, backscatter grey values, and the number of dredging days played also a significant role as structuring force.

2.8 Acknowledgements

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3 Benthic biodiversity changes in response to dredging activities during the construction of a deep-water port

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3.1 Abstract

During the construction of a deep-water port (JadeWeserPort), bathymetry, sediment distribution and macrofauna community structure were studied in the Inner Jade, a highly anthropogenically impacted tidal channel located in the southern North Sea. In order to assess the effects of additional disturbance by dredging activities, macrofaunal community compositions between 2002 (before the construction work had begun) and 2010 (during the final construction phase) were compared. The sand extraction for land reclamation and the redirection of the fairway changed the bathymetry markedly. While the old fairway in the centre of the study area remained mud dominated, a general increase in coarser sediments was detected in 2010. The dynamic nature of the study area in combination with the direct and indirect effects of dredging increased bathymetric heterogeneity (measured by singlebeam (2002) and multibeam (2010) echo-sounder). In 2010, the macrofauna community structure roughly resembled the different categories of dredging activities. The most recently dredged north-western area was inhabited by a community, which was different from the community in the regularly dredged old fairway. Both were different from the community in the north-eastern non-dredged area. In the southern area and in the transition areas between the other three communities a fourth community was found. A general increase of macrofaunal abundance and taxa number was observed in 2010, with the exception of the recently dredged area. The structure of the macrofauna community during the port construction phase seemed to be determined by secondary dispersal of the dominant taxa and re-colonisation by highly mobile and opportunistic species.

3.2 Keywords:

JadeWeserPort, sediment extraction, benthos, physical disturbance, re-colonisation

3.3 Introduction

Human use of coastal regions has a long history and various anthropogenic effects on the marine ecosystems have been documented (Halpern et al. 2008). In particular, the North Sea is highly frequented as a provider of food, energy and other resources and is used as a waterway for freight transport from all over the world (Lozán et al. 2003). The sustainable use of marine resources requires research of natural and anthropogenically induced changes in this already highly impacted ecosystem.

Macrofauna communities seem to be primarily determined by the substrate type (Greene et al. 1995; Auster and Langdon 1999), but hydrodynamically mediated food availability also plays a major role in their distribution, structure, and diversity (Rosenberg 1995; Pearson 2001; Wieking and Kröncke 2005; Kröncke 2006). Thus, the substrate in relation to the food availability determines to a large extent the occurrence of benthic species and may modify the recovery from disturbance. Many species living in hydrodynamically exposed sandy habitats, exhibit behaviors and feeding modes that enable them to survive daily tidal scouring events (Gorzelay and Nelson 1987; Reiss and Kröncke 2001; Nehmer and Kröncke 2003). Conversely, species found in low-energy muddy habitats are adapted to low oxygen, hydrogen sulphide enriched environments (Forbes and Depledge 1994; Reiss and Kröncke 2001; Kröncke et al. 2004). Thus, soft bottom macrofauna community structure is strongly related to both hydrodynamic force and sediment composition (Warwick and Uncles 1980; Roads et al. 1982; Yates et al. 1993). Therefore, macrofauna communities are often used as an indicator of physical disturbance such as dredging and dumping activities (Muxika et al. 2005; Taupp and Wetzel 2013; Whomersley et al. 2008), which affects the hydrodynamic regime as well as the sediment composition.

The impact of sediment extraction (e.g. dredging activities) on macrofauna has been well documented in European waters (e.g. Newell et al. 1998; Sardá et al. 2000; Van Dalfsen et al. 2000; Simonini et al. 2007). Direct effects of sediment extraction can include an initial reduction in species diversity, abundance, and biomass (Sutton and Boyd 2009). Even the areas around the dredging site can be indirectly affected by sediment re-suspension, the release of nutrients and chemicals, and changes in food resources by shifts of plankton bloom seasons (Boyd et al. 2005; Newell et al. 1998; Simonini et al. 2007; Van Dalfsen et al. 2000). Thus, the key question is not whether dredging activities have an impact, but to which extent the affected macrofauna communities can recover (MESL 2007). Although the recovery rates are highly site-specific (Boyd et al. 2004; Cooper et al. 2005; Kenny and Rees 1994; 1996; Kenny et al. 1998), some general principals are well known.

Based on the adaptive strategies of different assemblages and environmental conditions, there is evidence that communities found in hydrodynamically active sandy habitats will recover more quickly following physical disturbance than those found in less energetic muddy environments (Hall 1994; Kaiser 1998; Ferns et al. 2000). The recovery process of a disturbed habitat follows a succession of species composition over time (Pearson and Rosenberg 1978; Zajac et al. 1998). This sequence of colonization and extinction depends on the severity of the disturbance e.g. total or partial biota removal (Pearson and Rosenberg 1978; Gutt and Starmans 2001; Sousa 2001; Valdivia et al. 2005) and the coupling with additional disturbance events (e.g. Cifuentes et al. 2006; Sugden et al. 2007). The size of the patch to be colonized (e.g. Petraitis and Latham 1999; Petraitis and Dudgeon 2004; Norkko et al. 2006) and the seasonal variation in the supply of colonizers (e.g. Morgan 2001) determines the re-colonisation time. Moreover, succession is mediated by biological interactions (e.g. inhibition, facilitation, and tolerance) among early and late colonizing species (Connell and Slayter 1977). Any of these factors can complicate the community response to disturbance. In particular, when dredging activities remove the surface layers of sediments, the remaining substratum may be comprised of a totally different sediment type than the original one and might be unsuitable for re-colonization by the species that previously inhabited the area (Kenny and Rees 1996; Boyd et al. 2005).

However, the generated mosaic of different macrofaunal succession stages integrates spatial and temporal changes in the marine ecosystem (Johnson 1972). Thus, in environmental impact assessments, the macrofauna community composition is used as an essential tool for the evaluation of the status quo of the ecosystem (Warwick 1993, Borja et al. 2013). Knowledge about benthic macrofaunal succession patterns can help to understand the dynamics of community structure and the responses to human induced disturbances (Berlow, 1997). For the improvement of such succession models, an understanding of processes that occur throughout an ongoing disturbance is crucial (Vöge et al. 2008), but the intermediate state is often missing in the standard before/after disturbance analyses.

During the land reclamation for the construction of a deep-water port in the southern North Sea (JadeWeserPort (JWP), Germany), sediments were extracted from the Inner Jade, changing the physical conditions of the local marine environment. The Inner Jade is a naturally dynamic system (Dörjes et al. 1969, Schuchardt et al. 2007). Already by the 1960s, macrofauna community structure and sediment distribution in the Jade were influenced by the local fishery and dredging and dumping activities (Dörjes 1992). Based on differences in macrofauna and sediments between the 1960s and 2002, the western part of the Inner Jade

was classified as a “heavily modified water body” (Schuchardt et al. 2007). In qualitative comparison, one third of the formerly present polychaetes did not appear in 2002 and one third of the polychaetes was not found by Dörjes et al. in the 1960s. Additionally, less bivalves and more mobile crustaceans were detected by Schuchardt et al. in 2002. This altered macrofauna community structure was most likely caused by changes in hydromorphology due to land reclamations, construction of pile founded jetties, and deepening of the old fairway (Schuchardt et al. 2007).

Thus, the overarching aim of the present study was to assess the impact of the dredging and dumping activities for the JWP as additional stressors in the already anthropogenically disturbed Inner Jade. In order to evaluate the status quo of an ecosystem, it is recommended to utilize historical data of the formerly undisturbed state as a reference condition, if there is no pristine area nearby (Borja et al. 2012). Due to the natural and anthropogenically induced heterogeneity in the Inner Jade, the areas adjacent to dredged parts of the study area were not suitable to represent an undisturbed condition and probably also (indirectly) affected by the dredging activities for the JWP. Thus, changes in bathymetry, sediment distribution, biodiversity, taxa number, abundance, and macrofauna community structure were compared between the period before the port construction (2002) and during the final construction phase (2010). An earlier comparison between the 2002 dataset and the historic references study from the 1960s by Dörjes et al. (1969) was carried out by Schuchardt et al. (2007). The specific objectives of the present study were i) to document the physical disturbance caused by the dredging and dumping activities for the JWP and ii) to study the direct and indirect effects of these activities on the spatial distribution of sediments and macrofauna communities.

3.4 Material and methods

3.4.1 Study area

The Inner Jade is a tidal channel in the German Bight of the southern North Sea, which is bordered by the Outer Jade to the North and the Jade Bay to the South. It is classified as an upper mesotidal regime with semi-diurnal tides ranging from 2.8 m at the entrance of the channel in the north to 3.8 m at the Jade Bay in the south (Kubicki and Bartholomä 2011). The eastern channel margin of the Inner Jade is separated from the Weser estuary by a broad

tidal flat area. In March 2008, land reclamation started for the JWP, a deep-water port in the western Inner Jade. For completion in 2012, around 46 million m³ sand was required to create the 360 ha terminal area (Kluth and Ehmen 2010). The study area comprised the subtidal areas around the JWP with the redirected fairway in the Inner Jade between km 14.5 and km 7.1 of the old fairway (Fig. 3.1a).

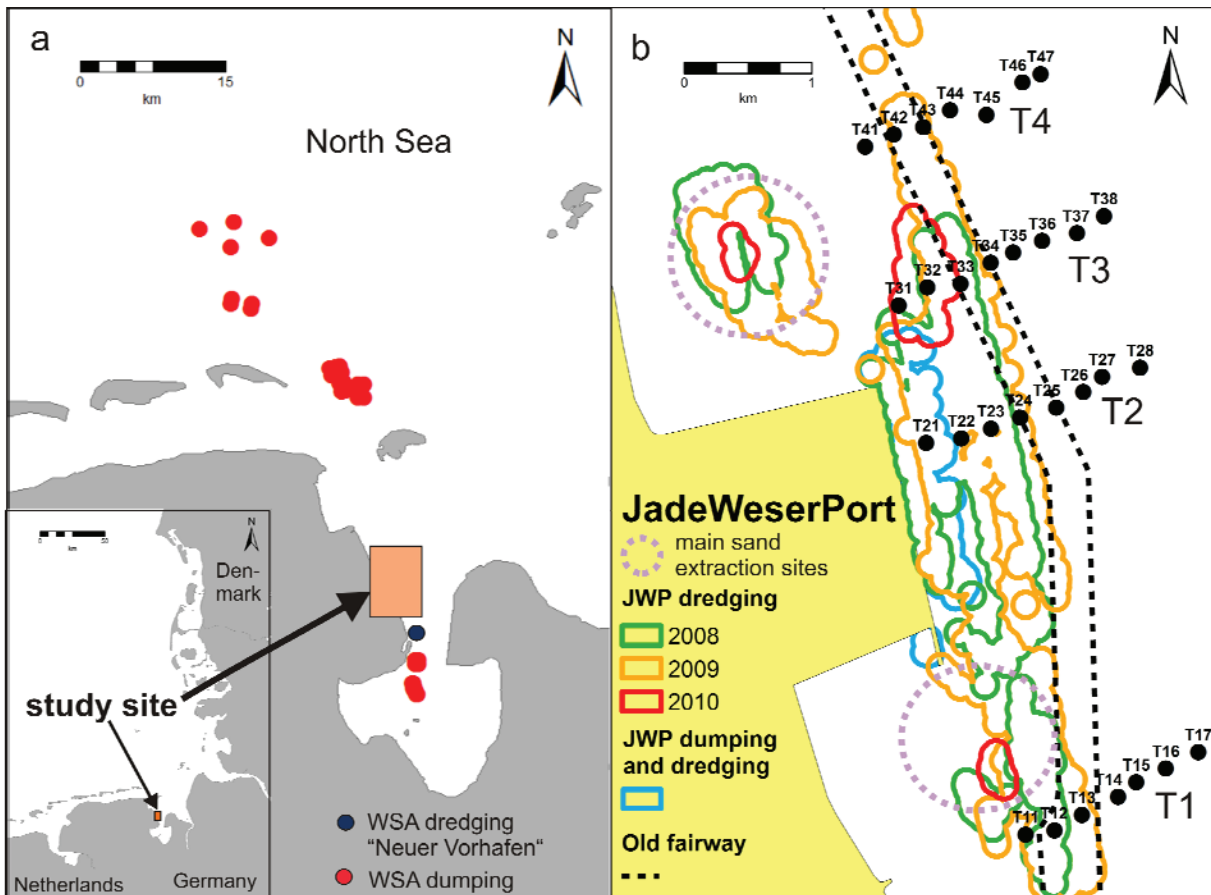


Figure 3.1 Location of a) the study area in the German Bight of the southern North Sea and b) the main features related to the modified coastline (yellow: land), the construction activities for the “JadeWeserPort” (JWP), and the regularly dredged old fairway (pointed lines). Along the transects (T1-T4) the location of the sampling stations (black dots) are shown in relation to the dredging and dumping activities for the JWP

The old fairway in the centre of the Inner Jade connects the harbours of Wilhelmshaven with the North Sea. Its width of 300 m and a minimum guaranteed depth of 20.1 m (referred to the local chart datum, Normalhöhennull (NHN)) are maintained by regular dredging with a hopper suction dredger (Kubicki and Bartholomä 2011). The local harbour “Neuer Vorhafen” at the southern Inner Jade is also periodically dredged (Fig. 3.1a).

Several dumping sites are located in the Outer and Inner Jade (BfG and WSA 2003; Fig. 3.1a). The closest site is located 4.7 km south of the southern border of the study area.

Dumping of fine, mobile sediments (e.g. extracted from the old fairway or the harbour “Neuer Vorhafen”) has potential effects on the sediment distribution in the study area.

In the 1960s, the seafloor of the study area was mainly dominated by medium to fine sand, while finer sediments (silt to silty fine sand) were present on the shallowest slopes of the channel (Dörjes et al. 1969). The Jade channel itself was characterised by medium sand, locally by fine or coarse sand (Dörjes et al. 1969; Irion 1994). At that time, the spatial distribution of the different macrofauna communities in the Jade largely corresponded to the sediment types in the study area (Dörjes et al. 1969). The *Petricolaria pholadiformis* community occurred, where finer sediments prevailed on the shallow slopes of the Jade channel. The *Magelona papillicornis* community appeared in medium sand on the current slopes, whereas the *Ophelia limacina* community was found on the coarser sediments of the Jade channel. Quantitative abundance data from the 1960s were not available.

3.4.2 Dredging and dumping data

For land reclamation sand was mainly taken from two extraction sites, north and south of the new port area (Fig. 3.1b). In order to enable access to the JWP, a new fairway was dredged (Fig. 3.2). Suction and suction cutter dredgers were mainly employed for sand removal. Backhoe dredgers were used for mining compact clay deposits underneath, the “Lauenburger Ton” formation. Since this clay was not suitable for land reclamation, the extracted “Lauenburger Ton” was dumped into the formerly exploited southern sand extraction site (Kluth and Ehmen 2010). Before piling, fine soft material had to be replaced by coarser sediments. Therefore, sand was dumped not only directly in the land reclamation zone, but also in front of the new bulkhead (Fig. 3.1b).

The JadeWeserPort Realization Company provided data on their dredging and dumping activities: position, date, time, and dredging volume (no data for the dumping of “Lauenburger Ton” into the southern pit). Since only midpoint coordinates were given, a buffer of 100 m was created around each dredging and dumping position. These data were merged according to four categories (Fig. 3.1b): dredging and dumping (2008-2010), dredging 2008 (March-December), dredging 2009 (January-December), dredging 2010 (January-May). Within the 100 m radius around each sampling station, all dredging and dumping activities before and during the sampling were summed up. All stations with dredging or dumping activities within the 100 m radius were classified as directly affected by these activities (Table 3.1).

The local harbour authority WSA (Wasser- und Schifffahrtsamt Wilhelmshaven) provided data on the yearly total sediment volumes, that were dredged in the old fairway (between km 8 and km 12) in the years 2000-2002 and 2008-2010.

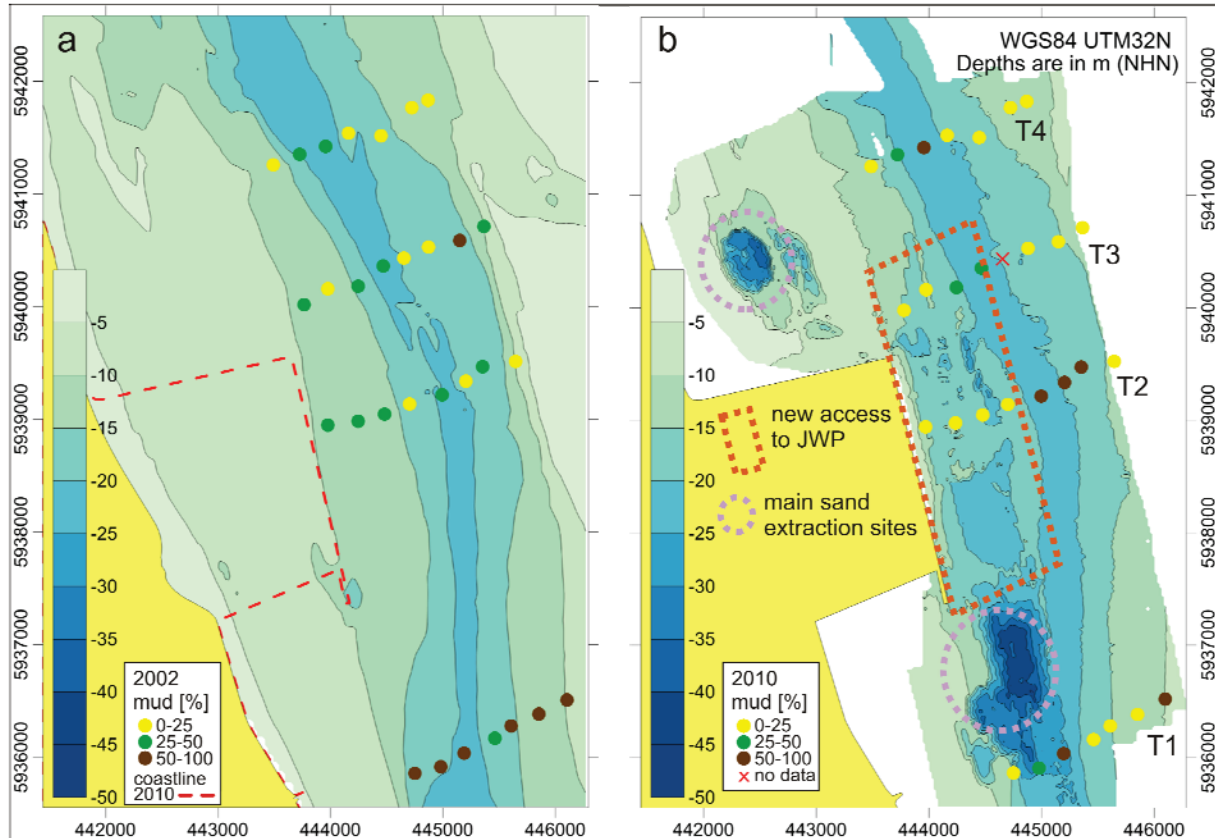


Figure 3.2 Bathymetry of the study area (depths in m referred to Normalhöhennull (NHN)) and mud content (percentage by weight) at the sampling stations in a) 2002 and b) 2010

3.4.3 Bathymetric data

In order to study the changes in seafloor topography between 2002 and 2010, two Digital Terrain Models (DTM) were generated based on bathymetric measurements.

For 2002, data was provided by the federal maritime and hydrographic agency BSH (Bundesamt für Seeschifffahrt und Hydrographie) and the WSA, measured by singlebeam echo-sounder (SBES).

In May 2010, bathymetric data was recorded on board the RV “Senckenberg” by means of a Reson 8125 multibeam 455 kHz echo-sounder (MBES) along 14 main transects parallel to the old fairway (north-south oriented). In order to obtain better coverage, the resulting dataset was combined with MBES data collected on behalf of the JadeWeserPort Realization Company in April 2010.

Both the 2002 and 2010 data were processed by means of Global Mapper 13TM for data cleaning, quality checking and interpolation. Two grid files were generated (25 m grid cell size). Depths were referred to the local chart datum (Normalhöhennull, NHN). The final maps (with 5 m interval contour lines) were generated by means of Surfer 10 of Golden SoftwareTM.

Table 3.1 Areas of interest according to the categories of disturbance in the study area with the involved sampling stations

categories of disturbance	stations
construction works for JWP	(n = 11)
dumping + dredging (2008-2010)	T21
dredged in 2010	T31, T32
dredged in 2009	T12, T13, T21-T24, T32, T33, T42, T43
dredged in 2008	T12, T21-T23, T32, T33
maintenance of the old fairway	(n = 8)
regularly dredged (also before 2002)	T12, T13, T24, T25, T33, T34, T42, T43
non-dredged areas	(n = 17)
	T11, T14-T17, T26-T28, T35-T38, T41, T44-T47

3.4.4 Sampling and sample procedure

The company BIOCONSULT (Bremen) provided data of the sediment and macrofauna distributions in the Inner Jade for April 2002 (Schuchardt et al. 2003). In total, they sampled 30 stations along 4 west-east oriented transects. One sample per station was collected using a 0.1 m² van Veen grab.

From each sample a subsample (approx. 200 ml) was removed for grain size analysis. The remaining sample was washed over a 1 mm mesh and macrofauna was fixed with 70% ethanol. At 3 stations (T17, T33, T41) no macrofauna was found by BIOCONSULT.

The sediment grain size composition for the 2002 sediments was determined by the company BÖL (Bremen) according to DIN 18123 (1983). For this procedure, wet and dry sieving with 6 mesh sizes according to DIN 4022 (1987) were used, after shells > 5 mm were discarded.

In May 2010, a survey was carried out with the RV “Senckenberg”. Sediment and biological samples were collected along 4 transects (T1-T4), matching the previously investigated stations (Fig. 3.1b). A total of 30 stations were sampled twice with a 0.1 m² van Veen grab.

One sample was used to take a subsample (approx. 150 ml) for laboratory grain size analysis. In the laboratories of Senckenberg am Meer the sediment samples were separated into mud fraction (<63 µm) and sand/gravel fraction by wet sieving over 63 µm mesh size. The sand fraction was analysed by means of settling velocity measurements in the MacroGranometer™ settling tube (Brezina 1979). The gravel content (>2000 µm) was determined by dry sieving over a 2000 µm mesh. At one station (T35) no sediment sample was collected for May 2010. Because of the different methods of analyses used by Senckenberg am Meer and BÖL, sediment data was presented as mud content (<63 µm) and sand content (>63 µm and <2000 µm). Only for 2010, gravel content (>2000 µm) was added.

The other sample was sieved over a 1 mm mesh and the retained macrofauna samples were fixed in a 4% buffered seawater formalin solution. Organisms were identified to the lowest taxonomic level possible. After counting, the sorted animals were preserved in 70% ethanol and their biomass (wet weight) was determined to an accuracy of ±0.0001g. Although the lack of replicates has the potential of misinterpretation, only one sample per station could be used to compare the macrofauna abundance with the 2002 dataset (also only one sample per station).

The biological data was taxonomically adjusted to allow for comparison between 2002 and 2010. For some taxa, the taxonomic resolution differed between BIOCONSULT and Senckenberg. As a consequence, taxa belonging to the genera *Ampharete*, *Autolytus*, *Caprella*, *Cheirocratus*, *Ensis* or the families Anoplodactylidae, Mytilidae sp. juv. or the order Anthozoa were all lumped at the genus/family/order level respectively. Hydrozoa, Bryozoa, Balanidae and single large, mobile epifauna were not sampled quantitatively by using the van Veen grab and were excluded from analysis.

3.4.5 Statistical data analyses

The effective number of taxa was chosen as the measure of community diversity, because it provides the true diversity (not the entropy) in units of the number of taxa (Jost 2006). Other diversity indices can easily be converted into this linear number of equally-common taxa, e.g. the exponent of the Shannon-Wiener index gives the effective number of taxa (Jost 2006). The significance of changes in taxa number, abundance and effective number of taxa was tested with one way ANOVA using PAST version 2.17.

Changes in the macrofauna community structure were determined by cluster analyses performed with abundance data from 2002 and 2010 after fourth root transformation using the

PRIMERTM v6 program package. Similarities between sampling sites were calculated with the Bray-Curtis coefficient and interpreted by means of the similarity profile permutation test SIMPROF, which tests the null hypothesis that a specific set of samples, which are not a priori divided into groups, do not differ from each other (Clarke and Gorley 2006). The similarity percentage routine, SIMPER, compares the taxa abundance between the clusters and identified which taxa characterised the different macrofauna communities (Clarke and Warwick 2001). Regarding the most common feeding type of species, they were characterised as omnivores/predators, deposit feeders, and suspension feeders. BIOENV tested for significant Spearman rank correlations (Clarke and Ainsworth 1993) between the community structure in 2010 and the dredging activities for the JWP (number of dredging days), depth or the sediment composition (gravel, sand, and mud content). Therefore the resemblance matrix of macrofauna abundance/biomass was compared with the resemblance matrix of the normalized abiotic variables. The significance of the correlation was determined using a permutation procedure. Results indicated which abiotic variable explained the highest percentage of the variability within the macrofauna dataset in 2010.

The routine RELATE was used to match the resemblance matrices of 2002 and 2010 in order to compare the similarity of patterns in the macrofauna abundances (Clarke and Gorley 2006). The significance of differences between clusters was tested with one-way PERMANOVA (Anderson et al. 2008) using fourth root transformed abundance data. The routine PERMDISP was used for testing the homogeneity of multivariate dispersions from group centroids on basis of the resemblance measure.

In addition, both datasets were combined in one cluster analysis. Following the approach of Kröncke et al. (2011), the similarity of the two corresponding stations was categorised into high (same sub-cluster), medium (same main cluster, but different sub-cluster) and low (different main cluster).

Using ArcMap10TM, GIS (Geographic Information System) maps were generated to visualize the changes in the patterns of macrofauna communities (clusters), taxa number, abundance, biomass, and selected species in relation to the dredging and dumping activities.

3.5 Results

3.5.1 Dredging and dumping

From the start of the construction work for the JWP (March 2008) until the sampling date for this study (May 2010), the dredging activities in the western Inner Jade overlapped (Fig. 3.1b, Table 3.1). Only one station (T21) in front of the bulkhead was affected by dredging and dumping. Two stations (T31, T32) were situated in the recently dredged area. In total, 11 stations were directly affected by dredging for the JWP (Table 3.1). 6 of these 11 stations were located in the regularly dredged old fairway. In 2009, the JadeWeserPort Realization Company extracted about 1.11 million m³ sediment at these 6 stations (according to the dredging data provided by the JadeWeserPort Realization Company).

In total, 8 stations were positioned in the regularly dredged old fairway. In the years 2000, 2001, 2002, and 2008 the volumes of sediment dredged by the WSA were similar with an annual mean of about 2.52 million m³. In 2009 and 2010 less dredging activities by the WSA were necessary for the maintenance of the old fairway (2009: 0.75 million m³ and 2010: 1.23 million m³). Thus, the total annual volume of removed material (1.86 million m³ in 2009) from the old fairway was lower in 2010 before the sampling campaign than in 2002.

All stations east of the old fairway represented the area which was not directly disturbed by the dredging and dumping activities.

3.5.2 Changes in seabed morphology

Despite the different data sources (SBES and MBES), specific morphologies were recognised in both the 2002 and 2010 contour maps (Fig. 3.2). However, as expected, the MBES data displayed a greater amount of details. In particular, the area close to the JWP showed geometries that matched the different dredging phases and corresponded to the new fairway under construction.

The main changes occurred close to the bulkhead and at the two extraction sites. While in 2002 the old fairway was the deepest part of the study area (approximately 20 m; Fig. 3.2a), the sand extraction resulted in two almost 50 m deep pits North and South of the JWP (Fig. 3.2b). The least disturbed environment was the area east of the old fairway, where no significant morphological changes were observed.

3.5.3 Changes in sediment composition and distribution

In 2002, sediments with medium and high mud content were dominant: 12 of 30 stations with 25-50% mud (percentage by weight) and 7 stations with more than 50% mud (Fig. 3.2a). The highest mud content was observed at the southernmost transect (T1), where 6 of 7 stations had a mud content of more than 50%.

In 2010, no sediment sample was collected at one station (T35; Fig. 3.2b). In comparison to 2002, 15 of 29 stations showed a change in sediment composition in 2010. Generally coarser sediments were found in 2010, 19 of 29 stations were classified as sand with low mud content (less than 25% by weight). Higher mud contents were still a specific signature of the old fairway (6 of 8 stations with 25-50% mud and 1 station with more than 50% mud).

In qualitative comparison, transects T1 and T2 were most affected by changes in sediment composition (Fig. 3.2). A reduction in mud content was found at 5 of 7 stations of transect T1 (T11, T12, T14-T16). Along transect T2, coarser sediments were found close to the JWP bulkhead (T21-T23) while mud contents increased further away from the construction site (T25-T27). An increase of coarse material was also observed at transect T3, where 3 of 7 stations showed a reduction of mud content; T31 was also close to the JWP, but T37 and T38 were the easternmost stations of transect T3. The northernmost transect T4 revealed the least changes, with a slight increase in mud content at the station within the fairway (T43).

In 2010, gravel with more than 10% by weight was present at 6 stations (T36-T38, T45-T47) in the north-eastern area (no data of the gravel content in 2002).

3.5.4 Changes in macrofauna diversity and abundance

In 2002, 428 individuals were collected and 31 taxa in total were identified. The samples from 2010 contained 1535 individuals, representing 57 taxa in total (Fig. 3.3).

At the 11 stations which were dredged for the JWP, the mean effective number of taxa decreased, the mean taxa number was similar to 2002, but the mean abundance increased (Table 3.2). These differences were not significant. At only one of the dredged stations (T22) 1160 ind./m² of the mysidacea *Gastrosaccus spinifer* were found in 2010. Even when this station is excluded, the mean abundance of the western dredged area was higher in 2010 than in 2002. At the station directly in front of the bulkhead (T21), which was affected by dredging and dumping activities, the same taxa number and a slight decrease in abundance were found in 2010. Only in the most recently dredged area (T31, T32) both, mean taxa number and mean abundance, were lower in 2010 than in 2002.

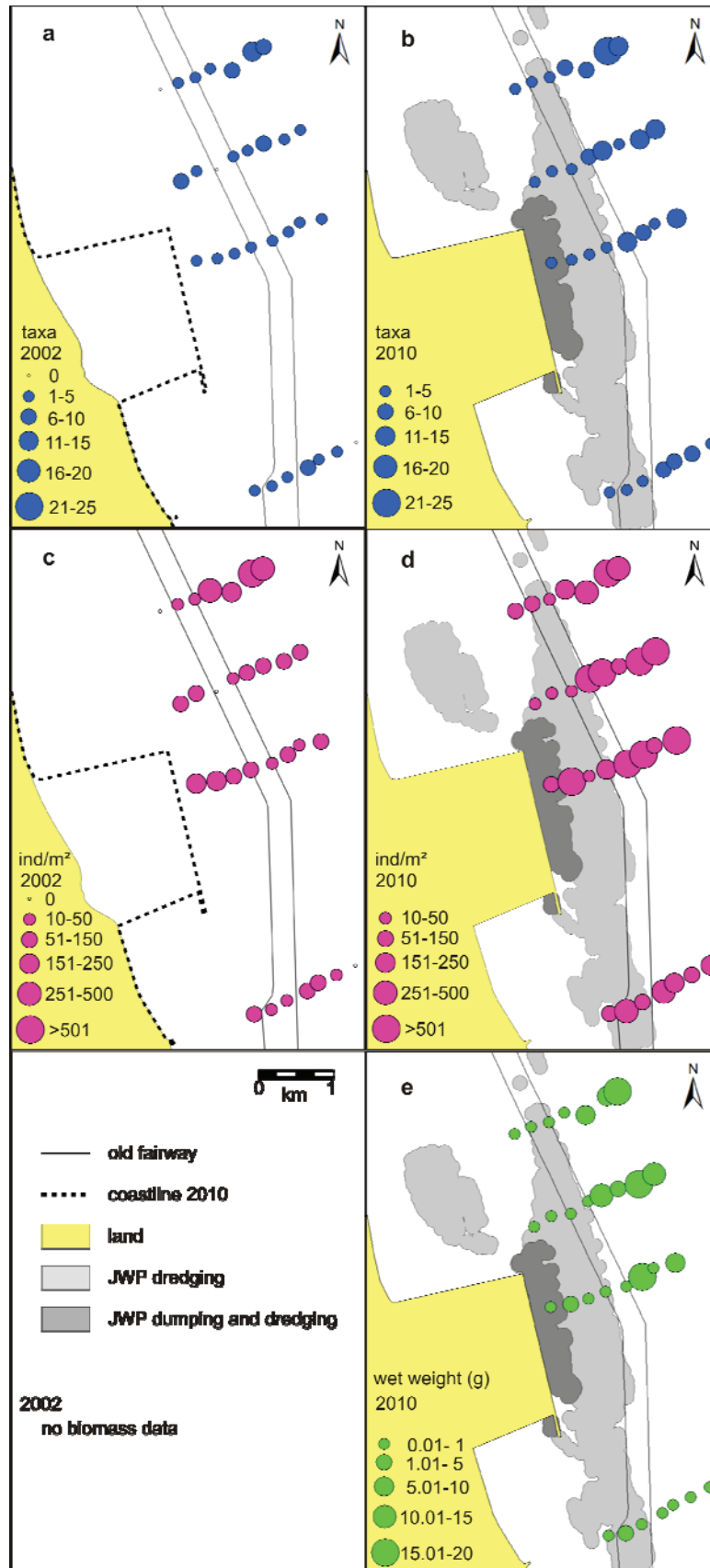


Figure 3.3 Macrofauna taxa number per sampling station (0.1m²) in a) 2002 and b) 2010, abundance of macrofauna (individuals/m²) per sampling station in c) 2002 and d) 2010, and biomass (wet weight in g) per sampling station in e) 2010 (no biomass data for 2002)

Table 3.2 Comparison of the defined areas of interest (see Table 3.1) in 2002 and 2010 referring to the taxa number, macrofauna abundance (individuals/m²), and effective number of taxa given as mean with standard deviation (sd), and the results of the performed ANOVAs; T17, T33, T41 were excluded, because at these stations no macrofauna was found in 2002; at T22 a high number of *Gastrosaccus spinifer* was found in 2010

areas of interest (see Table 1)		taxa number ANOVA					abundance [ind./m ²] ANOVA					effective number of taxa ANOVA					
		mean	(sd)	df	F	p	mean	(sd)	df	F	p	mean	(sd)	df	F	p	
JWP	dumping + dredging 2008-2010 n = 1	2002	5.0									4.1					
		2010	5.0				170.0				130.0		2.8				
JWP	dredged in 2010 n = 2	2002	6.0 (2.8)				135.0 (7.1)				4.8 (3.1)						
		2010	2.5 (0.7)				40.0 (0.0)				2.3 (0.8)						
JWP	dredged 2008-2010 n = 10 (without T33)				1,18	0.257	0.618			1,18	1.048	0.320			1,18	0.512	0.483
		2002	3.8 (2.1)				95.0 (62.2)				3.1 (1.8)						
	n = 9 (without T33,T22)	2010	3.4 (1.3)				208.0 (343.5)				2.6 (0.9)				1,16	0.076	0.786
		2002	3.7 (2.2)		1,16	0.000	1.000	84.4 (55.7)		1,16	0.286	0.600	3.0 (1.8)				
		2010	3.7 (1.1)				102.2 (82.7)				2.8 (0.7)						
		2002	2.4 (1.3)		1,12	5.454	0.038	44.3 (31.5)		1,12	5.242	0.041	2.2 (1.0)			1,12	5.645
old fairway	regularly dredged n = 7 (without T33)	2010	5.7 (3.5)				302.9 (297.1)				3.5 (1.4)						
		2002	4.9 (2.6)		1,28	10.800	0.003	217.3 (317.2)		1,28	4.370	0.046	3.4 (1.2)			1,28	8.770
	non-dredged n = 15 (without T17,T41)	2010	9.5 (4.8)				768.0 (969.8)				5.1 (1.9)						

In the old fairway, mean effective number of taxa, mean taxa number and mean abundance was lowest in 2002, but increased significantly in 2010. In areas that were not dredged the mean effective number of taxa increased in 2010, mean taxa number nearly doubled and a threefold increase in mean abundance was recorded. These differences were significant.

3.5.5 Changes in distribution and abundance of taxa between 2002 and 2010

In Table 3.3 only those taxa are listed which were present at least at 3 stations less or more in 2010 than in 2002, in order to shorten the taxa list of Table 3.3 and to stress the major changes in taxa presence. According to this arbitrary threshold (in total more than 10% change), the presence of only 5 taxa decreased at the 30 stations, the presence of 12 taxa increased in the old fairway, and the presence of 13 taxa increased in the JWP dredged area.

In 2002, a total of 14 taxa were found at the 11 stations that were directly affected by dredging activities for the JWP in 2008-2010. 11 of these 14 taxa were not listed in Table 3.3, because *Bathyporeia elegans*, *Diastylis bradyi*, *Eteone longa*, *Lagis koreni*, *Macoma balthica*, *Retusa obtusa*, *Retusa trunculata*, *Schistomysis spiritus*, *Scoloplos (Scoloplos) armiger*, *Spiophanes bombyx*, and *Tubificoides benedii* showed less than 10% change of their

absence/presence in the study area. These results would not differ much, if a slightly lower/higher threshold was chosen.

Table 3.3 Changes in the presence of all macrofauna taxa, which were found in 2010 at a minimum of 3 stations (10%) less (↓) or more (↑) than in 2002 (30 stations in total). Presence at the stations, which were affected by the dredging activities for the JWP (2008-2010) and in the old fairway, was listed in comparison to the presence at the not dredged stations

Taxa found in 2010 at a minimum of 3 stations with lower (↓) or higher (↑) presence than in 2002 (30 stations in total)	2002 presence (x) in the:			2010 presence (x) in the:		
	area later dredged for the JWP	regularly dredged old fairway	remaining non-dredged areas	area dredged for the JWP	regularly dredged old fairway	non-dredged areas
<i>Abra alba</i>			x			
Bivalvia spp. juv.					x	x
<i>Caprella</i> spp.			x	x	x	x
<i>Corophium volutator</i>				x	x	x
<i>Dyopodos monacantha</i>				x	x	x
<i>Eunereis longissima</i>		x	x			
<i>Gastrosaccus spinifer</i>			x	x	x	x
<i>Gattyana cf. cirrhosa</i>						x
<i>Heteromastus filiformis</i>	x		x			x
<i>Mesopodopsis slabberi</i>				x		x
<i>Monocorophium acherusicum</i>						x
Mytilidae sp. juv.			x	x	x	x
<i>Nephtys caeca</i>			x	x	x	x
<i>Nephtys hombergii</i>	x	x	x	x		x
<i>Nephtys</i> spp. juv.	x	x	x			x
<i>Peringia ulvae</i>				x	x	x
<i>Petricolaria pholadiformis</i>				x	x	x
<i>Photis reinhardi</i>						x
<i>Polydora cornuta</i>				x	x	x
<i>Pontocrates altamarinus</i>				x	x	
<i>Pygospio elegans</i>				x	x	x

3.5.6 Macrofauna community structure in 2002

Already in 2002, the taxa spectrum and the spatial distribution of the characteristic taxa changed markedly since the 1960s (Schuchardt et al. 2007). In particular, the formerly dominant species *Petricolaria pholadiformis*, *Magelona papillicornis*, and *Ophelia limacina* were absent at the 30 stations of the BIOCONSULT study used for this comparison. However, they were present in low abundance at some additionally sampled stations in 2002. The cluster analysis with integrated SIMPROF routine identified only 2 significant clusters ($p < 0.05$) which indicated 2 communities (“A” and “B”) among sampling stations in 2002 (Fig. 3.4a). These communities coincided less with the altered sediment distribution than in the 1960s (Table 3.4).

In the north eastern part, 6 stations with sand and low mud content were clustered within community “A” (2002), which was characterized by Anthozoa, *Scoloplos* (*Scoloplos*) *armiger*, juvenile Mytilidae, and *Gastrosaccus spinifer* (Fig. 3.4a,c, Tables 3.4, 3.5). While community “A” (2002) was dominated by omnivores, in community “B” (2002) deposit

feeders were the most abundant feeding type (Fig. 3.5). Community “B” (2002) represented the remaining 21 stations and was found on various sediments with low to high mud content (Fig. 3.4a,c, Table 3.4). The characteristic taxa were the polychaetes *Nephtys hombergii*, juvenile *Nephtys* spp., *Scoloplos (Scoloplos) armiger* and the bivalve *Macoma balthica* (Table 3.5). The mean abundance of this community was lower than in all communities in 2010 (Table 3.4).

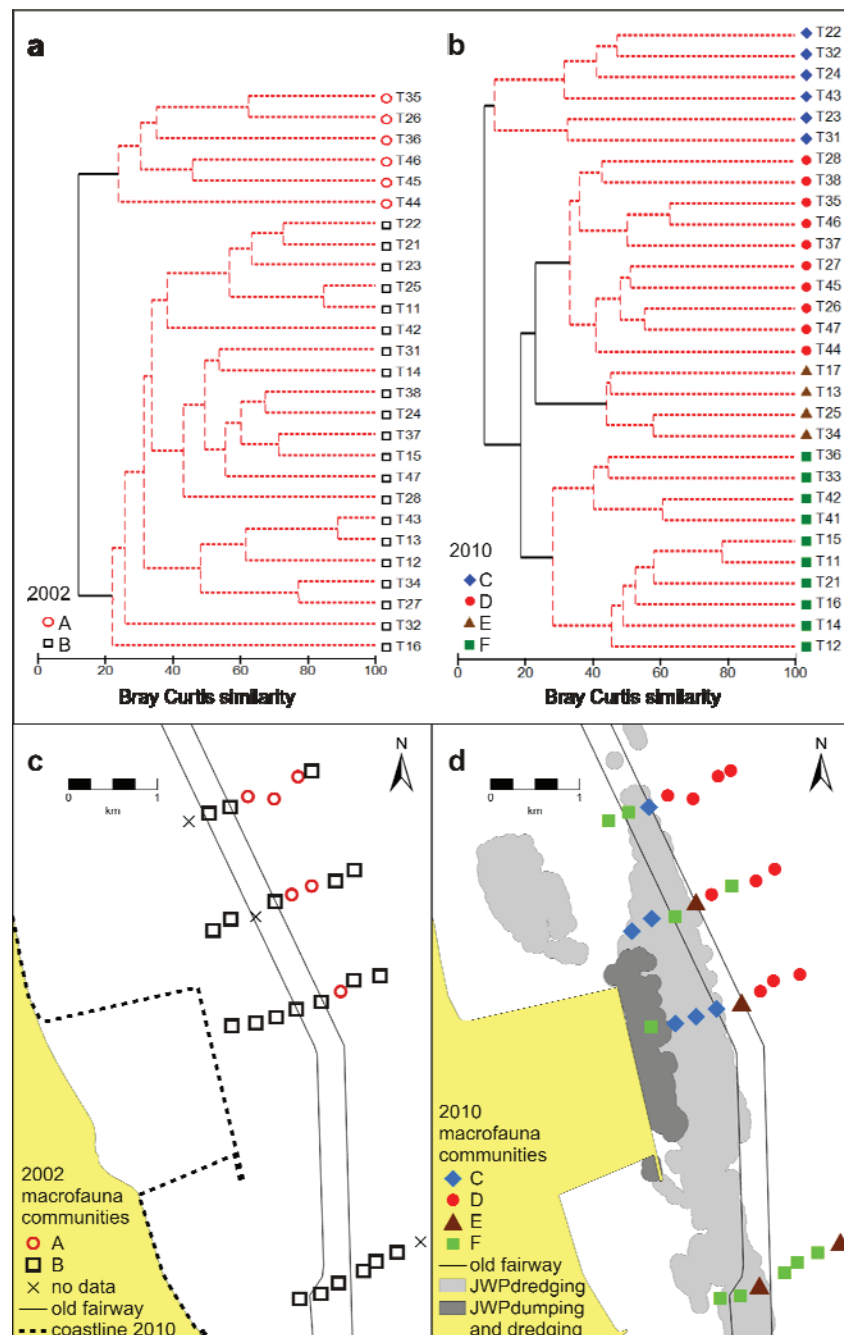


Figure 3.4 Cluster analyses of macrofauna data in a) 2002 and b) 2010, based on Bray-Curtis similarity, using fourth-root transformed taxa abundance data, black lines indicate the significantly different cluster according to the SIMPROF test ($p < 0.05$), and the concerning spatial alignment of the macrofauna communities in c) 2002 and d) 2010 in the study area

Table 3.4 Macrofauna communities of 2002 and 2010 with sediment categories at the concerning stations, total macrofauna taxa number per community, and macrofauna taxa number per station (0.1 m²), abundance (individuals/m²), and the diversity index effective number of taxa given as mean with standard deviation (sd)

macrofauna community	n	mud content			gravel >10%	taxa in total	taxa per station (0.1m ²)	abundance [ind./m ²]		effective number of taxa	
		0-25%	25-50%	50-100%				mean	(sd)	mean	(sd)
A (2002)	6	6	0	0	no data	22	6.0 (3.0)	37.0	(47.0)	3.7	(1.5)
B (2002)	21	4	11	6	no data	19	4.0 (2.0)	10.0	(8.0)	2.7	(1.5)
C (2010)	6	5	0	1	0	10	3.0 (1.0)	25.0	(45.0)	2.2	(1.5)
D (2010)	10	7	0	2	5	45	11.0 (5.0)	107.0	(108.0)	4.9	(1.5)
E (2010)	4	0	1	3	0	16	7.0 (4.0)	45.0	(32.0)	4.0	(1.2)
F (2010)	10	7	3	0	1	18	5.0 (2.0)	14.0	(10.0)	3.0	(1.8)

3.5.7 Macrofauna community structure in 2010

The macrofauna community structure in 2010 was clearly different from the macrofauna spatial distribution maps generated in the 1960s by Dörjes et al. (1969). The cluster analysis with integrated SIMPROF routine revealed 4 significant communities in 2010 (“C”, “D”, “E”, “F”; $p < 0.05$; Fig. 3.4b). This community structure provided a different pattern in the Inner Jade than in the 1960s and were dominated by different taxa (except for *Petricolaria pholadiformis* in community E”). In general, deposit feeders dominated the macrofauna communities in 2010 and only few suspension feeders were found (Fig. 3.5).

In the western dredged area, including the two recently dredged stations, community “C” (2010) exhibited a low taxa number (Table 3.4) at mainly sandy sediments. Characteristic species were *Macoma balthica*, *Gastrosaccus spinifer*, and *Pontocratus altamarinus* (Table 3.5).

Community “D” (2010) was situated in the north eastern part, which was not dredged for the construction works (Fig. 3.4d). Mainly sandy sediments, partly with relatively high gravel content (Table 3.4), and the highest mean biomass of the study area (10.1 ± 6.8 g; Fig. 3.3) were found in this area. Like community “A” (2002), community “D” (2010) was dominated by Anthozoa (Table 3.5). A relatively high number of accompanying species such as juvenile Mytilidae, *Pygospio elegans*, *Scoloplos (Scoloplos) armiger*, *Gattyana cf. cirrhosa*, *Caprella* sp., *Monocorophium acherusicum*, and *Nephtys caeca* led to the highest diversity of the study area in community “D” (2010) (Table 3.4). In community “D” (2010) omnivores occurred in similar numbers as deposit feeders.

Community “E” (2010) was mainly located within the old fairway (Fig. 3.4d) and characterised by medium to high mud content (Table 3.4). The amphipod *Corophium*

volutator dominated this community and *Caprella* sp., juvenile Mytilidae, the spionids *Pygospio elegans* and *Polydora cornuta*, and the bivalve *Petricolaria pholadiformis* were discriminating species (Table 3.5).

Table 3.5 Characteristic macrofauna taxa in a) 2002 and b) 2010 with mean abundance of not transformed data and mean similarity and percentage of their contribution to the community, based on Bray-Curtis similarity, using fourth-root transformed taxa abundance data

a)	2002	mean abundance	mean similarity	contribution %
community "A"				
			32.01	
	<i>Scoloplos (Scoloplos) armiger</i>	5.2	14.88	46.49
	Anthozoa spp.	16.0	10.54	32.92
	Mytilidae sp. juv.	2.3	3.13	9.78
	<i>Gastrosaccus spinifer</i>	0.3	1.23	3.85
community "B"				
			36.15	
	<i>Nephtys hombergii</i>	1.7	12.85	35.54
	<i>Nephtys</i> spp. juv.	2.1	9.78	27.04
	<i>Macoma balthica</i>	1.5	8.39	23.22
	<i>Scoloplos (Scoloplos) armiger</i>	2.3	3.30	9.13
b)	2010	mean abundance	mean similarity	contribution %
community "C"				
			22.67	
	<i>Gastrosaccus spinifer</i>	22.5	14.86	65.55
	<i>Pontocrates altamarinus</i>	0.5	5.39	23.76
	<i>Macoma balthica</i>	0.5	2.42	10.69
community "D"				
			37.87	
	Anthozoa spp.	19.3	8.25	21.78
	Mytilidae sp. juv.	26.2	7.89	20.83
	<i>Pygospio elegans</i>	15.4	6.78	17.90
	<i>Scoloplos (Scoloplos) armiger</i>	4.4	5.43	14.34
	<i>Gattyana cf. cirrhosa</i>	4.3	2.11	5.56
	<i>Caprella</i> spp.	21.5	1.78	4.70
	<i>Monocorophium acherusicum</i>	0.7	1.30	3.43
	<i>Nephtys caeca</i>	0.8	1.26	3.32
community "E"				
			46.42	
	<i>Corophium volutator</i>	19.0	18.74	40.37
	<i>Pygospio elegans</i>	7.0	7.33	15.79
	<i>Petricolaria pholadiformis</i>	1.0	6.80	14.66
	Mytilidae sp. juv.	2.5	5.06	10.91
	<i>Caprella</i> spp.	1.0	4.57	9.85
community "F"				
			38.00	
	<i>Scoloplos (Scoloplos) armiger</i>	3.7	14.89	39.18
	<i>Macoma balthica</i>	3.0	10.39	27.34
	Mytilidae sp. juv.	1.9	7.08	18.62
	<i>Peringia ulvae</i>	2.1	3.22	8.47

Community “F” (2010) was spread over the non-dredged eastern as well as in the dredged western areas (Fig. 3.4d), mainly at sandy sediments (Table 3.4). Characteristic species were *Scoloplos (Scoloplos) armiger*, *Macoma balthica*, *Peringia ulvae*, and juvenile Mytilidae (Table 3.5).

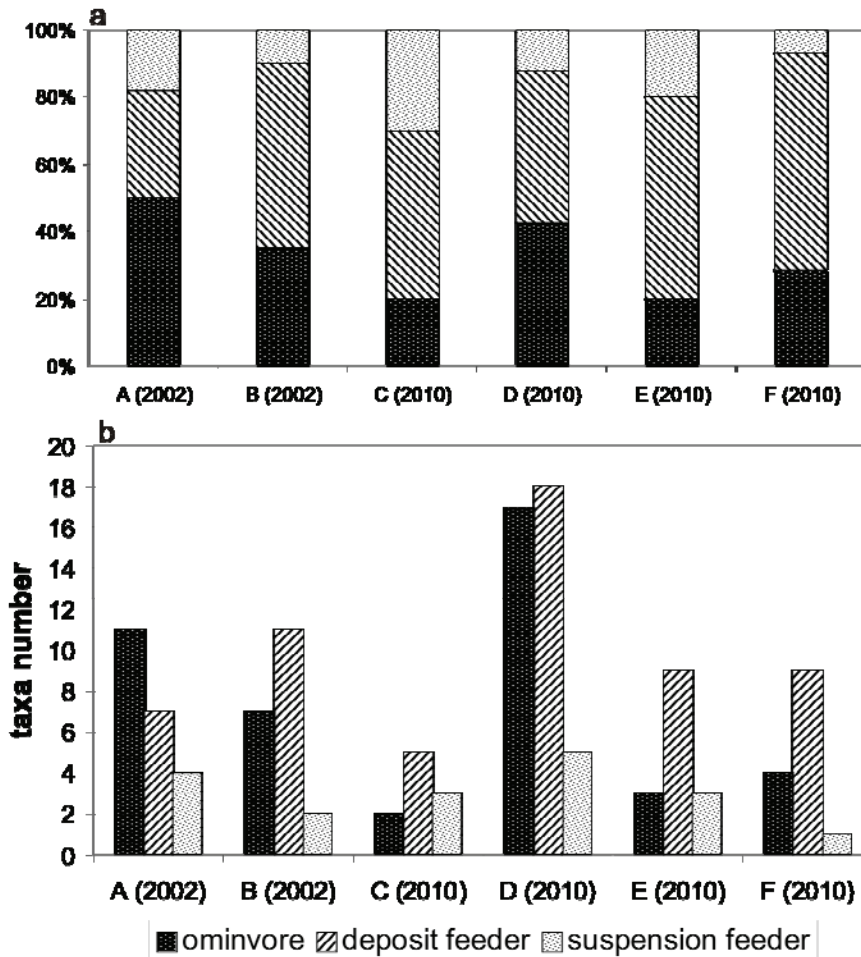


Figure 3.5 Relative and absolute dominance of the different feeding types in the macrofauna communities A-F

The community structure in 2010 was best explained by the dredging intensity of the JadeWeserPort Realization Company, although the correlation factors calculated by BIOENV ($p = 0.01$) revealed only a weak correlation between the macrofauna abundance data from 2010 and the number of JWP dredging days. Only about 36% of the variability within the resemblance matrix of the macrofauna abundance was explained by the number of JWP dredging days (Table 3.6). However, depth, gravel content, sand content, mud content, and the different combinations of these parameters correlated even less with the community structure in 2010. In contrast, macrofauna biomass correlated best with gravel content (Table 3.6).

Table 3.6 Results of the BIOENV analysis with fourth-root transformed macrofauna abundance and biomass data of 2010 and normalized abiotic variables

variables used for BIOENV analysis with macrofauna data 2010	df	abundance		biomass	
		%	p	%	p
number of JWP dredging days	11, 348	36.2	0.001	2.8	0.314
sand content (%)	29, 870	17.8	0.013	7.8	0.109
depth (m)	29, 870	10.4	0.116	0.2	0.428
mud content (%)	29, 870	9.3	0.144	10.7	0.053
gravel content (%)	29, 870	3.9	0.309	28.9	0.003

3.5.8 Changes in macrofauna community structure between 2002 and 2010

The RELATE routine determined no significant similarities between the patterns of the macrofauna communities in 2002 and 2010 ($R^2 = 0.0056$; $p = 0.18$). The SIMPROF test for the cluster analysis of the samples from 2002 revealed only two significantly separated clusters on a low similarity level: communities “A” and “B” (Fig. 3.4a,c). Despite equally low similarity levels, four significantly different clusters were found in 2010: communities “C”, “D”, “E”, and “F” (Fig. 3.4b,d). The PERMANOVA revealed significant differences between all the clusters (PERMANOVA main test, $df = 5$, mean squares = 16108, $F = 7.2684$, $p = 0.001$, $p(\text{Monte Carlo}) = 0.001$; Table 3.7). Sample dispersion was only not homogeneous between the groups (C,E). For all other groups PERMDISP generated p -values >0.05 (Table 3.7).

Table 3.7 Results of the PERMANOVA and PERMDISP pairwise test of all macrofauna communities in 2002 and 2010, statistically significant differences ($p < 0.05$) are marked in bold

macrofauna communities	df	PERMANOVA		PERMDISP	
		t	p	t	p
B (2002), A (2002)	25	2.8068	0.001	0.0611	0.960
B (2002), F (2010)	29	2.5975	0.001	0.6239	0.573
B (2002), C (2010)	25	2.5940	0.001	1.0524	0.381
B (2002), D (2010)	29	3.7460	0.001	0.6045	0.560
B (2002), E (2010)	23	3.1856	0.001	1.7883	0.172
A (2002), F (2010)	14	2.0893	0.003	0.4748	0.693
A (2002), C (2010)	10	2.0753	0.004	1.1937	0.350
A (2002), D (2010)	14	1.6856	0.007	0.5613	0.648
A (2002), E (2010)	8	2.5131	0.005	2.2511	0.096
F (2010), C (2010)	14	2.3407	0.001	1.4899	0.197
F (2010), D (2010)	18	2.6083	0.001	0.0746	0.951
F (2010), E (2010)	12	2.6997	0.004	1.3094	0.290
C (2010), D (2010)	14	2.6811	0.001	1.8520	0.130
C (2010), E (2010)	8	2.3058	0.004	2.8722	0.032
D (2010), E (2010)	12	2.1959	0.001	1.8986	0.137

The combined cluster analysis revealed that the similarity between community “A” (2002) and community “D” (2010) was high (Fig. 3.6). In contrast, the majority of stations from community “B” (2002) aligned in a separate cluster, which showed little overlap with the communities “C”, “E”, and “F” (2010). Even the splitting of community “B” (2002) into sub-clusters did not reveal any relationships between macrofauna patterns and regular dredging activities in the old fairway or the differences in sediment composition. It did also not improve the similarities with the macrofauna community structure in 2010.

Table 3.8 provides the abundance of 11 characteristic macrofauna taxa in 2002 and 2010. While the mean abundance of the polychaete *Nephtys hombergii* and juvenile *Nephtys* spp. decreased, the abundance of the bivalve *Macoma balthica* and the polychaete *Scoloplos (Scoloplos) armiger* remained almost stable. In contrast, the abundance of Anthozoa, *Corophium volutator*, *Gastrosaccus spinifer*, juvenile Mytilidae, *Peringia ulvae*, *Petricolaria pholadiformis*, and *Pygospio elegans* increased. Only the abundance of *Nephtys hombergii* and juvenile *Nephtys* spp. differed significantly in 2010 from 2002 (Table 3.8). The changes in abundances of *Corophium volutator*, *Peringia ulvae*, *Petricolaria pholadiformis*, and *Pygospio elegans* could not be tested with ANOVA, because these species were not present in 2002.

In 2010, *Gastrosaccus spinifer* was found mainly within or close to the areas dredged for the JWP (Fig. 3.7). *Nephtys hombergii* and juvenile Mytilidae occurred in the dredged areas as well as in the non-dredged eastern region. *Macoma balthica* and *Scoloplos (Scoloplos) armiger* were widely distributed over the entire study area. In contrast, the occurrence of *Peringia ulvae* was almost limited to the southern transect (T1). The distribution of *Corophium volutator* and *Petricolaria pholadiformis* coincided with medium or high mud contents, within the old fairway and in the eastern part. Anthozoa, juvenile *Nephtys* spp., and *Pygospio elegans* occurred in the areas which were not dredged.

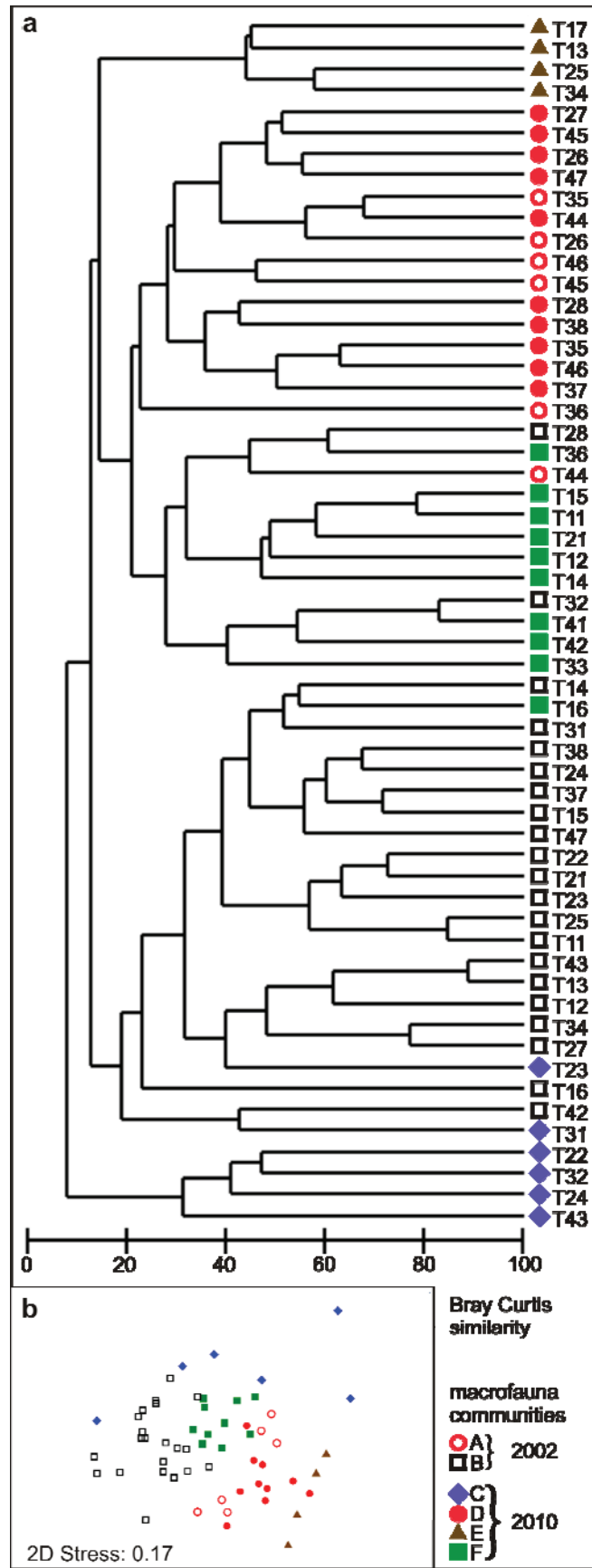


Figure 3.6 Combined cluster analyses (a) and MDS (b) of macrofauna data in 2002 and 2010, based on Bray-Curtis similarity, using fourth-root transformed taxa abundance data

Table 3.8 Comparison of mean abundances (individuals/m²) of 11 characteristic taxa at the 30 sampling stations in 2002 and 2010 with standard deviation (sd) and results of the performed ANOVAs

characteristic taxa (see Fig. 7)	2002 [ind./m ²]		2010 [ind./m ²]		df	ANOVA F	p
	mean	(sd)	mean	(sd)			
1 Anthozoa spp.	32.7	(144.2)	64.3	(164.2)	1,58	0.630	0.431
2 <i>Corophium volutator</i>	0.0	(0.0)	26.7	(80.0)	0 <i>C. volutator</i> in 2002		
3 <i>Gastrosaccus spinifer</i>	0.7	(2.5)	46.0	(212.3)	1,58	1.368	0.247
4 <i>Macoma balthica</i>	10.7	(16.4)	12.0	(26.7)	1,58	0.054	0.817
5 Mytilidae sp. juv.	5.0	(14.6)	97.0	(295.8)	1,58	2.895	0.094
6 <i>Nephtys hombergii</i>	12.0	(15.8)	2.0	(4.8)	1,58	10.930	0.002
7 <i>Nephtys</i> spp. juv.	15.3	(23.0)	1.0	(4.0)	1,58	11.300	0.001
8 <i>Peringia ulvae</i>	0.0	(0.0)	8.7	(20.3)	0 <i>P. ulvae</i> in 2002		
9 <i>Petricolaria pholadiformis</i>	0.0	(0.0)	2.3	(5.0)	0 <i>P. pholadiformis</i> in 2002		
10 <i>Pygospio elegans</i>	0.0	(0.0)	61.7	(169.4)	0 <i>P. elegans</i> in 2002		
11 <i>Scoloplos (Scoloplos) armiger</i>	26.7	(59.7)	27.3	(38.9)	1,58	0.003	0.959

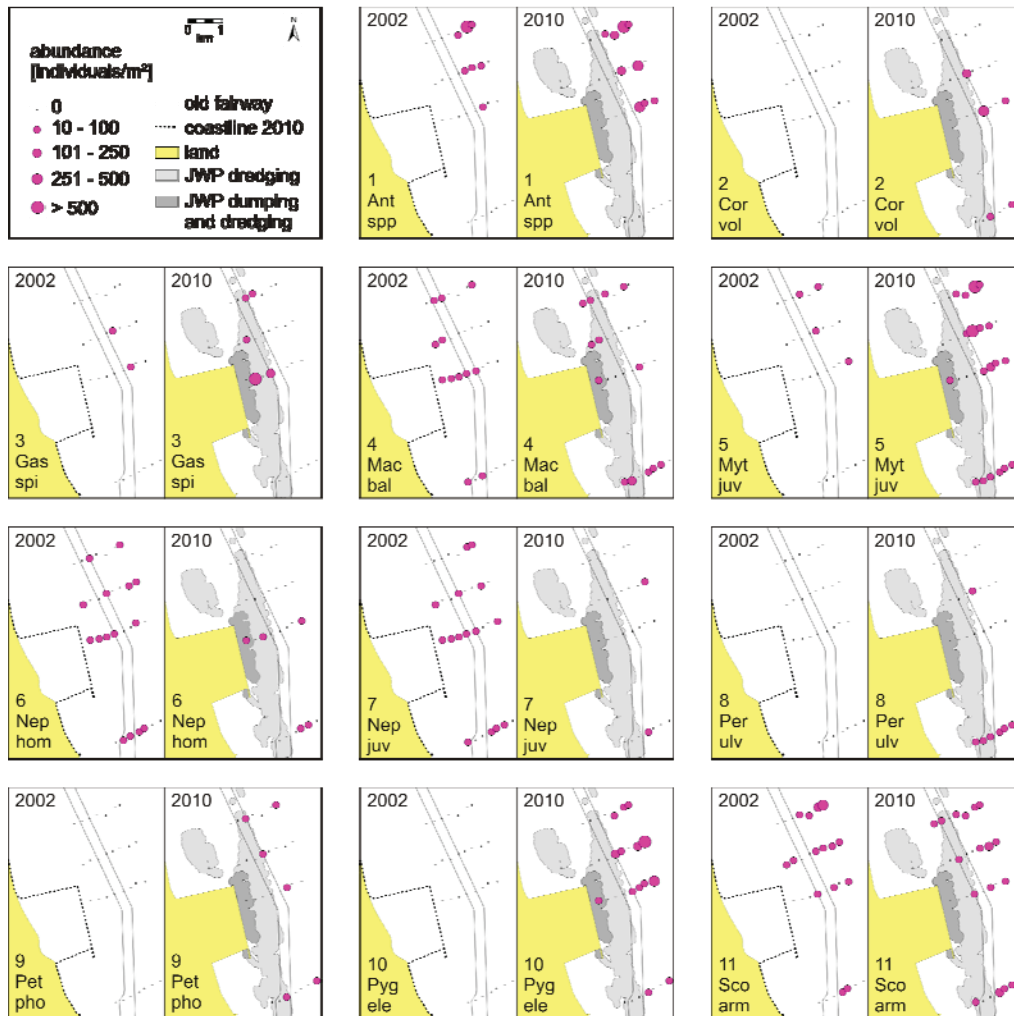


Figure 3.7 Abundance of characteristic macrofauna taxa (individuals/m²) in 2002 and 2010, 1 Anthozoa spp.; 2 *Corophium volutator*; 3 *Gastrosaccus spinifer*; 4 *Macoma balthica*; 5 juvenile Mytilidae sp.; 6 *Nephtys hombergii*; 7 juvenile *Nephtys* spp.; 8 *Peringia ulvae*; 9 *Petricolaria pholadiformis*; 10 *Pygospio elegans*; 11 *Scoloplos (Scoloplos) armiger*

3.6 Discussion

3.6.1 Physical effects of the construction work

The highly heterogeneous seafloor of Inner Jade was described by Capperucci and Bartholomä (2012). In 2010, this region was characterized by patchy small scale variations in composition and distribution of sediments, both in the dredged and in the non-dredged areas. The construction of the JWP, in particular, the dredging activities, transport and dumping of fine sediments (sand and mud) increased the complexity of the system. These effects were difficult to quantify and the impact of the JWP construction work was hardly distinguishable from the natural variance.

Most of the dredged sediments consisted of sand, which explained the observed coarsening trend in the study area, especially the increase of the sand fraction at the southern transect T1, close to the southern extraction site (Fig. 3.2). In fact, the region is dominated by a dynamic sediment transport regime, confirmed by the existence of large, very mobile bedform fields (Kubicki and Bartholomä 2011). The presence of a mobile sand layer, nourished by the dredging activities, could temporarily cover the previously existing fine deposits and/or replace them.

The coarsening of sediments observed along the western part of transect T2 (T21-T23), the closest to the construction site, could be attributed to the direct dumping of sand in the bulkhead area, or to the exposure of the Pleistocene sand deposits beneath the removed sea bottom.

In contrast, the eastern part of transect T2 showed an increase in mud fraction (T25-T27). This transect was the one closest to the “Lauenburger Ton” mining location. The intense reworking of the clay deposit and some unavoidable dispersion of the same material could potentially explain the increase of mud content recorded at stations T25-T27. On the other hand, different sources (e.g. Neuer Vorhafen dredging spoils; natural presence of fine sediments in the Jade Bay tidal flat areas) could not be excluded.

In contrast to earlier studies (Dörjes et al. 1969; Irion 1994), the old fairway was characterized by fine sediments in 2002 and 2010. Thus, this area was the most stable region of the system. The slight increase in mud content measured in 2010 could be linked to the “Lauenburger Ton” dredging and dumping operations (although different sources could not be excluded). In fact, beside the two sand extraction sites, the old fairway was the deepest part of the study area and seemed to act as a trap for soft sediments (ICES 1992).

For the land reclamation of the JWP terminal area, the original seafloor surface was removed, and the Pleistocene sand deposits below were exposed and exploited, especially from the two extraction sites in the Jade Channel (north and south of the new bulkhead). Underneath the sand cover, a thick deposit of consolidated clay (“Lauenburger Ton” formation) was dug, mainly in the area between the bulkhead and the old fairway. The removed material was dumped into the southern extraction site (Kluth and Ehmen 2010). Dredging and dumping operations are commonly associated with sediment re-suspension (mainly the fine sand and mud fractions of the suspended load near the bottom), as well as leaks and spills (Newell et al. 1998; Winterwerp 2002). This material can be easily re-mobilized and spread, especially at periods of maximum flow intensity.

There is no evidence that the observed sediment changes were controlled by a variation in the hydrodynamic conditions. Kahlfeld and Schüttrumpf (2006) modelled the impact of deepening and narrowing the Inner Jade on the morphodynamics of the area. They predicted that only local changes in flow velocity of the Inner Jade would occur in the immediate proximity of the JWP. However, the predicted values (mean ebb flow velocity increased up to +0.1 m/s) were too low for inducing sediment changes, in comparison with the maximum average flow velocities (generally larger than 1.5 m/s, Grabemann et al. 2004).

3.6.2 Changes in macrofauna community structure

In 2002, the patchy distribution of the few characteristic taxa in low abundances reflected the study area as a more homogeneous habitat than in 2010. Only community “A” (2002) in the north eastern area was distinguishable from the predominating community “B” (2002) in the remaining area (Fig. 3.4a,c). Community “B” (2002) showed the characteristics of an early succession stage already: low taxa number, low abundance, and dominance of opportunistic or stress tolerant species.

The spatial distribution of the macrofauna communities in 2010 matched roughly with the division of the study area according to the different categories of disturbance: the most recently dredged north western area (community “C”), the regularly dredged old fairway (community “E”), and the north eastern non-dredged area (community “D”). The southern area (T1) was mainly inhabited by community “F”, which also occurred in the transition areas between the other communities (Fig. 3.4b,d).

3.6.3 Direct dredging effects on the macrofauna community structure in 2010

The BIOENV analysis proved the dredging activities for the JWP as the most important structuring parameter in 2010 (Table 3.6). According to known effects of dredging activities on macrofauna (e.g. Kenny et al. 1998; Sardá et al. 2000; van Dalftsen et al. 2000; van Dalftsen and Essink 2001; Newell et al. 2002; Sutton and Boyd 2009), a decrease in diversity, taxa number, and abundance was expected in the area that was directly affected by the dredging activities for the JWP. Thus, the very low taxa number in the north western area (community “C”, 2010) was probably a direct effect of the recently conducted dredging activities (Kenny and Rees 1994; 1996). In community “C” (2010) the high number of the mysidacea *Gastrosaccus spinifer*, which actually belongs to the hyperbenthos, and the occurrence of the amphipod *Pontocrates altamarinus* (Table 3.5), which is also a very mobile species, hinted at an early stage of re-colonisation in the newly available substrate.

For the old fairway the date of the last dredging activity by the WSA is not exactly known, but the increased taxa number and abundance in community “E” (2010) indicate re-colonisation in the regularly disturbed area with relatively stable sediment composition. This re-colonisation by opportunistic (r-selected) species such as *Corophium volutator* and *Pygospio elegans* is a typical response after dredging (e.g. Newell et al. 1998).

This study confirmed that quick re-colonisation is possible after physical disturbance in highly dynamic areas (Borja et al. 2010). Post-settlement dispersal may have resulted in dispersal of juvenile and adult *Macoma balthica* over the wide range of different habitats in the entire study area (Fig. 3.7). Juvenile Mytilidae can disperse by byssus drifting (Armonies 1996), probably originating from the mussel farms and banks in the Inner Jade (Herlyn and Millat 2000). The appearance of the mud snail *Peringia ulvae* in the southern transect (T1) could also be explained by drifting. This species occurred in very high abundance in the adjacent Jade Bay (Schückel et al. 2013) and disperses by floating at the water surface (Armonies and Hartke 1995).

Thus, re-colonisation by opportunistic and highly mobile species as well as secondary dispersal of several dominant species seemed to follow the construction phase of the JWP. Despite the high re-colonisation potential of the study area, it is unlikely that full recovery to the state of the 1960s is attainable.

3.6.4 Indirect dredging effects on the macrofauna community structure in 2010

The combination of naturally very mobile bedforms (Kubicki and Bartholomä 2011) and the different dredging activities in the Inner Jade formed a dynamic mosaic of microhabitats. In 2002 and 2010, the presence of some dominant species (e.g. *Macoma balthica*, *Scoloplos (Scoloplos) armiger*) in different communities (Table 3.5) indicated the high tolerance of these species to variable environmental conditions (Schückel et al. 2013).

Overall, the macrofauna pattern in 2002 was obviously less influenced by the sediment distribution than in the 1960s. Nevertheless, despite the lack of information about the gravel content of the study area in 2002, the dominance of Anthozoa in community “A” (2002) indicated the presence of hard substrate in the north eastern area. Indeed, the expanded dominance of Anthozoa in the north eastern area (community “D”, 2010) coincided with the presence of gravel in 2010. Within eight years between the two sampling campaigns, the spatial extension of the Anthozoa dominated community “A” (2002) shifted slightly towards the shallower eastern Jade slope (community “D”, 2010). The hard ground characteristics of the coarse gravel bed supported the settlement of Anthozoa and their presence explained the high biomass in the north eastern area (Table 3.6). For the other characteristic taxa in 2002 no strict sediment preferences are known.

In 2010, a more heterogeneous seabed morphology and sediment distribution (Capperucci and Bartholomä 2012) coincided with the more complex macrofauna community structure in comparison to 2002. Community “E” (2010) was restricted to areas with medium or high mud content (Table 3.4), because the characteristic species *Corophium volutator* and *Petricolaria pholadiformis* prefer fine sediments (Fenchel et al. 1975; Tebble 1976). The majority of stations belonging to the communities “C” and “F” (2010) coincided with sandy areas, but (according to the BIOENV analysis, Table 3.6) a significant relationship between the macrofaunal community structure in 2010 and the altered sediment distribution was not determined.

The increased taxa number and abundance in the old fairway and the not dredged areas (Table 3.2) could not be explained by the presence of invasive species. All taxa from the 2010 samples are typical inhabitants of the southern North Sea, which were found in the study area prior to the JWP construction (Dörjes et al. 1969; Schuchardt et al. 2003). In the Australian Moreton Bay Poiner and Kennedy (1984) observed a fast increase of biodiversity and population density outside dredged areas. They suggested that the macrofauna expanded, because of the increase in suspended organic material due to the sediment plume of fine

particles generated by the dredging activities. Transferred to the study area in the Inner Jade, the old fairway and even the non-dredged areas were indirectly affected by the JWP construction. In 2010, re-suspension and spilling of the dredged sediments could explain the increased abundance of some macrofauna taxa, which probably profited from the enhanced food availability. In the non-dredged areas, the number of omnivores and deposit feeders increased markedly (Fig. 3.5).

In contrast, the abundance and spatial distribution of the polychaete *Nephtys hombergii* declined significantly in 2010, even in the non-dredged areas (Fig. 3.7, Table 3.8). Brooks et al. (2006) assumed that the predator *Nephtys hombergii* benefits from organisms that were injured or died during the dredging process. Its main prey, the polychaete *Scoloplos (Scoloplos) armiger* (Beukema et al. 2000), was still abundant in 2010, suggesting that food shortage could not explain the decrease in *Nephtys hombergii*. Instead, its sensibility to low winter temperatures (Beukema et al. 2000) has to be taken into account, because the mean temperatures of January (-0.2°C) and February (0.9°C) 2010 were lower than in January (0.6°C) and February (6.0°C) 2002. Monthly CTD time series data, measured by the RV “Senckenberg”, revealed up to 5°C difference in February at ton 48 (geographic position according to WGS84 UTM32N: Easting 445722.91099; Northing 5937336.36463) in the study area between 2002 and 2010. This suggests a temperature dependent decrease of the predator *Nephtys hombergii*, which may have contributed to the relatively high abundance of its prey *Scoloplos (Scoloplos) armiger* in 2010. This example highlights the importance of interannual variability, which can have a strong influence on the abundance of several species (Kröncke et al. 2013) and may have masked the impact of the dredging activities for the JWP in the Inner Jade.

3.7 Conclusion

For decades, the Inner Jade has been classified as a dynamic ecosystem characterised by both natural and anthropogenic factors. In comparison to the local hydrodynamic regime, the predicted increase in current velocity due to the harbour construction was negligible. The dredging and dumping activities for the JWP changed the bathymetry and contributed to the permanent re-distribution of sediments within the study area. Opportunistic and mobile macrofauna species, without strict sediment preferences, had colonized the area from the 1960s to 2002. Nevertheless, the community structure in 2010 was clearly different. Although

interannual variability has to be taken into account, the distribution pattern of the re-colonising species in 2010 was best explained by the dredging activities for the JWP.

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4 Comparison of adult-juvenile interactions of a deposit-feeding and a suspension-feeding bivalve under controlled conditions

R. Gutperlet and C.A. Pilditch

4.1 Abstract

The effects of the presence of two adult bivalve species with different feeding modes on the post-settlement dispersal of their juveniles were examined in a flume experiment. The treatments consisted of 4 deposit-feeding *Macomona liliana*, 10 suspension-feeding *Austrovenus stutchburyi*, and a control without adults. Flow speed was set at a velocity that did not cause sediment erosion but was high enough to give the juveniles a chance to actively move. At the end of each experimental run, the capture position in the flume (acrylic floor, bedload traps, plankton net) was related to the different dispersal modes of the juveniles (crawling, rolling as bedload transport, and drifting). Over 90% of the juvenile *Austrovenus stutchburyi* remained in the sediment cores, regardless of the treatment. In contrast, higher percentages of juvenile *Macomona liliana* left the *Austrovenus* treatment (30%), the *Macomona* treatment (50%) and the control (50%). The differences of total dispersal between the treatments were not significant. The differences in dispersal mode were significant for both, *Austrovenus* and *Macomona* juveniles. Most *Austrovenus* juveniles dispersed by crawling on the acrylic floor of the flume, only few individuals were found in the bedload traps and none drifted into the plankton net. For juvenile *Macomona* a significant interaction between dispersal mode and treatment was detected, because in the control significantly more juveniles were found in the bedload traps than on the acrylic floor or in the plankton net. The *Macomona* juveniles which drifted in the plankton net were significantly smaller than those on the acrylic floor or in the bedload traps.

4.2 Introduction

Dispersal is a key process determining spatial and temporal patterns of macrofauna communities in soft sediment ecosystems (Commito et al. 1995; Norkko et al. 2001; Pethua et al. 2006; Pilditch et al. 2015). Drifting of pelagic larvae is widely recognised as the main procedure for the re-colonisation of large disturbed habitats (Günther 1992), but recently the role of post-settlement dispersal appears to be at least similarly important (Pilditch et al.

2015). Many (40-60%) soft-sediment species lack any pelagic larvae (Grantham et al. 2003), but all have the potential to disperse as juveniles (Pilditch et al. 2015). The competence of juvenile and adult dispersers is even higher than of vulnerable larvae (Pilditch et al. 2015), because fitness and the probability of survival increases with age (Gosselin and Qian 1997). Many taxa use post-settlement movement for their redistribution after their initial settlement, including polychaetes (Tamaki 1987; Shull 1997; Stocks 2002), crustaceans (Grant 1980; Hedvall et al. 1998; Blackmon and Eggleston 2001; Moksnes 2002), gastropods (Levinton 1979; Levinton et al. 1995) and bivalves (Sirgurdsson et al. 1976; Beukema and de Vlas 1989; Armonies 1992, 1996; Commito et al. 1995; Cummings et al. 1995; Hewitt et al. 1997; Turner et al. 1997; Hunt and Scheibling 1998; Hunt et al. 2003).

Passive transport of sediments and organisms is correlated with hydrodynamic forces, such as waves and currents (Commito 1995; Hewitt et al. 1997). Active dispersal involves a behavioural component like crawling or swimming (Pilditch et al. 2015). Emergence from the sediment and the release of mucous or byssal threads promotes dispersal (Lundquist et al. 2004). In contrast, burrowing and attaching to the substrate with byssus fibres reduce the likelihood of dispersal (Armonies 1994). Thus, at flow speeds that are subcritical to sediment erosion, but high enough to disperse, post-settlers can actively move into areas, which are more suitable e.g. due to higher food availability, and escape from unfavourable conditions, e.g. due to anthropogenic chemical or physical disturbance or due to biological factors such as presence of predators and sediment disturbers, competition or high population densities (Commito et al. 1995). One possible motivation to avoid dispersal could be the presence of con-specifics, which indicate a suitable habitat.

Adult-larval interactions have been relatively well studied since Woodin (1976) presented the hypothesis that the often sharp boundaries between assemblages of suspension feeders and deposit feeders are due to interactions of the present adults and the settling larvae. For a description of the spatial separation between assemblages of deposit feeders and suspension feeders see Rhoads and Young (1970). Suspension feeders filter particles and larvae out of the water column (Woodin 1976). Deposit feeders can also ingest larvae and disturb settling larvae and juveniles by sediment reworking during their siphonal activities (Woodin 1976). Several studies reported negative effects of dense adult bivalve assemblages on the settlement of larvae (André and Rosenberg 1991; Möller 1986; Williams 1980).

Relatively little is known about post-settlement dispersal (Pilditch et al. 2015) and adult-juvenile interactions. Trap studies showed that organisms of multiple taxa disperse more or less continuously as juveniles and adults (Armonies 1994; Valanko et al. 2010). Thus, post-settlement dispersal might contribute to the maintenance of discrete beds as often observed in the field, e.g. on an intertidal flat of the Whitford embayment (36° 54.5'S, 174° 59.5'E), Auckland, New Zealand. There are distinct patches, where the suspension-feeding bivalve *Austrovenus stutchburyi* and the mainly deposit-feeding bivalve *Macomona liliana* occur separately, although there is no obvious abiotic gradient that could explain this separation (Thrush et al. 2006). Competition for space and food between adults and juveniles might be one possible motivation for the dispersal of juveniles. Disturbance due to bioturbation activities in particular by the deposit-feeding bivalve *Macomona liliana*, but also by the highly mobile, surface-dwelling suspension-feeding bivalve *Austrovenus stutchburyi* (juveniles of both species live in the upper 2cm of sediment; Thrush et al. 2006) is another hypothesis. On the other hand, settlement in the vicinity of the adult con-specifics promises a suitable habitat.

Legendre et al. (1997) found no support for adult-juvenile interactions for both bivalve species *Austrovenus stutchburyi* and *Macomona liliana*. In their study no positive/negative correlations between the spatial distribution patterns of juveniles and adults were detected (Legendre et al. 1997). In contrast, Thrush et al. (1992) reported facilitation of the colonisation of juvenile *Macomona liliana* in the vicinity of adult con-specifics. In other studies, high densities of *Macomona liliana* had negative impacts on juvenile con-specifics and other taxa (Thrush et al. 1994, 2000; Turner et al. 1997). Turner et al. (1997) explained the reduced colonisation by macrofauna in high density *Macomona liliana* areas by the ingestion of larvae and juveniles and/or by physical disturbance of the sediment surface associated with activity of the inhalant siphon of this deposit-feeding bivalve. In the study of Thrush et al. (2000), the adult-juvenile interactions were clearly related to energy dissipation by waves, implying site specific effects. These contrasting outcomes from field experiments can be easily misinterpreted due to high levels of natural variability, or by failing to take into account the effects of factors that were not investigated (Pillay et al. 2007). Laboratory experiments on the other hand have the advantage of controlled conditions.

The objective of this study was to investigate, if the presence of adult *Macomona liliana* and *Austrovenus stutchburyi* promotes active dispersal of juvenile con-specifics in a flume under

controlled laboratory conditions. The difference in the feeding methods of these two bivalves made it possible to compare the effects on juvenile settlement of a deposit feeder, *Macomona liliana* with a suspension feeder, *Austrovenus stutchburyi* (Olivier et al. 1996). To our knowledge adult-juvenile interactions of *Austrovenus stutchburyi* and *Macomona liliana* have not been investigated in flume experiments before.

4.3 Material and Methods

4.3.1 Study species

The bivalves *Austrovenus stutchburyi* and *Macomona liliana* are common species in the soft sediment ecosystems of New Zealand (Pridmore et al. 1990). *Austrovenus stutchburyi* (hereafter referred to as *Austrovenus*) is a suspension-feeding venerid bivalve with short siphons. Its shell protrudes the sediment surface. Juvenile *Austrovenus* live also in the top 2 cm of the sediment (Thrush et al. 2006). In contrast, *Macomona liliana* (hereafter referred to as *Macomona*) is a deposit feeding tellinid bivalve with a long inhalant siphon that lives up to 10 cm below the sediment surface. Juvenile *Macomona* are restricted to the top 2 cm of the sediment (Thrush et al. 2006).

4.3.2 Observation site characteristics

Taupiro Point is a sheltered inter-tidal sandflat in the Bay of Plenty, New Zealand (37° 29'20''S, 175°57'12''E). Mean salinity was 30.0 and mean temperature was 20.4°C, measured during the 12 days for sediment or bivalve collection. Surface sediments at the *Austrovenus* sites consisted primarily of fine sand with an average of 4.74% silt/clay (<63µm) and low organic content. At the *Macomona* sites contained also fine sand with an average of 2.03% silt/clay (<63µm) and low organic content. In both, the *Austrovenus* and the *Macomona* sites there was a distinct oxic layer (indicated by colouration differences), approximately 2 cm deep.

4.3.3 Field collection and acclimation

For an oxidised layer, surface sediments (0-2 cm) were taken and for an anoxic layer deeper sediments (below 2 cm) were assembled. Both oxidised and anoxic sediments were separately sieved through a 500 µm mesh, in order to get rid of the macrofauna. In the laboratory first

the anoxic sediment was filled in the deeper 13 cm of the cores (13 cm diameter, 15 cm deep) and then the oxidised sediment was placed on top (upper 2 cm). The prepared sediment cores were acclimated for 48 hours in aerated aquariums for the reestablishment of a natural gradient between the two sediment layers, before insertion into the flume.

Adult *Austrovenus* were found by digging the surface sediments at the *Austrovenus* sites of Taupiro Point. For the collection of adult *Macomona* one had to dig in the sandflat bottom of the *Macomona* sites. Juveniles were found by sieving (500 μ m mesh) surface sediments (0-2 cm) at the *Austrovenus* and *Macomona* sites respectively. For each experimental run 100 juvenile *Austrovenus* were collected. Since the density of juvenile *Macomona* in the field samples were lower, only 40-50 individuals of that species could be used for each experimental run. Adult and juvenile bivalves were transported to the laboratory and held in aerated seawater at ambient temperatures.

The adult individuals were placed on the surface of the prepared sediment cores, which were inserted in the flume. They had 24 hours to bury and acclimate in the cores with a low flow speed (2 cm/s). Juvenile bivalves were immediately sorted using a dissecting microscope with attached micrometer. Only active individuals (foot out and moving around) in a size range between 2-5 mm were selected. The sorted juvenile bivalves were acclimated overnight in aerated seawater containers before being used in experiments. One half of the juveniles were stained with fluorescein, in order to be able to reconstruct from which core the dispersed juveniles originated from. It is proven, that fluorescein does not change the behaviour of the juveniles (Norkko et al. 2001). Fresh sediments and bivalves were collected for each experimental run.

4.3.4 Laboratory flume

Experiments were conducted in the re-circulating flume described by Miller et al. (2002). It consists of a 7.23-m long, 50-cm wide and 50-cm deep acrylic channel. Beneath the flume runs a 40-cm diameter return pipe, in which an impeller regulates the flow speed via an AC motor. The flume was filled to 15 cm with artificial seawater (mean salinity: 30.8). Experiments were conducted at ambient temperatures (mean temperature: 20.5°C) and ambient photoperiod (12light/12dark). In the working section of the flume (Fig. 4.1) two

holes were cut in the flume floor to allow the insertion of cores containing sediments. Cores were inserted flush with the flume floor.

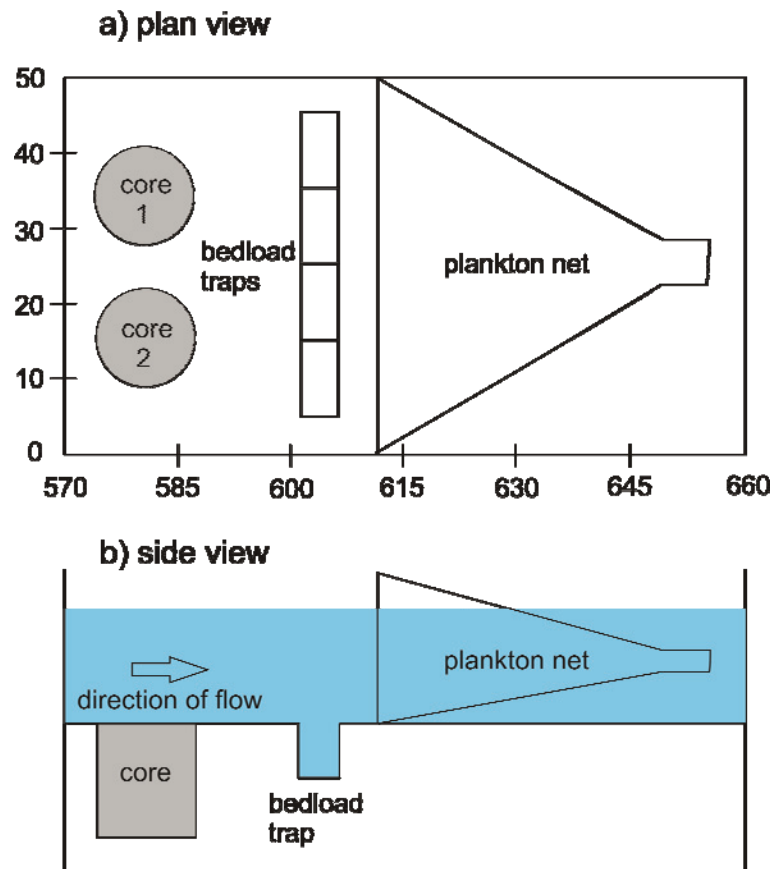


Figure 4.1 The working section of the flume in a) plan view and b) side view

15 Hz was chosen as flow motor speed. Lundquist et al. (2004) found highest dispersal rates at a motor speed of 18 Hz (16.6 cm s^{-1}). 15 Hz is high enough to give the juveniles a chance to move, but low enough that it did not cause sediment erosion. Thus, active behaviour was required for post-settlement transport. Dispersing bivalves were captured either on the acrylic flume floor, in one of four bedload traps (each 2.5 cm wide by 15 cm deep) or a plankton net (500 μm mesh) that extended the full width and height of the flume located downstream of the cores.

To characterise the variation in flow and boundary-layer dynamics in detail, vertical profiles of flow velocity were made in the centre of the cores using a Sontek 10-MHz Acoustic Doppler Velocimeter (ADV). Profile measurements were made at heights of 0.6, 0.8, 1, 1.5, 2, 2.5, 3, 4, 5, and 6 cm above the flume floor. The minimum height above the flume floor was chosen to insure that the bottom boundary was not included in the ADV sample volume (Finelli et al. 1999). At each height, velocity measurements were collected for 120 s at a sampling frequency of 2 Hz.

4.3.5 Experimental treatments and protocol

Adult treatments consisted of sediment cores with either 10 *Austrovenus* or 4 *Macomona* (Fig. 4.2). These chosen densities in the adult treatments corresponded approximately with the mean densities of the both species, which were found in a former study at Tuapiro Point (CA Pilditch, unpublished data). As a control, sediment cores without adult bivalves were used. In total, the three treatments were replicated four times. Since there was only space for two cores in the flume, six experimental runs were conducted. The order of the treatments in each replicate was randomized, in order to limit the impact of any behavioural changes during the six weeks over which the experiments were performed.

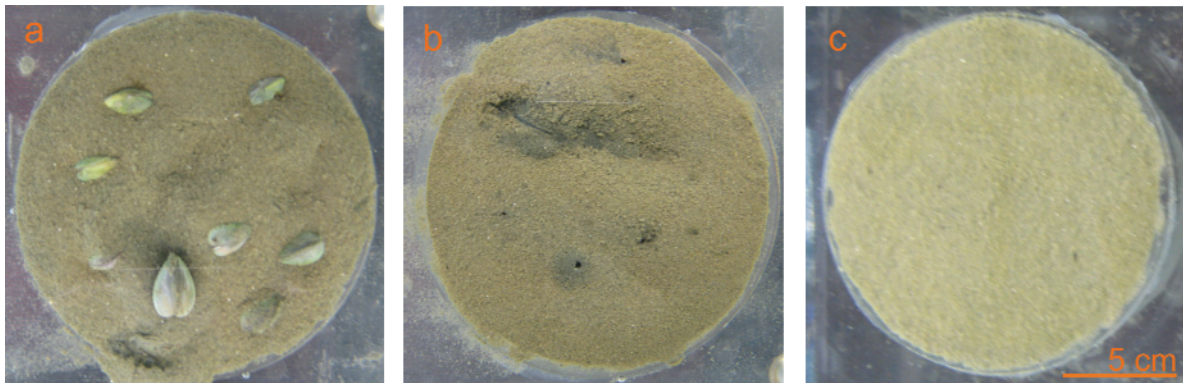


Figure 4.2 Photographs of the core surface in the three treatments: a) 10 adult *Austrovenus*, b) 4 adult *Macomona*, c) control without adult bivalves after 24 hours acclimation time

Using a barrel the juveniles were carefully put on top of the cores (100 *Austrovenus* and 40-50 *Macomona* per core). After insertion in the flume, the juveniles had time to bury themselves in the sediment cores. After two hours the flow was switched on. After 48 hours dispersal time the flow was switched off and the juveniles were recovered from the different areas in the working section of the flume. Each area in the flume corresponded to different dispersal modes. The acrylic floor before the bedload traps was probably reached by crawling. Bedload transport led into the bedload traps. Drifting juveniles were caught in the plankton net at the end of the working section. Juveniles, which got stuck on the rims of each core were recovered separately, because it was assumed, that these juveniles tried to move. Finally, all juveniles were recovered, which remained in the cores. Immediately after their recovery, juveniles, which were found at the acrylic floor, in the bedload traps and in the plankton net were sorted under blue light excitation, in order to determine if they were fluorescent. Additionally, the exact shell length of all bivalves, which were involved in the experiments, was measured.

4.3.6 Statistical analysis

Using the programme PAST, a one way ANOVA determined the significance of differences in juvenile total dispersal between the two adult treatments and the control without adult bivalves. Shapiro Wilk tested for normal distribution of the data and Levene's test was used to check the homogeneity of variance. A two way ANOVA was performed, in order to test for significant differences between the two factors "treatment" and "dispersal mode". In the case of a significant interaction between these two factors, a separate ANOVA (equal variances are given) or Welch test (unequal variances are given) were calculated per treatment. Tukey's HSD (Honestly Significant Difference) test was used to identify the significant differences of dispersal mode per treatment. The significance of differences in size per capture position in the flume was determined by Kruskal Wallis tests (normal distribution of size data was not given, even after trying several different transformations). The Mann-Whitney test was used to detect significant differences in size of the juveniles between the different capture positions. .

4.4 Results

4.4.1 Flow conditions

At the motor speed of 15 Hz the mean free stream flow velocity (u) 6 cm above the flume floor was $14.98 \pm 0.93 \text{ cm s}^{-1}$. The flow conditions varied between the two cores. Without adult bivalves u was 7.66% higher in core 1 (16.18 ± 0.22) than in core 2 (14.94 ± 0.22). The difference of flow conditions across the width of the flume was due to wall-effects and the displacement of the fastest flows in the channel slightly to the right of centre, when looking upstream into the flow (Lundquist et al. 2004).

The presence of adult bivalves decreased the mean u above both cores. The *Austrovenus* treatment decreased u by 8.10% in core 1 (14.87 ± 0.20). The *Macomona* treatment decreased u by 6.83% in core 2 (13.92 ± 0.32). The order of adult treatments in the cores was randomized between the 6 runs of the experiment, thus, the flow variability between the two cores had no influence on the mean dispersal of juveniles.

4.4.2 Effects of adult treatments

Most juveniles were buried after the flow was switched on. The number of dispersing juveniles differed markedly between *Austrovenus* and *Macomona*. Over 90% of *Austrovenus* juveniles remained in the cores, regardless of the treatment (Fig. 4.3a). $8.5 \pm 5.0\%$ *Austrovenus* juveniles dispersed away from their adult con-specifics. Less ($6.0 \pm 5.6\%$) *Austrovenus* juveniles left the cores containing adult *Macomona*. Only $4.3 \pm 2.8\%$ *Austrovenus* juveniles dispersed from the controls without adults. These differences between treatments were not significant (Table 4.1).

In contrast, 30-50% juvenile *Macomona* dispersed away from the cores (Fig. 4.3b). While $30.8 \pm 24.4\%$ *Macomona* juveniles left the cores containing adult *Austrovenus*, $49.2 \pm 33\%$ *Macomona* juveniles dispersed from the *Macomona* treatment and $51.6 \pm 16.6\%$ from the control cores. These differences were also not significant (Table 4.1).

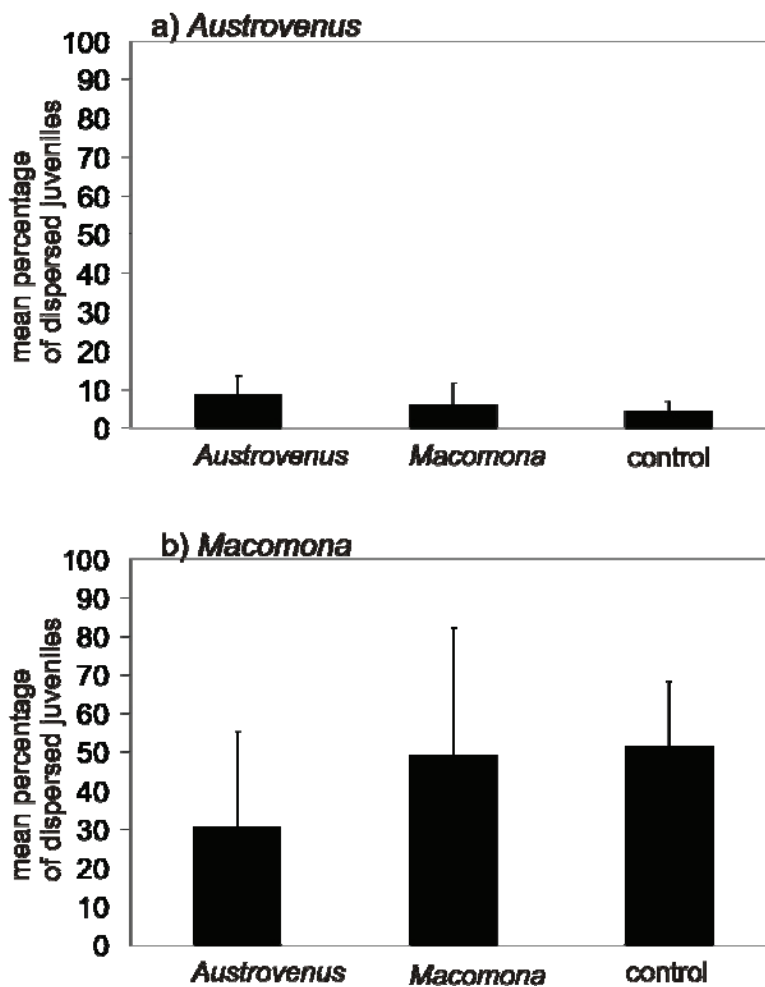


Figure 4.3 Mean percentage of total dispersal of a) juvenile *Austrovenus* and b) juvenile *Macomona* in response to the 3 treatments with standard deviation

Table 4.1 Results of the one way ANOVA of total dispersal of juvenile *Austrovenus* and *Macomona* in response to the different treatments

	df	sum of squares	F-ratio	p-value
<i>Austrovenus</i>	2	36.5	1.112	0.3703
<i>Macomona</i>	2	123.5	1.051	0.3888

4.4.3 Dispersal mode

In all treatments, most *Austrovenus* juveniles (4-8%) were recovered from the acrylic flume floor and only a small amount (0.3-0.5%) was found in the bedload traps (Fig. 4.4a). No *Austrovenus* juvenile was caught in the plankton net.

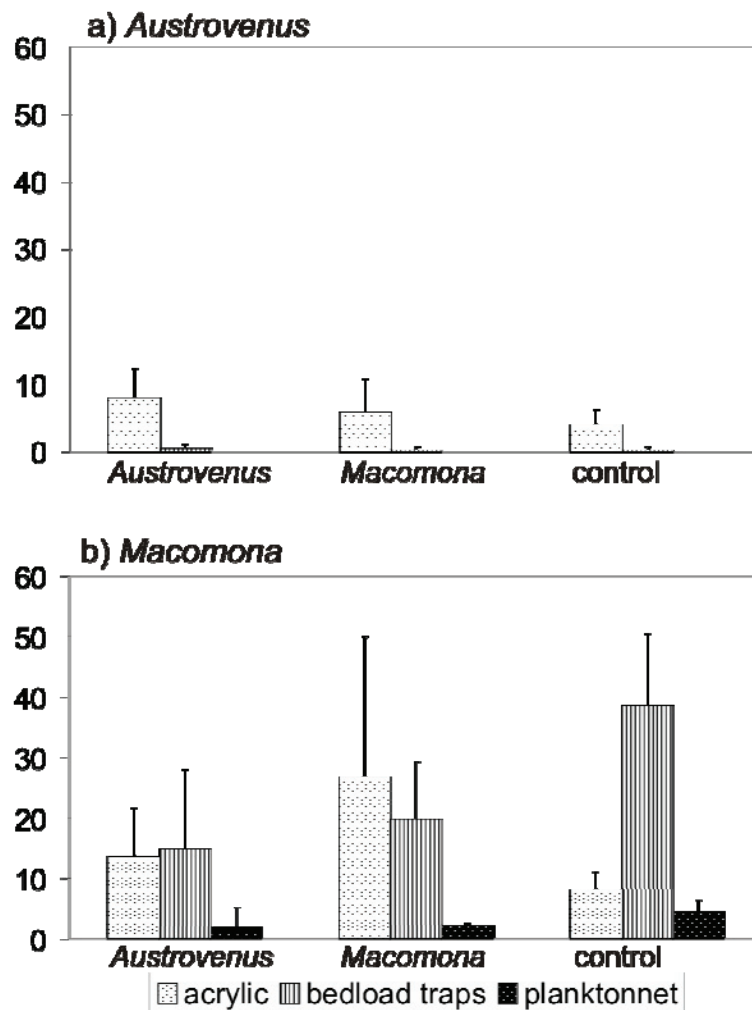


Figure 4.4 Mean percentage of dispersed juveniles in relation to their dispersal modes per treatment of a) juvenile *Austrovenus* and b) juvenile *Macomona* with standard deviation

The numbers of *Macomona* juveniles, which were recovered from the acrylic, the bedload traps and the plankton net differed between treatments (Fig. 4.4b). Dispersing from the *Austrovenus* treatment, almost equal numbers of *Macomona* juveniles were found on the acrylic (13.7%) and in the bedload traps (14.9%). The amount of juveniles in the plankton net was equal in the *Austrovenus* treatment (2.2%) and the *Macomona* treatment (2.3%). Dispersing from the *Macomona* treatment, most *Macomona* juveniles were found on the acrylic (27.0%) and a bit less were caught in the bedload traps (19.9%). In contrast, the majority of *Macomona* juveniles originating from the control cores were found in the bedload traps (38.6%) and only a few juveniles were recovered from the acrylic (8.4%) and the plankton net (4.7%). These results confirmed that *Austrovenus* juveniles mainly disperse by crawling, because the majority only reached the acrylic flume floor. Only some *Austrovenus* juveniles rolled into the bedload traps. In contrast, most juvenile *Macomona* rolled into the bedload traps, some crawled on the acrylic and some floated into the plankton net. These differences of dispersal mode were significant for *Austrovenus* and *Macomona* (Table 4.2).

Table 4.2 Results of the two way ANOVA of dispersal of juvenile *Austrovenus* and *Macomona* versus treatment and dispersal mode

Source	df	sum of squares	F-ratio	p-value
<i>Austrovenus</i>				
treatment	2	12.080	1.153	0.3308
dispersal mode	2	266.800	25.460	6.11E-07
treatment x dispersal mode	4	20.040	0.956	0.4475
Error	27	141.500		
<i>Macomona</i>				
treatment	2	347.100	1.526	0.2355
dispersal mode	2	2802.000	12.320	0.0002
treatment x dispersal mode	4	1654.000	3.637	0.0170
Error	27	3069.000		

For *Macomona* a significant interaction between treatment and dispersal mode was detected. Levene's test showed unequal variances for the dispersal data of the *Austrovenus* and *Macomona* treatment, therefore the Welch test was performed. The dispersal modes of juvenile *Macomona* in the *Macomona* treatment revealed a significant difference (Table 4.3), but with Tukey's pairwise comparisons of the different dispersal modes no significant difference could be detected. In contrast, the ANOVA of the control data showed a significant difference of the dispersal mode and Tukey's pairwise comparison revealed significant

differences between crawling (acrylic floor) and rolling (bedload trap) and between rolling (bedload trap) and drifting (plankton net) for juvenile *Macomona* (Table 4.3).

Table 4.3 Results of the Welch test/ANOVA per treatment for dispersal of juvenile *Macomona* with results of the post hoc test (Turkey’s HSD) for differences in their capture position (acrylic floor, bedload trap, plankton net)

dispersal of juvenile <i>Macomona</i>									
treatment	test	df	sum of squares	F-ratio	p-value	Tukey’s pairwise comparison of dispersal mode	Q-value	p-value	
<i>Austrovenus</i>	Welch	4.772	395.669	4.767	0.07282				
						acrylic floor/bedload trap	0.272	0.98000	
						acrylic floor/plankton net	2.579	0.21660	
						bedload trap/plankton net	2.851	0.16410	
<i>Macomona</i>	Welch	4.006	1288.330	7.763	0.04186				
						acrylic floor/bedload trap	0.983	0.77250	
						acrylic floor/plankton net	3.411	0.09034	
						bedload trap/plankton net	2.428	0.25140	
control	ANOVA	2	2771.670	26.590	0.00017				
						acrylic floor/bedload trap	8.379	0.00073	
						acrylic floor/plankton net	1.017	0.75900	
						bedload trap/plankton net	9.396	0.00041	

The dispersal mode differed slightly with the size of the juvenile bivalves (Fig. 4.5). The smallest juveniles dispersed furthest. *Austrovenus* juveniles that were found in the bedload traps were slightly (not significantly) smaller than those, which were recovered from the acrylic (Table 4.4). *Macomona* juveniles that floated into the plankton net were slightly smaller than those, which crawled on the acrylic or rolled into the bedload traps. For *Macomona* the differences in size per capture position in the flume were significant (Table 4.4). The post hoc test (Mann-Whitney) identified significant differences between the size of *Macomona* juveniles which remained in the core and those which rolled in the bedload traps (Table 4.5). Furthermore the size of *Macomona* juveniles which drifted into the plankton net was significantly smaller than the size of *Macomona* juveniles which remained in the cores or crawled on the acrylic floor or rolled into the bedload traps (Table 4.5).

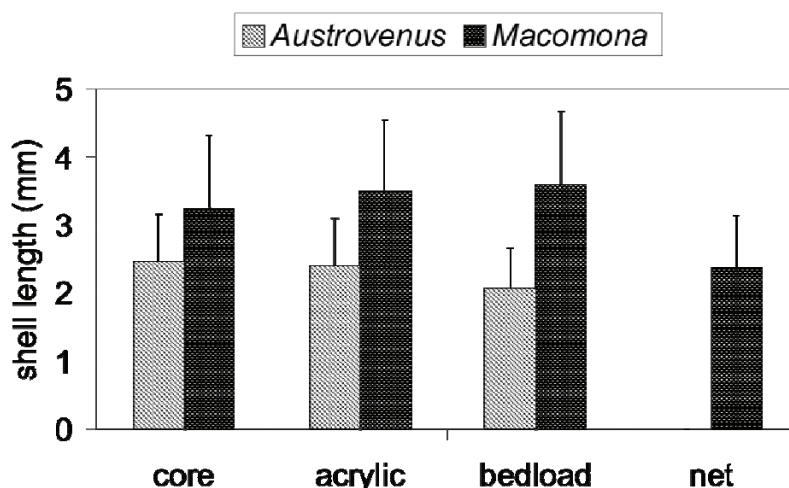


Figure 4.5 Mean size of juvenile *Austrovenus* and *Macomona* at the different locations in the flume with standard deviation

Table 4.4 Results of the Kruskal Wallis test of size of juvenile *Austrovenus* and *Macomona* in relation to their capture position in the flume (acrylic, bedload traps, plankton net)

	H(chi ²)	Hc(tie corrected)	p-value
<i>Austrovenus</i>	2.137	2.142	0.34260
<i>Macomona</i>	22.62	22.65	0.00005

Table 4.5 Results of the post hoc test of juvenile *Macomona* sizes per capture position in the flume

Mann-Whitney pairwise comparisons of <i>Macomona</i> sizes per capture position	Bonferroni corrected p-values
inside core/acrylic floor	0.4012
inside core/bedload traps	0.0244
inside core/plankton net	0.0101
acrylic floor/bedload traps	1.0000
acrylic floor/plankton net	0.0009
bedload traps/plankton net	0.0002

4.5 Discussion

In comparison to the control, the treatments with adult *Austrovenus* and adult *Macomona* had no significant effect on the post-settlement dispersal of juvenile *Austrovenus* and *Macomona*. Lundquist et al. (2004) compared the dispersal of juvenile *Austrovenus* and *Macomona* in response to 3 different flow velocities (in average 4.8, 11.0, and 16.6 cm s⁻¹) and 2 different substrates (defaunated natural sediment versus glass beads) in the same flume that was used for this study. For juvenile *Austrovenus* the authors reported a similar mean percentage of total dispersal from natural sediment at 11.0 cm s⁻¹ as in this study at 14.98 cm s⁻¹. For

juvenile *Macomona* the mean percentage of total dispersal from the adult *Austrovenus* treatment was slightly higher in this study than from natural sediment at 11.0 cm s^{-1} in the experiment of Lundquist et al. (2004). The total dispersal of juvenile *Macomona* from the adult *Macomona* treatment and the control was slightly higher than from the natural sediment at 16.6 cm s^{-1} in the study of Lundquist et al. (2004). The lack of significant results in response to the adult treatments might be a consequence of the low number of replicates, although Lundquist et al. (2004) also had only 4 replicates in their experiment and found significant effects of their treatments (flow and substrate). The effects of adults on juvenile dispersal might be so small that it cannot be detected with a relatively small number of replicates. In addition, the natural variability of these effects might be high. For example, Thrush et al. (2000) found increased negative effects of adult *Macomona liliana* on juveniles at average wave velocity at the seabed, but maximum wave velocity decreased the strength of the observed adult-juvenile interactions, implying highly site specific effects. That would explain the mixed outcomes of field studies dealing with adult-juvenile interactions of *Austrovenus* and *Macomona* (Legendre et al. 1997; Thrush et al. 1992, 1994, 2000; Turner et al. 1997). Although flume experiments have the advantage of controlled conditions, they have the disadvantage that there might be factors in nature which trigger adult-juvenile interactions which were not present in the flume.

Another hypothesis is that the bottom roughness created by moving adult *Austrovenus* protected the juveniles from the flow and therefore their dispersal was slowed. Maybe the juveniles were even passively buried by the adult *Austrovenus*. It was expected that the siphon activities in particular by adult *Macomona* would disturb the settlement of juveniles (Woodin 1976). Maybe the density of adults was too low in the treatment cores to measure such an effect. Ólafsson et al. (1994) argued that most negative effects were detected at unnatural high adult densities. Furthermore, they pointed out in their review that mainly experiments with measured effects were published and only few articles without effects are available. This study is an example of no effects of the presence of adult bivalves on the dispersal of juveniles, because no significantly more/less juveniles dispersed away from the control without adults than from the treatments with adults.

As described by Lundquist et al. (2004), the observed dispersal modes of the juveniles confirmed, that *Austrovenus* mainly dispersed by crawling and only few individuals rolled into the bedload traps. In contrast, juvenile *Macomona* were mainly found in the bedload

traps. Only some juvenile *Macomona* crawled on the acrylic floor of the flume and some floated into the plankton net. It was expected, that smallest individuals dispersed furthest (into the plankton net), because heavier juveniles are less mobile. Thus, the use of more small *Macomona* juveniles probably would have led to enhanced dispersal by drifting.

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5 Synthesis

5.1 Characteristics of the Inner Jade in May 2010

The Inner Jade is a highly anthropogenically impacted tidal channel with a very heterogeneous sediment distribution (Capperucci and Bartholomä 2012). Areas of interest comprised the regularly dredged old navigation channel in the centre, the eastern non-dredged area, and the western area which was dredged for the construction of the deep-water port JWP. Only two stations in the north-western area were recently (in 2010) dredged for the JWP. In the regularly dredged old navigation channel the date of the last dredging activity is not exactly known, because the WSA provided only data about the annual volume of dredged material. The acoustic classification (chapter 2) reflected various dredge marks in the western area which was dredged for the JWP and in the regularly dredged old navigation channel. In contrast, in the undisturbed eastern area natural bedforms dominated which were already reported by Kubicki and Bartholomä (2011).

5.2 Benthic habitat mapping in the Jade

Many studies demonstrated that acoustic seabed classification using sidescan sonar systems (SSS) is a suitable tool for the detection of benthic habitats in various environments (Brown et al. 2004b; Ehrhold et al. 2006; Zajac et al. 2003; Franklin et al. 2003; Brown and Collier 2008). SSS were developed in the 1940s (Kenny et al. 2003). For many years geologists used the acoustic backscatter from SSS to segment the seafloor into geological classes (i.e. surficial sediment types; Brown et al. 2011). Collier and Brown (2005) reported a close association between acoustic backscatter strength and geotechnical properties of the seafloor. Many sedimentological factors (e.g. grain size, volumetric heterogeneity, fine-scale roughness of surface sediment) and significant slope variation may play an important role in the acoustic response (Urlick 1983). Thus, the relationships between backscatter and sediments are not always clear (Ehrhold et al. 2006).

Conventionally, segmentation of the backscatter data was done by manual expert interpretation, whereby the mosaicked imagery is divided into areas of similar texture or backscatter strength “by eye” (Brown et al. 2011). This approach of expert classification was

employed for mapping discrete biological characteristics from a range of environments (e.g. Brown et al. 2002; Cook et al. 2008; Greene et al. 2007; Nitsche et al. 2007). More recently, automated methods of segmenting SSS backscatter data have been explored (Brown et al. 2011), which have the advantage of eliminating the subjectivity of the expert segmentation process (Ehrhold et al. 2006; Brown and Collier 2008). However, in the Inner Jade the attempt to use automated and semi-automated classification tools did not succeed, due to the high variability of both sediments and morphologies. The sediment heterogeneity of the study area was increased by the construction works for the JWP with the introduction of new sources of different sediments (e.g. the clay formation “Lauenburger Ton”, whose outcrops were extremely rare in the Jade system, before the JWP construction works had begun). In addition, specific features (i.e. different generations of dredging marks, in some cases partially reworked by the high dynamic sediments) generated patterns, which lead to misclassification. Therefore, manual expert classification was used for the identification of habitats in the Inner Jade.

The high degree of sediment heterogeneity (patchy distribution of 10 sediment classes) was problematic for the identification of discrete boundaries between the physical habitats (Brown et al. 2004a). The manual expert classification revealed 10 acoustic classes (A-J), which did not coincide with the 10 sediment classes (the RELATE routine identified no significant relationship between the resemblance matrices of the acoustic classes and the sediment classes). Low backscatter intensities (acoustic class A) were detected in areas, where muddy sand and slightly gravelly sand dominated in front of the bulkhead and in the southern area. In contrast, shells are known as strong and characteristic acoustic reflectors (Wienberg and Bartholomä 2005), therefore the north eastern area was clearly identifiable as high backscatter region (acoustic class I). The medium backscatter classes (B-H) were dominated by various sediments (slightly gravelly sand, sandy mud, muddy sand, slightly gravelly sandy mud). Thus, the acoustic classification represented the dredge marks and natural bedforms, but not the full heterogeneity of sediments in the Inner Jade. Brown and Collier (2008) concluded that in certain environments it is not possible to extrapolate substrate maps based on acoustic signatures. Due to the high anthropogenic impact in combination with natural variability the Inner Jade seemed to be an example for such an environment.

The SIMPROF analysis of the macrofauna abundance data (55 stations) revealed 5 different communities (I-V) in the study area, whereby “community I” consisted of only 4 stations and

was a group of statistical outliers. Two communities (III and IV) prevailed in the non-dredged north eastern area (acoustic class I, high backscatter). The non-dredged south eastern area (acoustic class C, medium backscatter) and the old navigation channel (acoustic class F, medium backscatter) were dominated by another community (II). The western area which was dredged for the JWP (acoustic classes A (low backscatter), B, D, E, G, (medium backscatter), J (high backscatter)) was dominated by community V. The low, but significant correlation between the resemblance matrices of the acoustic classification and the macrofauna community structure stressed the heterogeneity in the Inner Jade.

The low average similarity of the macrofauna communities (4-49%, results of the SIMPER test) indicated a high level of spatial heterogeneity also within the species distribution. According to other studies in heterogeneous environments (Brown et al. 2004a; Markert et al. 2015) this spatial heterogeneity of species distribution was probably linked to the high heterogeneity of sediments. Indeed, a low, but significant correlation between the macrofauna community structure and the 10 sediment classes was detected by the RELATE routine. However, only few taxa with known sediment preferences were characteristic taxa in the Inner Jade. These were Anthozoa which settled on gravel and shells in the undisturbed north eastern area (communities III and IV). In contrast, *Corophium volutator* and *Petricolaria pholadiformis* prefer fine sediments (Fenchel et al. 1975; Tebble 1976) and were found in the regularly dredged old navigation channel and at some stations in the undisturbed south eastern area (communities I and II). *Scoloplos (Scoloplos) armiger* (communities III, IV, V) is more cosmopolitan without a real sediment preference (Coosen et al. 1994) and the opportunist *Pygospio elegans* (communities II, III, IV, V) has also a wide habitat tolerance (Bolam and Fernandes 2003). Therefore, these taxa cannot be used as indicators for a particular sediment type. Additionally, the impoverished macrofauna abundance in the areas, which were dredged for the JWP, was most likely a result of the physical disturbance by the conducted dredging activities and not on sedimentary characteristics of the bottom. In general, the macrofauna data proofed that quick re-colonisation after the cessation of dredging activities is possible in highly dynamic areas (Borja et al. 2010), such as the Inner Jade. Nevertheless, the dominating community (community V) showed still the characteristics of an early succession state (low taxa number, low abundance, and dominance of cosmopolitan and opportunistic taxa).

5.3 Factors determining macrofauna community structure in the Inner Jade

The DISTLM analysis (chapter 2) revealed that the number of days after the last dredging/dumping activities for the JWP was the most important parameter structuring the variability of macrofauna communities in the Inner Jade, followed by sediment characteristics (content of sand, mud and shell debris). Depth, high and low backscatter grey values and dredging intensity (expressed as the number of dredging days for the JWP) played also a significant role. Gravel content was less important, because only a small community in the north eastern area (community IV) appeared on undisturbed stations with elevated gravel content. The spatial distribution of the other community in the undisturbed north eastern area (community III) was best explained by the presence of shell debris. In and close to the old navigation channel a community (community II) prevailed which showed an affinity to elevated mud contents. The dominating community (community V) occurred mainly in the area which was dredged for the JWP and which was also the deepest site of the study area and dominated by sand. However, the total degree of variation explained by all these variables was rather low at 40%, indicating that there were additional structure forces active in the study area.

The BIOENV analysis (chapter 3) confirmed the importance of the number of JWP dredging days for the subset of macrofauna abundance data (30 stations) in 2010. Sediments (content of sand, mud and gravel) and depth explained less of the macrofauna community structure than the dredging intensity (36% of the variability within the resemblance matrix of the macrofauna abundance was explained by the number of JWP dredging days). In contrast, the biomass data were best explained by the gravel content, because Anthozoa made up the highest biomass in the study area and settled on coarse material.

The unknown dredging intensity in the old navigation channel could be also helpful information to describe the species composition in the study area. In the adjacent Jade Bay Schückel et al. (2015) found that the macrofauna community structure was best explained by the variability of tidal current velocity and depth, followed by sediment characteristics (mud, total organic carbon, gravel and median grain size). By using these natural parameters, Schückel et al. (2015) could also only explain 30% of the total variability in the species composition. Therefore the authors suggested that variables related to food availability (e.g. chlorophyll a content), predation or topographical characteristics could be responsible for the unexplained variability.

5.4 Effects of dredging activities

The impacts of dredging activities on the seabed and the associated macrofauna have been widely reviewed (e.g. Newell et al. 1998; ICES 1992, 2016; Boyd et al. 2003). Direct removal of sediments and the extraction of associated fauna results in a decrease in species abundance, diversity, and biomass (Kenny et al. 1998; Newell et al. 1998, 2002; Sardá et al. 2000; van Dalfsen et al. 2000; van Dalfsen and Essink 2001; Sutton and Boyd 2009; ICES 2016). Adjacent areas can be also affected by the deposition of material mobilised by dredging and transported outside the boundaries of the dredge site (Newell et al. 2002, 2004; Hitchcock and Bell 2004). Thus, the key question is not whether dredging activities have an impact, but to which extent the affected macrofauna communities can recover (MESL (Marine Ecological Surveys Limited) 2007). Within the JWP project the intensity of dredging activities peaked in 2009, with a total of 19.05 million m³ being extracted for construction and fill purposes (ICES 2016). Due to the ongoing dredging activities, the study in 2010 could only investigate the intermediate effects of physical disturbance in the Inner Jade. Thus, the recovery potential of the study area can only be hypothesized.

During the construction of the JadeWeserPort, the sand extraction for land reclamation and the redirection of the old navigation channel changed the bathymetry of the study area in the Inner Jade markedly (see comparison of data measured by singlebeam (2002) and multibeam (2010) echo-sounder, chapter 3). The western area close to the JWP showed geometries that matched the different dredging phases close to the bulkhead. While in 2002 the old navigation channel was the deepest part of the study area (approximately 20m), the sand extraction resulted in two almost 50m deep pits north and south of the JWP.

Physical recovery from dredging activities is complete when dredge tracks and pits are no longer detectable and where sediment composition is similar to either pre-dredge conditions or local reference sites (Foden et al. 2009; Sutton and Boyd 2009; ICES 2016). The length of time that dredge tracks and pits remain as distinctive features on the seabed can range from a month to decades (Foden et al. 2009). In stable gravelly areas of moderate hydrodynamics, dredge tracks were visible for several years or even decades (Cooper et al. 2007; Sutton and Boyd 2009). In contrast, in areas with mobile sands and high hydrodynamics, such as the Inner Jade (Kubicki and Bartholomä 2011), the dredge tracks may be smoothed within a few months after cessation of the dredging activities (ICES 2016). The sedimentation of material

in the two deep extraction pits depends on trapping efficiency and sediment transport, which depends on flow rate as well as wave and sediment properties (Hoogewoning and Boers 2001). Several decades are sometimes insufficient for physical recovery, especially in areas with low hydrodynamics and weak sediment transport (Kubicki et al. 2007). However, in the Jade highly mobile sands dominate (Kubicki and Bartholomä 2011) and current velocity is relatively high (maximum average flow velocity is generally greater than 1.5m/s, Grabemann et al. 2004). Thus, it is expected, that the natural rate of infill of the two pits will happen faster than decades. In addition, the extracted clay formation “Lauenburger Ton” (which is not suitable for land reclamation) was dumped into the formerly exploited southern extraction site (Kluth and Ehmen 2010).

Studies have shown that sediment change may delay or prevent recovery to a pre-dredged state (Cooper et al. 2011; Wan Hussin et al. 2012). In comparison to 2002, the composition and distribution of sediments had changed markedly in 2010, but the impact of the JWP construction works was hardly distinguishable from the natural variance. In 2002, the study area was dominated by sediments with medium and high mud content. In contrast, sand dominated the Inner Jade in 2010. This coarsening trend in the construction area could be attributed to the direct dumping of sand in the bulkhead area, or the exposure of the Pleistocene sand deposits beneath the removed sea bottom. Naturally, the region is dominated by a dynamic sediment transport regime, confirmed by the existence of large, very mobile bedform fields (Kubicki and Bartholomä 2011). The mobile sand layer, nourished by the dredging activities, could temporally cover the previously existing fine deposits and/or replace them. In contrast, the reworking and dispersion of the clay deposit “Lauenburger Ton” could potentially explain the increase of mud content at some eastern stations, although other sources (e.g. dredging spoils of the dredging area “Neuer Vorhafen”; natural presence of fine sediments in the Jade Bay) could not be excluded. The old navigation channel was the most stable area with fine sediments in 2002 and 2010. The slight increase in mud content measured in 2010 could also be linked to the “Lauenburger Ton” dredging and dumping activities (although different sources could not be excluded). Beside the two sand extraction pits the old navigation channel was the deepest part of the study area and seemed to act as trap for sediments (ICES 1992).

There is no evidence that the observed sediment changes were controlled by a variation in the hydrodynamic conditions. Kahlfeld and Schüttrumpf (2006) modelled the impact of

deepening and narrowing the Inner Jade on the morphodynamics. They predicted that only local changes in flow velocity would occur in the immediate proximity of the JWP. In comparison with the maximum average flow velocities (generally larger than 1.5m/s, Grabemann et al. 2004), the predicted values (mean ebb flow velocity increased up to +0.1m/s) were too low for inducing sediment changes.

The distribution of macrofauna communities is strongly related to hydrodynamic, morphological, and sediment parameters (Gray 1974; Pearson and Rosenberg 1978; Snelgrove and Butman 1994; Rosenberg 1995; Kröncke and Bergfeld 2003; Baptist et al. 2006; Kröncke 2006; see also chapter 1). Thus any physical changes in the seabed will lead to a response in the macrofauna community structure (ICES 2016). The cluster analysis of the 2002 macrofauna dataset revealed, that only one community in the north-eastern area (community “A” (2002)) was distinguishable from the predominating community (community “B” (2002)) in the remaining study area. Thus, the study area seemed to be more homogeneous in 2002 than in 2010, where four significantly different communities (communities “C”, “D”, “E”, “F” (2010)) were found. In 2010, these four communities roughly resembled the different categories of dredging activities.

While Schuchardt et al. (2003) found mainly pelophilous species in the western Inner Jade, the new analysis of the 30 stations revealed characteristic taxa (*Nephtys hombergii*, *Nephtys* spp. juv., *Macoma balthica*, *Scoloplos (Scoloplos) armiger*) in the predominating community (community “B” (2002)) without strict sediment preferences. The predominating community in 2002 (community “B” (2002)) showed the characteristics of an early succession stage (low taxa number, low abundance and low diversity) already. This was problematic for identifying effects of the dredging activities for the JWP. Nevertheless, a reduction of taxa number, abundance and diversity was found at the two recently dredged stations in 2010. This north-western area (community “C” (2010)) was re-colonised by highly mobile species (*Gastrosaccus spinifer* and *Pontocrates altamarinus*).

The date of the last dredging activity by the WSA in the regularly dredged old navigation channel is not exactly known, but the dominating taxa (*Corophium volutator* and *Pygospio elegans*) inhabiting that area were typical opportunistic (r-selected) species which indicate an early succession stage (community “E” (2010)). This community was restricted to areas with medium or high mud content, because the characteristic species *Corophium volutator* and

Petricolaria pholadiformis prefer fine sediments (Fenchel et al. 1975; Tebble 1976). The sampling campaign in April 2002 (before the construction works for the JWP had begun) comprised 199 samples in the Inner Jade (Schuchardt et al. 2003) whereof 30 sample positions coincided with the sampling design in May 2010 (during the final construction phase; chapter 3). The larger extension of the area (between km 40 and km 5 of the old navigation channel) sampled by Schuchardt et al. (2003) explains why the investigators found mainly psammophilous species in the old navigation channel (see chapter 1). The northern part of the old navigation channel (between km 40 and km 15) was dominated by coarse sand (Schuchardt et al. 2003). The study area of chapter 3 comprised only the southern part between km 14.5 and km 7.1 of the old navigation channel and this part was dominated by fine sand with elevated mud contents, already in 2002 (Schuchardt et al. 2003).

The Anthozoa dominated community (community “A” (2002)) in the non-dredged north-eastern area was still present in 2010 (community “D” (2010)), but expanded by four stations. In the north-eastern area the highest taxa number, abundance and diversity was detected. The dominance of Anthozoa coincided with the presence of gravel in 2010 and explained the high biomass in the north-eastern area. At the southern transect and in the transition areas between the other three communities, a fourth community (community “F” (2010)) was found mainly on sandy sediments.

All taxa from the 2010 samples are typical inhabitants of the southern North Sea, which were found in the study area prior to the JWP construction (Dörjes et al. 1969; Schuchardt et al. 2003). Thus, the increased taxa number and abundance in the old fairway and the not dredged areas could not be explained by the presence of invasive species. Poiner and Kennedy (1984) suggested that the observed fast increase of biodiversity and population density outside the dredged areas in the Australian Moreton Bay was due to the sediment plume of fine particles generated by dredging activities, because this increase in suspended organic material enhanced the food availability. In fact, the number of omnivores and deposit feeders in the Inner Jade increased markedly in the non-dredged areas. In the UK, Newell et al. (2002) reported an enhancement of benthic biomass at distances beyond the suppressed area (>500m northwest). The authors suggested that this enrichment was due to organic matter released either from the water column or from benthic boundary layer plumes (Newell et al. 2002). Newell et al. (2004) reported also an enhancement of species diversity, population density, biomass and mean body size of the macrofauna in the sediments surrounding the dredge site.

The possibility that this increase reflects organic enrichment needs further investigations (Newell et al. 2004).

In contrast, the abundance and spatial distribution of the polychaete *Nephtys hombergii* declined significantly in 2010, even in the non-dredged areas. Its sensitivity to low winter temperatures (Beukema et al. 2000) has to be taken into account, because the mean temperatures of January (-0.2 °C) and February (0.9 °C) 2010 were lower than in January (0.6 °C) and February (6.0 °C) 2002. Monthly CTD time series data, measured by the RV “Senckenberg” revealed up to 5°C difference in February at ton 48 (geographic position according to WGS84 UTM32N: Easting 445722.91099; Northing 5937336.36463) in the study area between 2002 and 2010. This suggests a temperature-dependent decrease of the predator *Nephtys hombergii*, which may have contributed to the relatively high abundance of its main prey the polychaete *Scoloplos (Scoloplos) armiger* in 2010. Cold winters can have a strong influence on the abundance of several species (Kröncke et al. 2013) and interannual variability may have masked the impact of the dredging activities for the JWP in the Inner Jade.

Chapter 3 confirmed that quick re-colonisation is possible after physical disturbance in highly dynamic areas (Borja et al. 2010). Recovery rates after cessation of the dredging activities are highly site specific (Boyd et al. 2004; Cooper et al. 2005; Kenny and Rees 1994, 1996; Kenny et al. 1998). In general, macrofaunal recovery after dredging proceeds from initial colonisation beginning within days to recovery of diversity within months, recovery of population density after several months and biomass recovery after one or more years (ICES 1992; Newell 2004; Foden et al. 2009). When dredging activities remove the surface layers of sediments, the remaining substratum may be a totally different sediment type than the original one and might be unsuitable for re-colonisation by the species that previously inhabited the area (Kenny and Rees 1996; Boyd et al. 2005; ICES 2016). Thus, despite the high re-colonisation potential of the study area, it is unlikely that full recovery to the state of the 1960s (Dörjes et al. 1969) or 2002 (Schuchardt et al. 2003) is attainable.

5.5 Re-colonisation by post-settlement dispersal

Drifting of pelagic larvae is widely recognised as the main procedure for the re-colonisation of large disturbed habitats (Günther 1992), but recently post-settlement dispersal appears to be

at least similarly important (Pilditch et al. 2015). Most likely post-settlement dispersal played a crucial role for the re-colonisation of the dredged area in the Inner Jade. The observed distribution of juvenile and adult *Macoma balthica* over a wide range of different habitats in the entire study area was probably a result of post-settlement dispersal. Juvenile Mytilidae can disperse by byssus drifting (Armonies 1996) and originated possibly from the mussel farms and banks in the Inner Jade (Herlyn and Millat 2000). The appearance of the mud snail *Peringia ulvae* in the southern area could also be explained by drifting. This species occurred in very high abundances in the adjacent Jade Bay (Schückel et al. 2013) and disperses by floating at the water surface (Armonies and Hartke 1995). Trap studies showed that organisms of multiple taxa disperse more or less continuously as juveniles and adults (Armonies 1994; Valanko et al. 2010). The competence of juvenile and adult dispersers is even higher than of vulnerable larvae (Pilditch et al. 2015), because fitness and the probability of survival increases with age (Gosselin and Qian 1997).

5.6 Adult-juvenile interactions of a deposit-feeding and a suspension-feeding bivalve in a flume

The effects of the presence of two adult bivalve species, the suspension-feeding *Austrovenus stutchburyi* (hereafter *Austrovenus*) and the deposit-feeding *Macomona liliana* (hereafter *Macomona*), on the post-settlement dispersal of their juveniles were examined in a flume experiment (chapter 4). In comparison to the control without adult bivalves, the treatments with adult *Austrovenus* and adult *Macomona* had no significant effect on the post-settlement dispersal of juvenile *Austrovenus* and *Macomona* (see results of the one way ANOVA, Table 4.1). The experimental set up of this study was inspired by the study of Lundquist et al. (2004) who compared the dispersal of juvenile *Austrovenus* and *Macomona* in response to 3 different flow velocities (in average 4.8, 11.0, and 16.6 cm s⁻¹) and 2 different substrates (defaunated natural sediment versus glass beads) in the same flume that was used for this study. For juvenile *Austrovenus* Lundquist et al. (2004) reported a similar mean percentage of total dispersal from natural sediment at 11.0 cm s⁻¹ as in this study at 14.98 cm s⁻¹. For juvenile *Macomona* the mean percentage of total dispersal from the adult *Austrovenus* treatment was slightly higher in this study than from natural sediment at 11 cm s⁻¹ in the experiment of Lundquist et al. (2004). The total dispersal of juvenile *Macomona* from the adult *Macomona* treatment and the control was slightly higher than from the natural sediment at 16.6 cm s⁻¹ in the study of Lundquist et al. (2004). The lack of significant results in

response to the adult treatments might be a consequence of the low number of replicates, although Lundquist et al. (2004) also had only 4 replicates in their experiment and found significant effects of their treatments (flow and substrate). The effects of adults on juvenile dispersal might be so small that it cannot be detected with a relatively small number of replicates.

The two way ANOVA revealed significant differences between the dispersal modes of juvenile *Austrovenus* and *Macomona* (Table 4.2). As described by Lundquist et al. (2004), most *Austrovenus* juveniles dispersed by crawling on the acrylic floor of the flume, only few individuals were found in the bedload traps and none drifted into the plankton net. In contrast, juvenile *Macomona* were mainly found in the bedload traps. Only some juvenile *Macomona* crawled on the acrylic floor of the flume and some floated into the plankton net. For juvenile *Macomona* a significant interaction between the factors “treatment” and “dispersal mode” was detected (Table 4.2), because in the control significantly more juvenile *Macomona* were found in the bedload traps than on the acrylic floor or in the plankton net (see results of the ANOVA, Table 4.3). The Welch test for the *Macomona* treatment revealed also a significant *p*-value for the dispersal mode of juvenile *Macomona* (Table 4.3), but the post hoc test (Tukey’s Honestly Significant Difference) showed no significant differences in the pairwise comparisons of dispersal mode. These non significant results can be probably explained by the small effect size versus the relatively small number of replicates. The Kruskal Wallis test identified a significant difference in the size of juvenile *Macomona* per capture position in the flume (Table 4.4). The Mann-Whitney pairwise comparisons showed that the *Macomona* juveniles in the plankton net were significantly smaller than those recovered from inside the cores, the acrylic floor or the bedload traps (Table 4.5). It was expected, that smallest individuals dispersed furthest (into the plankton net), because heavier juveniles are less mobile. Thus, the use of more small *Macomona* juveniles probably would have led to enhanced dispersal by drifting.

The natural variability of the effects of adults on juvenile dispersal is most likely high. For example, Thrush et al. (2000) found increased negative effects of adult *Macomona* on juveniles at average wave velocity at the seabed, but maximum wave velocity decreased the strength of the observed adult-juvenile interactions, implying highly site specific effects. That would explain the mixed outcomes of field studies dealing with adult-juvenile interactions of *Austrovenus* and *Macomona* (Legendre et al. 1997; Thrush et al. 1992, 1994, 2000; Turner et al. 1997). Although flume experiments have the advantage of controlled conditions, they have

the disadvantage that there might be factors in nature which trigger adult-juvenile interactions which were not present in the flume.

During the flume experiment, it was observed, that adult *Austrovenus* were highly mobile. Their movements in the cores created a bottom roughness, which probably protected the juveniles from the flow and therefore their dispersal was slowed. Maybe some juveniles were even passively buried by the moving adult *Austrovenus*. Adult *Macomona* were buried in the cores and showed siphon activities at the surface. It was expected that the siphon activities in particular by deposit feeding adult *Macomona* would disturb the settlement of juveniles (Woodin 1976). Probably the density of adults was too low in the treatment cores to measure such an effect. Ólafsson et al. (1994) argued that most negative effects were detected at unnatural high adult densities. Furthermore, they pointed out in their review that mainly experiments with measured effects were published and only few articles without effects are available. This study is an example of no effects of the presence of adult bivalves on the dispersal of juveniles, because no significantly more/less juveniles dispersed away from the control without adults than from the treatments with adults.

5.7 Suggestions for future research

By sampling in study areas such as the Inner Jade a higher number of replicates is advisable, in order to catch the full heterogeneity of sediments and macrofauna. Ideally, the same worker processes the samples in the lab, in order to avoid artefacts by different accuracy in species determination. Furthermore, the company BIOCONSULT did not collect biomass data, but this would have been useful information by which one could determine if lighter/heavier individuals dominated the study area during the reference state in 2002. If for instance more juveniles or small opportunistic (r-selected) species were present, this would give a hint to an early re-colonisation state. In contrast, the dominance of big adult K-selected species indicates an equilibrium state of the ecosystem.

Adult-juvenile interactions of *Austrovenus stutchburyi* and *Macomona liliana* seem to have only a small effect size. Most likely a higher number of replicates would have produced significant results in the flume experiment. The use of more small *Macomona liliana* juveniles probably would have led to an increased number of drifting individuals. Maybe the number of adults in the treatments was too low to measure an effect. Nevertheless, natural adult densities should be chosen, in order to make the results meaningful.

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6 Summary

6.1 Summary

The objectives of this thesis were to:

- I) compare patterns of hydroacoustics, sediments and macrofauna in the Inner Jade, a heterogeneous study area, which is naturally highly dynamic and influenced by various anthropogenic stressors.
- II) study the direct and indirect effects of ongoing dredging activities on the spatial distribution of sediments and macrofauna in the Inner Jade.
- III) assess the impact of the presence of two adult bivalve species (*Austrovenus stutchburyi* and *Macomona liliana*) on the post-settlement dispersal behaviour of juveniles in a flume.

During the construction of a deep-water port (JadeWeserPort), bathymetry, sediment distribution, and macrofauna community structure were studied in the Inner Jade, a tidal channel located in the southern North Sea. The relationships between macrofauna community structure and natural as well as anthropogenic environmental variables were investigated in this very heterogeneous study area. The manual expert hydroacoustic classification of the backscatter image derived by side scan sonar was successful to detect the different dredging activities and the natural bedforms in the undisturbed areas. The sediment distribution was very patchy and no significant congruence with the hydroacoustic classification could be identified. In contrast, low, but significant relationships between the hydroacoustic classification and the macrofauna community structure as well as the sediment distribution and the macrofauna communities were found. The most important impact on the spatial community structure was the number of days after the last dredging/dumping activity for the JadeWeserPort (JWP), followed by the sediment characteristics explained by grey values of the backscatter image. Sand dominated the western stations, which were dredged for the JWP and were inhabited by a characteristic macrofauna community. Another community occurred mainly on stations with elevated mud content in the regularly dredged old navigation channel and the undisturbed south eastern area. The communities in the north eastern undisturbed area coincided with elevated contents of gravel and shells. This study stresses the problems of benthic habitat mapping in such a heterogeneous area.

In order to assess the effects of physical disturbance by dredging activities, macrofaunal community compositions between 2002 (before the construction work had begun) and 2010 (during the final construction phase) were compared. The sand extraction for land reclamation and the redirection of the navigation channel changed the bathymetry markedly. While the old navigation channel in the centre of the study area remained mud dominated, a general increase in coarse sediments was detected in 2010. The dynamic nature of the study area in combination with the direct and indirect effects of dredging increased the bathymetric heterogeneity (measured by singlebeam (2002) and multibeam (2010) echo-sounder). In 2010, the macrofauna community structure roughly resembled the different categories of dredging activities. The most recently dredged north western area was inhabited by a community, which was different from the community in the regularly dredged old navigation channel. Both were different from the community in the north eastern, non-dredged area. In the southern area, and in the transition areas between the other three communities, a fourth community was found. A general increase in macrofaunal abundance and taxa number was observed in 2010, with the exception of the recently dredged area. The structure of the macrofauna community during the port construction phase seemed to be determined by secondary dispersal of the dominant taxa and recolonisation by highly mobile and opportunistic species.

The effects of the presence of two adult bivalve species with different feeding modes on the post-settlement dispersal of their juveniles were examined in a flume experiment. The treatments consisted of 4 deposit-feeding *Macomona liliana*, 10 suspension-feeding *Austrovenus stutchburyi*, and a control without adults. Flow speed was set at a velocity that did not cause sediment erosion, but was high enough to give the juveniles a chance to actively move. At the end of each experimental run, the capture position in the flume (acrylic floor, bedload traps, plankton net) was related to different dispersal modes of the juveniles (crawling, rolling as bedload transport, and drifting). Over 90% of the juvenile *A. stutchburyi* remained in the sediment cores, regardless of the treatment. In contrast, higher percentages of juvenile *M. liliana* left the *A. stutchburyi* treatment (30%), the *M. liliana* treatment (50%) and the control (50%). The differences of total dispersal between the treatments were not significant. The differences in dispersal mode were significant for both, *A. stutchburyi* and *M. liliana* juveniles. Most *A. stutchburyi* juveniles dispersed by crawling on the acrylic floor of the flume, only few individuals were found in the bedload traps and none drifted into the plankton net. For juvenile *M. liliana* a significant interaction between dispersal mode and

treatment was detected, because in the control significantly more juveniles were found in the bedload traps than on the acrylic floor or the plankton net. The *M. liliانا* juveniles, which drifted in the plankton net were significantly smaller than those on the acrylic floor or in the bedload traps.

6.2 Zusammenfassung

Die Zielsetzungen dieser Arbeit waren:

- I) die Muster von Hydroakustik, Sedimenten und Makrofauna in der Inneren Jade, einem heterogenen Untersuchungsgebiet, das natürlicherweise sehr dynamisch ist und von verschiedenen anthropogenen Stressoren beeinflusst wird, zu vergleichen.
- II) die direkten und indirekten Effekte der andauernden Baggerarbeiten auf die räumliche Verteilung von Sedimenten und Makrofauna in der Inneren Jade zu ermitteln.
- III) den Einfluss der Anwesenheit von zwei adulten Muschelarten (*Austrovenus stutchburyi* and *Macomona liliana*) auf das sekundäre Verbreitungsverhalten von Juvenilen in einem Strömungskanal zu untersuchen.

In der Inneren Jade, einem Tidekanal in der südlichen Nordsee, wurden während der Bauphase eines Tiefwasserhafens (JadeWeserPort) Bathymetrie, Sediment-Verteilung und die Makrofaunagemeinschaftsstruktur erforscht. In diesem sehr heterogenen Untersuchungsgebiet wurden die Beziehungen zwischen der Makrofaunagemeinschaftsstruktur und natürlichen sowie anthropogenen Umweltparametern untersucht. Die manuelle Hydroakustikklassifizierung der Sonographie, die durch einen Seitensicht-Sonar erzeugt wurde, identifizierte erfolgreich die verschiedenen Baggeraktivitäten und die natürlichen Bodenstrukturen in den ungestörten Bereichen. Die Sedimentverteilung war sehr ungleichmäßig und es konnte keine signifikante Übereinstimmung mit der Hydroakustikklassifizierung festgestellt werden. Im Gegensatz dazu, wurden geringe, aber signifikante Übereinstimmungen sowohl zwischen der Hydroakustikklassifizierung und der Makrofaunagemeinschaftsstruktur als auch zwischen der Sedimentverteilung und den Makrofaunagemeinschaften belegt. Den größten Einfluss auf die räumliche Gemeinschaftsstruktur hatte die Anzahl der Tage nach der letzten Bagger- bzw. Verklappungsaktivität für den JadeWeserPort (JWP), gefolgt von Sedimenteigenschaften, die durch die Grauwerte der Sonographie erklärt wurden. Sand dominierte die westlichen Stationen, die für den JWP gebaggert wurden und von einer charakteristischen Makrofaunagemeinschaft besiedelt waren. Eine andere Gemeinschaft trat vor allem an Stationen mit erhöhtem Schlickgehalt in der alten Fahrrinne und dem ungestörten südöstlichen Bereich auf. Die räumliche Verbreitung der Gemeinschaften in dem ungestörten

nordöstlichen Gebiet stimmte mit erhöhten Gehalten an Kies und Schalen überein. Diese Studie hob die Probleme der benthischen Habitatkartierung in einem heterogenen Untersuchungsgebiet hervor.

Um die Auswirkungen der physikalischen Störung durch die Baggararbeiten zu erforschen, wurden die Zusammensetzungen der Makrofaunagemeinschaften in 2002 (vor Beginn der Bauarbeiten) und 2010 (während der letzten Bauphase) verglichen. Die Sandextrahierung zur Landgewinnung und die Verlegung der Fahrrinne veränderten die Bathymetrie deutlich. Während die alte Fahrrinne im Zentrum des Untersuchungsgebietes von Schlick dominiert blieb, wurde in 2010 eine generelle Zunahme grober Sedimente festgestellt. In Kombination mit direkten und indirekten Auswirkungen der Baggararbeiten erhöhte die dynamische Natur des Untersuchungsgebietes die bathymetrische Heterogenität (gemessen mit Einstrahl-Echolot in 2002 und Fächer-Echolot in 2010). In 2010 stimmte die Makrofaunagemeinschaftsstruktur grob mit den verschiedenen Kategorien der Baggararbeiten überein. Die Gemeinschaft im nordwestlichen Gebiet, das erst vor kurzem gebaggert worden war, unterschied sich von der Gemeinschaft in der regelmäßig gebaggerten alten Fahrrinne. Beide Gemeinschaften unterschieden sich von der Gemeinschaft im Nordosten, dem nicht gebaggerten Gebiet. Im südlichen Gebiet und den Übergangsbereichen zwischen den anderen drei Gemeinschaften wurde eine vierte Gemeinschaft gefunden. In 2010 wurde ein genereller Anstieg der Makrofaunaabundanz und Artenzahl beobachtet, mit Ausnahme des zuletzt gebaggerten Gebietes. Die Makrofaunagemeinschaftsstruktur während der Hafenbauphase schien durch sekundäre Verbreitung der dominanten Arten und durch die Wiederbesiedlung mobiler und opportunistischer Arten geprägt zu sein.

Die Einflüsse der Präsenz von zwei adulten Muschelarten mit unterschiedlichen Ernährungsweisen auf die sekundäre Verbreitung ihrer Nachkommen wurden in einem Strömungskanal-Experiment untersucht. Die Behandlungen bestanden aus 4 Ablagerung fressenden *Macomona liliana*, 10 Suspension fressenden *Austrovenus stutchburyi* und einer Kontrolle ohne Adulte. Die Strömungsgeschwindigkeit wurde auf eine Geschwindigkeit eingestellt, die keine Sedimenterosion verursachte, aber hoch genug war, um den Juvenilen eine Chance gab sich aktiv zu bewegen. Am Ende jedes Versuchsdurchlaufs wurde die Auffangposition im Strömungskanal (Acrylboden, Geschiebefallen, Planktonnetz) den verschiedenen Verbreitungsmechanismen der Juvenilen zugeordnet (Krabbeln, Rollen im Geschiebetransport und Driften). Über 90% der juvenilen *A. stutchburyi* blieben in den

Sedimentkernen, unabhängig von der Behandlung. Im Gegensatz verließen höhere Prozentsätze juveniler *M. liliana* die *A. stutchburyi* - Behandlung (30%), die *M. liliana* - Behandlung (50%) und die Kontrolle (50%). Die Unterschiede in der Gesamtverbreitung zwischen den Behandlungen waren nicht signifikant. Die Unterschiede im Verbreitungsmechanismus war dagegen signifikant für beide juvenile Arten, *A. stutchburyi* und *M. liliana*. Die meisten juvenilen *A. stutchburyi* verbreiteten sich durch Krabbeln auf dem Acrylboden des Strömungskanals, nur wenige Individuen wurden in Geschiebefallen gefunden und keine drifteten in das Planktonnetz. Bei juvenilen *M. liliana* wurde eine signifikante Interaktion zwischen Verbreitungsmechanismus und Behandlung festgestellt, weil in der Kontrolle signifikant mehr Juvenile in Geschiebefallen gefunden wurden als auf dem Acrylboden oder im Planktonnetz. Die juvenilen *M. liliana*, die in das Planktonnetz drifteten, waren signifikant kleiner als die Juvenile auf dem Acrylboden oder im Planktonnetz.

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Peer-reviewed publications

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Conference poster

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