Macrozoobenthic response to fishery

trophic interactions in highly dynamic coastal ecosystems

Jennifer Dannheim

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Alfred Wegener Institute
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Makrozoobenthische Reaktion auf Fischerei – trophische Interaktionen in hochdynamischen Küstenökosystemen

Jennifer Dannheim

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„Viele kleine Leute,
an vielen kleinen Orten,
die viele kleine Dinge tun,
werden das Gesicht der Welt
verändern.“

(Afrikanisches Sprichwort)

Summary

The German Bight is a highly dynamic coastal ecosystem driven by strong hydrodynamics and anthropogenic impacts. Intense bottom trawling has been the most severe impact on the German Bight benthos over the last century. Besides the removal of fish and bycatch, bottom trawling has two major impacts on benthic communities: a direct physical impact that causes reduction of habitat complexity, disturbance of sediment and resuspension, as well as dislocation, damage and mortality of benthic organisms; and indirect trophic effects through an alteration of sedimentary biogeochemistry and through fishery bycatch and discards which become a significant food source for predators and scavengers.

The consequences of bottom trawling for benthic trophic functioning are less well studied than the direct effects on community structure descriptors such as species richness, abundance and biomass. Trophic interactions, however, are the principle type of organism-organism relationships and thus are a significant determinant of ecological functioning.

This thesis aims at achieving deeper insights into the ecological functioning of German Bight benthos: I looked for trophic properties of the ecosystem that might explain the resistance of the system in the light of decades of frequent bottom trawling, and focused on recovery patterns of the benthic system during 14 months of trawling cessation.

In order to accomplish this aim, a number of approaches were developed and applied:

(i) Stable isotope ratios served as an indicator for species trophic elevation, i.e. the relative distance of a species to the primary food source within the food web hierarchy. Community trophic complexity and species trophic niche width were determined by means of interspecific and intraspecific variability of trophic elevation. Trophic significance, i.e. a metabolism scaled abundance, served as an indicator of trophic flow through particular populations.

(ii) A new two-dimensional approach to trophic complexity (horizontal and vertical diversity) was developed. It was applied to the German Bight ecosystem, but concurrently provides a robust and standardised tool for the comparison of species and ecosystem trophic properties.

(iii) The response of macrozoobenthos to trawling cessation was investigated over the course of 14 months by two approaches: firstly, multivariate community analyses using numerical measures which follow changes at different system levels: the community level, the level of compartments (e.g. feeding guilds) and the species level; secondly community and species trophic properties, i.e. trophic elevation and trophic significance. For the first time, this approach identified significant changes due to trawling cessation on a short time-scale within a highly dynamic coastal ecosystem.

The synthesis of all results provides a detailed picture of trophic functioning of the German Bight benthos: (a) Most species are trophic generalists, i.e. they are connected by many and mainly ‘weak’ trophic links. (b) Trophic redundancy is comparatively high, i.e. the loss of one species may be compensated functionally by one or more other species. (c) In terms of size distribution, the system is characterised by small-sized organisms with corresponding high turnover rates. These particular food-web properties correspond to high system resistance, i.e. the current state can be maintained despite the severe impact of continuing bottom trawling.

A return of the benthos towards a ‘pre-trawling’ state is rather unlikely. Bottom trawling caused irreversible changes to the habitat and ecosystem structure, and the impact of external synergistic forcing factors persists or might even gain importance in the future, e.g. climate warming and species invasion. A large-scale and long-term fishery ban, however, may cause a benthic regime shift towards a system with lower turnover rate, higher biodiversity and higher trophic complexity. The offshore windmill farms planned in the German Bight might offer a chance for this regime shift in an area of considerable extension, as bottom trawling will be banned here. In view of the current state of the German Bight benthos, the positive effects of a fishery ban may outweigh potential negative effect of windmill farms on the environment.

Zusammenfassung

Die Deutsche Bucht ist ein hochdynamisches Küstenökosystem, welches durch starke Hydrodynamik und anthropogene Einflüsse gesteuert wird. Intensive Grundschleppnetzfischerei, Scherbrett- vor allem jedoch Baumkurrenfischerei, hatte den stärksten Einfluss auf das Benthos der Deutschen Bucht während des letzten Jahrhunderts. Neben der Entnahme von Fisch und Beifang hat Grundschleppnetzfischerei zwei wesentliche Einflüsse auf die benthische Gemeinschaft: einen direkten physikalischen Einfluss, welcher Reduzierung der Habitatkomplexität, Störung und Resuspension des Sediments sowie Dislokation, Schädigung und Mortalität von benthischen Organismen verursacht; und indirekte trophische Effekte durch die Änderung der Sedimentbiogeochemie und des fischereilichen Beifangs und Rückwurfs, welche eine bedeutende Nahrungsquelle für Räuber und Aasfresser darstellen.

Die Konsequenzen der Grundschleppnetzfischerei für die trophische Funktionalität des Benthos sind weniger gut untersucht als die direkten Effekte auf die Gemeinschaftsstruktur anhand von Deskriptoren wie Artenreichtum, Abundanz und Biomasse. Trophische Interaktionen sind jedoch die grundlegendste Art von Beziehungen zwischen Organismen und daher eine aussagekräftige Steuergröße ökologischer Funktionalität.

Ziel dieser Arbeit ist es, tiefere Einsichten in die ökologische Funktionalität des Benthos der Deutschen Bucht zu erhalten: Ich habe trophische Eigenschaften des Ökosystems untersucht, welche die Resistenz des Systems im Hinblick auf jahrzehntelange und häufige Fischerei erklären könnten und mich auf Eigenschaften der Erholung des benthischen Systems während einer Fischereischließung über 14 Monate konzentriert.

Um dieses Ziel zu erreichen, wurden verschiedenste Ansätze entwickelt und angewendet:

(i) Stabile Isotopenverhältnisse dienten als Indikator der trophischen Erhöhung von Arten, d.h. als Indikator der relativen Distanz einer Art zur primären Nahrungsquelle innerhalb der Hierarchie des Nahrungsnetzes. Die trophische Komplexität der Gemeinschaft und die trophische Nischenweite der Arten wurden mittels interspezifischer und intraspezifischer Variabilität der trophischen Erhöhung bestimmt. Die trophische Signifikanz, d.h. eine metabolismus-skalierte Abundanz, diente als Indikator für den trophischen Fluss durch einzelne Populationen.

(ii) Für die trophische Komplexität (horizontale und vertikale Diversität) wurde ein neuer zweidimensionaler Ansatz entwickelt. Dieser wurde auf das Ökosystem der Deutschen Bucht angewendet und bietet gleichzeitig ein robustes und standardisiertes Hilfsmittel für den Vergleich der trophischen Eigenschaften von Arten und Ökosystemen.

(iii) Die Antwort des Makrozoobenthos auf fischereiliche Schließung wurde über den Zeitraum von 14 Monaten durch zwei Ansätze untersucht: Erstens durch multivariate Gemeinschaftsanalysen, welche auf numerischen Maßen basieren, wurde die Veränderung auf verschiedenen systemaren Ebenen untersucht: der Gemeinschaftsebene, der Ebene von verschiedenen Kompartimenten (z.B. Nahrungsgilden) und der Artebene; zweitens, anhand trophischer Eigenschaften, d.h. der trophischen Erhöhung und trophischen Signifikanz, der Gemeinschaft und Arten. Zum ersten Mal wurden mit Hilfe dieses Ansatzes signifikante Veränderungen durch die Schließung der Fischerei über solch einen kurzen Zeitraum und in einem hoch dynamischen Küstensystem identifiziert.

Die Synthese aller Ergebnisse liefert ein detailliertes Bild über die trophische Funktionalität des Benthos der Deutschen Bucht: (a) Die meisten Arten sind trophische Generalisten, d.h. sie sind durch viele und hauptsächlich ‚lose' trophische Verbindungen verbunden. (b) Die trophische Redundanz ist verhältnismäßig hoch, d.h. der Verlust einer Art kann durch eine oder mehrere Arten funktionell ausgeglichen werden. (c) In Bezug auf die Größenverteilung ist das System durch kleine Organismen mit entsprechend hohen Umsatzraten charakterisiert. Diese speziellen Eigenschaften des Nahrungsnetzes entsprechen einer hohen Resistenz im System, d.h. dass der aktuelle Zustand trotz des schweren Einflusses von kontinuierlicher Grundschleppnetzfischerei aufrechterhalten werden kann.

Die Rückkehr des Benthos hin zu einem ‚vorfischereilichen' Zustand ist eher unwahrscheinlich. Grundschleppnetzfischerei hat irreversible Schäden des Habitats und der ökosystemaren Struktur verursacht, und die Wirkung äußerer, synergetischer Einflussfaktoren bleibt bestehen bzw. dürfte in der Zukunft eher noch an Bedeutung zunehmen, z.B. der Einfluss der Klimaerwärmung und der Einwanderung von Arten. Jedoch würde eine großräumige und langfristige Schließung der Fischerei zu einem benthischen System mit geringer Umsatzrate, hoher Biodiversität und hoher trophischer Komplexität führen. Die geplanten Windenergieanlagen vor der Küste der Deutschen Bucht könnten eine Möglichkeit für diese Verlagerung des benthischen Systems in einem Areal von beträchtlicher Ausdehnung sein, da Grundschleppnetzfischerei hier verboten werden soll. In Anbetracht des derzeitigen Zustandes des Benthos der Deutschen Bucht dürfte der positive Effekt der fischereilichen Schließung den möglichen negativen Effekt der Windenergieanlagen auf die Umwelt überwiegen.

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1 Preface

The world's human population is increasing continuously. While in 1950 there were 2.5 billion people on earth, there were already 6.1 billion people in 2003 and the population will further increase (UNO 2004). Concurrently, the demand for food, water and natural resources rises. This has led and will lead to a more and more exceeding economic utilisation of the earth's landscapes and oceans by e.g. agriculture, forestry and mining of natural resources. Between one-third and one-half of the land surface already reached an intensely artificial state. In marine ecosystems, the spatial quantification of human alteration is difficult. The alterations, however, are as well substantial and today only a few pristine sites have remained of marine ecosystems such as parts of the the deep sea and the Antarctic ecosystem (e.g. Vitousek et al. 1997).

Humanity took ecosystem services (benefits provided by an ecosystem to humans) at all times for granted and used the services and goods without knowledge on and thoughtfulness for ecological consequences. Every kind of human utilisation, however, is in some way an interference in the respective ecosystem. Human intervention primarily decreases ecosystem complexity through simplification of habitat structure and reduction of overall biodiversity. Within ecosystems, the number and kinds of the existent species define the organismal traits that constitute ecologcial processes (e.g. Chapin III et al. 2000, McCann 2000). Removing one species from the system means that one link within the trophic web is eliminated. In 1859 Darwin already proposed that diverse polycultures will be more efficient, have lower nutrient losses and more sustainable soils than even the 'best' species monoculture. This has been asserted by current scientific studies (Tilman & Downing 1994, Tilman et al. 1996, Buschmann et al. 2005, Cardinale et al. 2006). Thus, there is a rekindeled interest in the potential effects of species richness and functional diversity on ecosystems (e.g. Tilman 2000, Worm et al. 2006) largely because of the consequences for ecosystem services.

Marine ecosystems provide several services, primarily living and non-living resources, means of transport, waist disposal and processing, leisure and recreational space. About 60 % of the world's population is concentrated near the ocean coasts (within 100 km, Vitousek et al. 1997), and the coastal margins have been affected most strongly by humans. To fulfil the demand for seafood of the steadily growing human population, overall fishing effort has continuously increased over the years. Hitherto, for each fishery the short-term most effective catch stands in the foreground. Overfishing is primarily caused by the lack of individual disposal rights (Gordon 1954), an example for the non-cooperative game theory (e.g. Hardin 1968), provided by the proceeding mechanisation and industrialisation of fishery (Pauly et al. 2003).

Fishing, in particular bottom trawling, is the most severe anthropogenic impact on marine environments (e.g. Dayton et al. 1995, Jennings & Kaiser 1998, Lindeboom & de Groot 1998, Thrush et al. 2001, Kaiser et al. 2006). Besides the removal of fish and bycatch, bottom-trawling has two mayor impacts on benthic communities: On the one hand, a direct physical impact that causes reduction of habitat complexity (e.g. biogenic reefs), disturbance of sediment and resuspension (e.g. Jennings et al. 2001b, Watling et al. 2001), as well as dislocation, damage and mortality of benthic organisms. On the other hand, an indirect trophic effect through fishery bycatch and discards which become a considerable food source for predators and scavengers. Long-term bottom-trawling pushes the soft-bottom communities towards smaller, short-lived and fast growing species. After 100 years of intense trawling (Lindeboom & de Groot 1998, Rijnsdorp et al. 1998, Rumohr & Kujawski 2000) changes add up to a shift from high to low diversity and from a high biomass-low turnover to a low biomass-high turnover system (reviewed in Jennings & Kaiser 1998, Hall 1999, Fonteyne 2000, Kaiser et al. 2002, Gray et al. 2006, Kaiser et al. 2006). Most likely, complex feedback processes are invoved here that will affect overall ecosystem services, particularly fishery itself, too. Scientists, having realised this already, call for a comprehensive management at the ecosystem level to make fisheries sustainable (e.g. Pauly et al. 2002, Browman & Stergiou 2005, Cury et al. 2005). Therefore, the actual question is how and to what extent bottom-trawling affects the ecosystem as a whole (Jennings & Kaiser 1998, Malakoff 2002).

My dissertation deals with the trawling impact on soft-bottom communities in the German Bight, one of the most heavily trawled areas in the world. Trophic interactions within benthic communities are less studied than numerical parameters (e.g. abundance and biomass), but constitute the mayor part of organism-organism interactions (May 1974, Cohen 1978, Pimm 1982), i.e. a significant determinant of ecological functioning and the response of communities to perturbations. In this context, I put my emphasis on the trophic functioning of benthos, asking:

> How is the benthic community in the subtidal German Bight trophically structured?
>
> What causes species diet variability and which role does it play for the food web structure of soft-bottom benthic communities?
>
> How is the benthic community structure affected by cessation of bottom trawling?
>
> Which are the main effects of trawling cessation on the benthic trophic complexity?
>
> How can benthic communities sustain resistance in spite of bottom-trawling impact?

2 Outline

2.1 Macrozoobenthic communities in the German Bight

In this first chapter, I give an overview on the numerous environmental factors that govern the benthic community of my study area and that often hamper cause and effect studies of one certain impact factor such as bottom trawling, which I have investigated in my thesis.

The first studies on benthic communities in the German Bight were carried out already at the beginning of the last century (e.g. Blegvad 1922, Hagmeier 1925, Davis 1923, 1925 cited in Kingston & Rachor 1982). Since that time, there was a considerable interest to monitor the state of the benthos owing to the impact of the rapid industrial development on the marine environment (Kingston & Rachor 1982).

On the one hand, benthic communities are suited for long-term investigations since they are considerably stable in space and time (e.g. Salzwedel et al. 1985). Temperature, sediment and depth are the main environmental parameters governing the distribution of benthic species (e.g. Glémarec 1973, Duineveld et al. 1991). Traditionally, benthos is classified into associations according to species dominance patterns. Such accociations, however, have no strict boundaries but rather are descriptions of typical species assemblages along a gradient (e.g. Stripp 1969, Dyer et al. 1983, Salzwedel et al. 1985, Duineveld et al. 1991, Heip et al. 1992, Kuenitzer et al. 1992, Rachor & Nehmer 2003). In the German Bight, silty sands are inhabited by the *Amphiura filiformis* association and silt by the *Nucula nitidosa* association. Coarser sands are inhabited by the *Goniadella Spisula* association and fine sands are characterised by the *Tellina fabula* association (e.g. Salzwedel et al. 1985, Rachor & Nehmer 2003), the association of my study area.

On the other hand, benthic communities in shallow, boreal coastal systems such as the German Bight life in an extremely dynamic environment (e.g. Clark & Frid 2001) that becomes manifest in high temperature variability (e.g. Dyer et al. 1983, Dörjes et al. 1986, Kröncke et al. 2001, Schröder 2005), in strong tidal currents, in significant albeit variable riverine input including nutrient and sediment load (Lozán et al. 1990, Becker et al. 1992, Lozán et al. 2003) as well as in wind induced swell and sediment resuspension (Rachor & Gerlach 1978, Dörjes et al. 1986). Moreover, rare events such as extremely cold winters (e.g. Ziegelmeier 1964, Dörjes et al. 1986, Kröncke et al. 1998, Armonies et al. 2001, Schröder 2005) and anoxia (Niermann et al. 1990, Duineveld et al. 1991, Beukema 1992) affect significantly recruitment and survival of species.

The climate of the North Sea is also driven by the North Atlantic Oscillation (NAO, Becker et al. 1992) that manifests itself in regional oscillations of environmental parameters such as temperature, salinity and surface currents. The periodic changes of the NAO affects significantly benthic communities (e.g. Kröncke et al. 1998, Tunberg & Nelson 1998, Kröncke

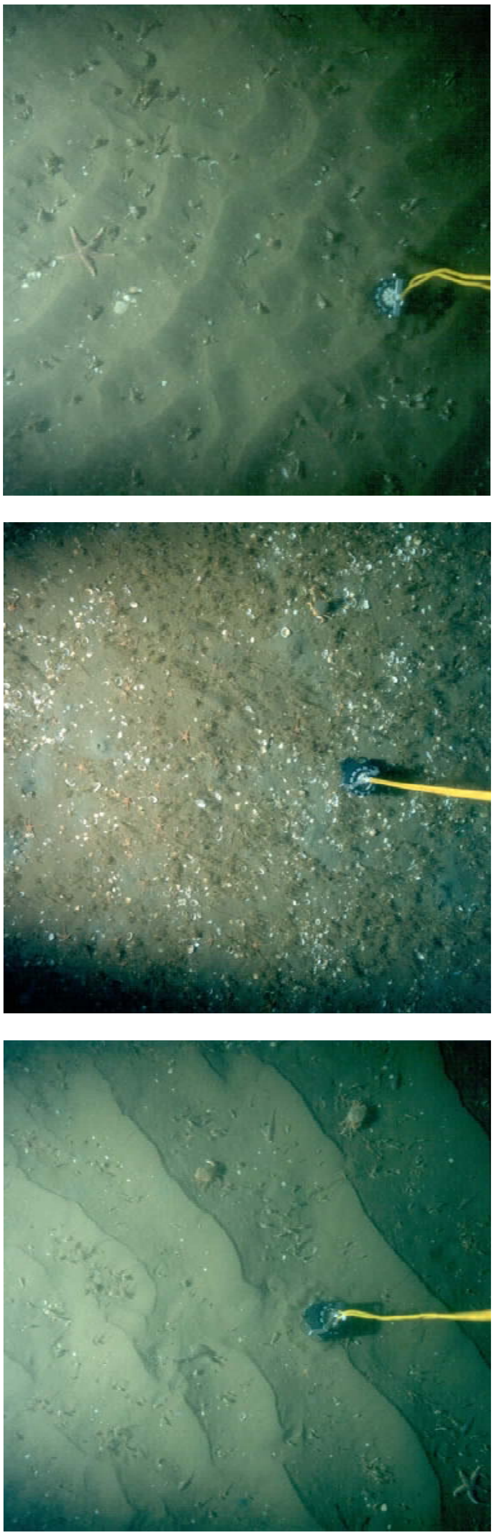


Figure 1: Example for sea bottom variability in the study area: photos of the same station taken in March (upper photo), July (middle) and November 2003 (lower photo).
Scale: 1 m^2.

et al. 2001, Schröder 2005). The oscillations in environmental parameters cause alterations in nutrient supply for the plankton which may result in an increased planktonic biomass (Hickel et al. 1993, Reid et al. 2001), passed to the benthos through sedimentation (benthic-pelagic coupling, e.g. Tunberg & Nelson 1998, Kirby et al. 2007). Particularly the southern North Sea, however, is an ecosystem where nutrient supply is high by riverine pollutants and allochthonous input (Clark & Frid 2001, Kröncke et al. 2004). Therefore, Kröncke et al. (2001) suggested that the benthos of the southern North Sea is primarily affected by changes in storm activity. Moreover, the North Sea ecosystem is affected by the trend of natural climate change, resulting in an ongoing shifting baseline (Frid 2006, Pörtner & Knust 2007).

Superimposed on natural variability, anthropogenic disturbances affect the benthos. These can be local such as dumping (e.g. Stronkhorst et al. 2003, Witt et al. 2004) and sand extraction (e.g. Van Dalfsen et al. 2000) or concern larger areas such as pollution and eutrophication (e.g. Pearson & Rosenberg 1978, Rachor 1990, Duineveld et al. 1991, Basford et al. 1993, Kröncke 1995) and bottom trawling (e.g. Ehrich 1998, Rumohr et al. 1998, Jennings et al. 1999, Clark & Frid 2001), which is itself unevenly distributed in space and time (e.g. Rijnsdorp et al. 1998, Jennings et al. 1999).

High variability in environmental conditions, both natural and anthropogenic, governs not only directly the benthic community structure, but cause other modified ecological conditions such as larval drifting and recruitment, competition, predation and variable food supply (e.g. Clark & Frid 2001, Kröncke et al. 2001, Kröncke et al. 2004, Williams et al. 2004).

The naturally and anthropogenically induced variability causes a consistent noise in abundance, biomass and species inventory of the benthic community. Cause and effect studies that single out one certain effect such as bottom trawling (Brylinsky et al. 1994, Kaiser 1998, Collie et al. 2000, Kaiser et al. 2002) or indirect effects such as trophic interactions are often hampered by complex multi-factorial interactions (e.g. Jennings et al. 2001a, Tillin et al. 2006).

2.2 Food-web descriptors and ecosystem resistance

Here, the measures I used to describe trophic complexity are discussed with respect to modern theory and praxis of food web analysis, and I will focus on trophic features that enhance community resistance against natural or anthropogenic disturbance.

Some of the earliest studies on food webs and trophic interactions were carried out in marine environments: the quantification of benthic species serving as fish food (e.g. Blegvad 1914, Petersen 1918, Boysen-Jensen 1919). Volterra (1926) made the first attempt to model trophic interactions, i.e. fluctuations in fish and shark populations after the cessation and restart of fisheries brought about by the World War I, to understand the roles of natural predation and fishing in European Seas. This was the nucleus of the general Lotka-Volterra model (see e.g. Begon et al. 1996).

Trophic interactions are, besides environmental conditions, the main forcing factors for the occurence, distribution and behaviour of organisms (e.g. MacArthur 1955, May 1974, Cohen 1978, Pimm 1982, McCann 2000). Amongst species interactions which constitute mutualistic, competitive and trophic interactions, feeding relations are the most important ones, they constitute the biological base of ecological functioning (May 1983, Chapin III et al. 2000). Pioneering work on food-web properties and descriptors was carried out by May (1974), Cohen (1978) and Pimm (1982). Since then, scientists have been searching for appropriate and universally valid properties that allow to describe and to compare food webs. This search is far from being over, particularly the suitability of food webs attributes and the crucial significance of taxonomic and functional resolution have been and are still controversially discussed (e.g. Yodzis 1980, May 1983, Martinez 1991, Hall & Raffaelli 1993, Goldwasser & Roughgarden 1997, Moore 2005). All feeding relations in a community, i.e. the trophic interactions between species, constitute the food web of a system (e.g. May 1983, Briand & Cohen 1987). Hence, feeding type and the trophic role of each species is, in theory, of equal significance for ecological functioning, but concurrently its determination in diverse food webs is forstalled by limited resources of manpower (e.g. McCann 2000, Dunne et al. 2002, Cardinale et al. 2006, Montoya et al. 2006). To capture all species trophic links that define a food web is beyond any scientific feasibility in all but the most simply structured systems. Accordingly, food-web analysts restrain to approximate descriptors for trophic properties of webs such as species size spectra or trophic compartments.

Species body size approximates species trophic position within the trophic hierarchy, since predators are usually one to three orders larger in magnitude than their prey (Cohen et al. 1993). The larger an organisms is, the larger its prey spectrum might become and the higher its trophic position within the food web will be (e.g. Sheldon & Kerr 1972, Davenport & Bax 2002, Pauly & Palomares 2005, Brose et al. 2006). Hence, the size-based approach takes an instantaneous look at biological properties and interactions at the individual level (e.g. Cohen et al. 1993, Jennings et al. 2002b, 2002c, Brose et al. 2006), as well as a temporally integrative look at ontogenetic diet shifts during organism life span (e.g. Arntz 1977-1978, Post 2003). One potential weakness of the size-based analysis is that the positive relationship between body size and trophic position becomes weaker in higher size classes (Jennings 2005). Some of the largest organisms feed on small prey: e.g. whale – krill, elephant – plants, or within marine benthic communities heart urchin – detritus (Dinmore & Jennings 2004).

Conventional food-web research is based on the number of trophic compartments in a web (Lindeman 1942, Pimm 1982, Hall & Raffaelli 1993). Trophic compartments combine species that are taxonomically and/or functionally similar (Dunne et al. 2005). The broadest approach combines species with similar trophic levels (e.g. Williams & Martinez 2004), i.e. in the most simplified system (Briand & Cohen 1984) the web consists of three compartments, basal (producers and primary consumers), intermediate (consumers and prey), and a top compartment (top consumers with no further predators). A higher resoluted approach is grouping species into feeding types. These can be (a) functional groups, i.e. where within trophic level species perform in similar ways, (b) feeding guilds, similar to functional groups, but including taxonomically similar species and (c) trophospecies, a group of species that share similar interaction patterns within a food web (Yodzis 1988, Martinez 1991, Morris et al. 2005).

Lumping species together or structuring the community by body size is, however, always associated with a loss of taxonomic and particularly functional resolution. Moreover, the way of forming compartments affects both food-web model structure and properties. For example, over-aggregation of basal species or putting the emphasis on commercially important or “charismatic” species may introduce serious bias (Hall & Raffaelli 1993, Arntz et al. 1999, Dunne et al. 2005, Pinnegar et al. 2005). Particularly in systems with a large heterogeneous food pool, such as terrestrial leaf communities or benthic soft-bottom communities species trophic interactions are difficult to disentangle (Ponsard & Averbruch 1999, Eggers & Jones 2000). Stable nitrogen isotope ratios, a proxy for an organism’s position within the trophic continuum (see chapter 3.2), might offer a lever to tackle this problem.

The question how ecological functioning affects the stability of ecosystems is not new, but still significant (e.g. Forbes 1887, Elton 1927, Nicholson 1933). Over the last century the definition of the term “stability” evolved permanently (see Ives 2007 for an abbreviated history). Multiple inconsistent definitions of “stability” made any meaningful synthesis of theoretical and empirical work rather impossible (Pimm 1984), and the mere term “stability” has no practical meaning in ecology, i.e. it is but a generic term for several stability properties (Grimm et al. 1992). To avoid confusion, in the further course of my thesis, the term “stability” is defined and used in the sense of the different stability properties inherent of a community following Boesch & Rosenberg (1981), Pimm (1984) and Grimm et al. (1992), i.e.

(1) persistence: remaining essentially unchanged through time;
(2) resistance: remaining essentially unchanged despite the presence of disturbances; and
(3) resilience: returning to the reference state (or dynamics) after a temporary disturbance.

In terms of resilience, the reference state does not strictly refer to the pristine state, but to the *status quo ante* or one of a number of multiple stable points (Sutherland 1974, Gray 1977). The speed of return to a reference state after a temporary disturbance is the recovery rate, i.e. the elasticity (Boesch & Rosenberg 1981, Grimm et al. 1992, Dittmann & Grimm 1999), which depends on the strength of perturbations and their frequency (intermediate disturbance hypothesis, Connell 1978).

Trophic interactions constitute a significant aspect of community stability properties (e.g. Gray 1977, Hall & Raffaelli 1993, Dunne et al. 2005). Since the 1950s (MacArthur 1955), much attention has been payed to the connection between food-web properties and ecosystem resilience, resistance and persistence (e.g. Elton 1958, May 1972, 1974, Pimm 1982, 1984, Martinez 1992).

Food-web theory has been developed principally from freshwater and terrestrial food webs. Marine webs resemble terrestrial and freshwater systems to a large extent, but differ to a certain extent in their openness, in their predominantly higher connectivity and number of links per species, and in their higher degree of omnivory (Hall & Raffaelli 1991, Bengtsson 1994, Link 2002, Dunne et al. 2004, Link et al. 2005). Nevertheless, marine food webs are not unique, but represent at least specific food-web types in the sense of common food-web theory (e.g. Link et al. 2005).

In the last decades, the lively discussion of ecosystem-stability properties (‘diversity – stability debate’) was fed by contradictionary experimental outcomes and unclear definitions of stability and diversity (Ives 2007). Different ways of food-web construction and modelling led to points of view (for discussion see e.g. Eggers & Jones 2000, Kaiser 2000, Loreau et al. 2001, Dunne et al. 2005, Moore 2005). Owing to their slightly different settings, marine food webs might add a different angle to this discussion (*sensu* Link et al. 2005).

Nevertheless, there is a general understanding that certain food-web properties enhance ecosystem resistance, irrespective of the habitat or type of ecosystem looked at. The more species a system has, the greater the trophic variety among species might become (MacArthur 1955, Hooper et al. 2005), and the more capacity a system may have to buffer stress (insurance hypothesis, e.g. Yachi & Loreau 1999, McCann 2000, Moore 2005, Thébault & Loreau 2005, Ives 2007). This buffering effect refers to the increased chance of trophic redundancy with increased number of species (Naeem & Shibin 1997, Yachi & Loreau 1999), i.e. the replacement of lost species by others capable of trophic compensation. Hence, an increase in both, trophic complexity and redundancy, is positively related to ecological functioning in terms of resistance (Duffy 2003, Duffy et al. 2007). Against this background, a growing number of empirical studies demonstrate positive diversity-resistance relationships (see e.g. Duffy et al. 2007, Ives & Carpenter 2007).

Trophic redundancy is not merely having similar trophic elevations, but depends on the nature of trophic interactions species may share. Seemingly trophically 'similar' species may have non-identical sets of trophic links and may differ in the strength of links to the same prey or predator (Pimm & Lawton 1978, Paine 1992). To date, there is increasing evidence that especially the number of 'weak trophic links' is crucial for system resistance. 'Weak links' represent consumers that can choose between many food species as well as species that are prey items to many consumers. On the one hand, "multi-choice" consumers can switch between different prey items and thus dimish prey population osscilations and prevent one single species from becoming dominant (Post et al. 2000, McCann et al. 2005). On the other hand, 'weak interactions' can buffer strong and unstable consumer-resource interactions within a web (McCann et al. 1998, Berlow 1999, McCann 2000). Fagan (1997) and McCann & Hastings (1997) suggested that omnivory, defined as feeding over more than one trophic level (Pimm & Lawton 1978, Pimm 1980), might as well increase ecosystem resistance.

Niche models showed that specialisation in resource use leads to increased species richness, while an increased number of generalists does not (Thébault & Loreau 2003, Ives et al. 2005). The latter, however, comprehends a high degree of trophic redundancy (e.g. Eggers & Jones 2000). Accordingly, high species diversity does not necessarily imply enhanced resistance. Ecosystem-stability properties might rather be a function of the mixture between specialised and generalistic species, and between community trophic complexity and redundancy. Knowledge on food-web structure and species feeding strategies is essential to understand the community's ability to cope with perturbations such as bottom trawling.

2.3 Fishery in the North Sea and its impact on macrozoobenthos

The impact of fishing on the benthic fauna of the North Sea has been intensively studied. In this chapter, I give an overview of bottom fishery and summarise its main effects on benthic community structure.

Fishery has a long tradition in the North Sea. Before 1884, rowing boats or sailing vessels and mainly passive gears (long lines, nets and traps) were used. In 1884, steam vessels were introduced that allowed the use of actively towed gears (otter trawls). Between 1910 and 1930 the North Sea was already intensively fished (Lindeboom & de Groot 1998). The intensity of fishery increased further in the 50s and 60s due to the introduction of more powerful diesel engine vessels that were able to tow heavy beam trawls. Today's strong boats, heavy gear, modern technics to locate profitable fishing grounds (e.g. navigation systems, fish finders), and substancial subsidies result in high fishing intensity with serious effects on the benthic fauna (Lindeboom & de Groot 1998).

While in the northwestern part of the North Sea otter trawls are the most common gear, targeting cod (*Gadus morhua*), haddock (*Merlanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and saithe (*Pollachius virens*), beam trawling is the predominant type of fishery in the southeastern part (Ehrich 1998, Lindeboom & de Groot 1998, Jennings et al. 1999), targeting particularly sole (*Solea solea*) and plaice (*Pleuronectes platessa*) (Lozán et al. 2003). The fleets fishing in the southeastern North Sea are primarily Dutch and German ones. French, Belgian and Danish fleets are of lesser importance. Vessel types fishing in the study area are mainly large beam trawlers >300 hp (see Figure 2).

Figure 2: Modern beam trawler with a 12 meter beam trawl at either side, typical of the study area.

Trawling intensity is neither spatially (Ehrich 1998, Jennings et al. 1999) nor seasonally (Piet & Rijnsdorp 1998, Pastoors et al. 2000, Figure 3) homogenously distributed over the North Sea. In 1995 the total trawling effort was 2.25 million hours yr^{-1} and 55 % of these hours were spent on beam trawling, within specific areas. Only 5 % of the North Sea bottom is trawled less than once in 5 years, 29 % less than once in a year, 30 % is trawled 1 – 2 times yr^{-1} and 9 % of the sea bottom is trawled more than 5 times yr^{-1}. In intensively fished areas the sea bottom is trawled more than 10 times yr^{-1} (Rijnsdorp et al. 1998). The study site is situated in one of the most heavily trawled areas of the North Sea (Figure 3, Figure 4).

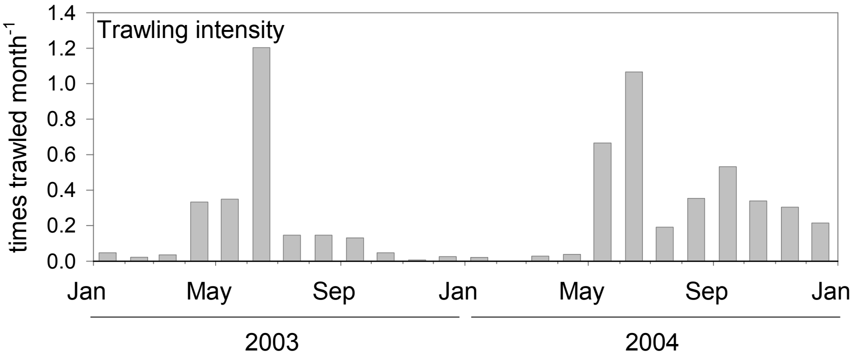


Figure 3: Seasonal variation of trawling intensity (times trawled month^{-1}) in the study area over time of investigation. Data were calculated from Vessel Monitoring System (VMS-data). Modified after Schröder & Dannheim 2006.

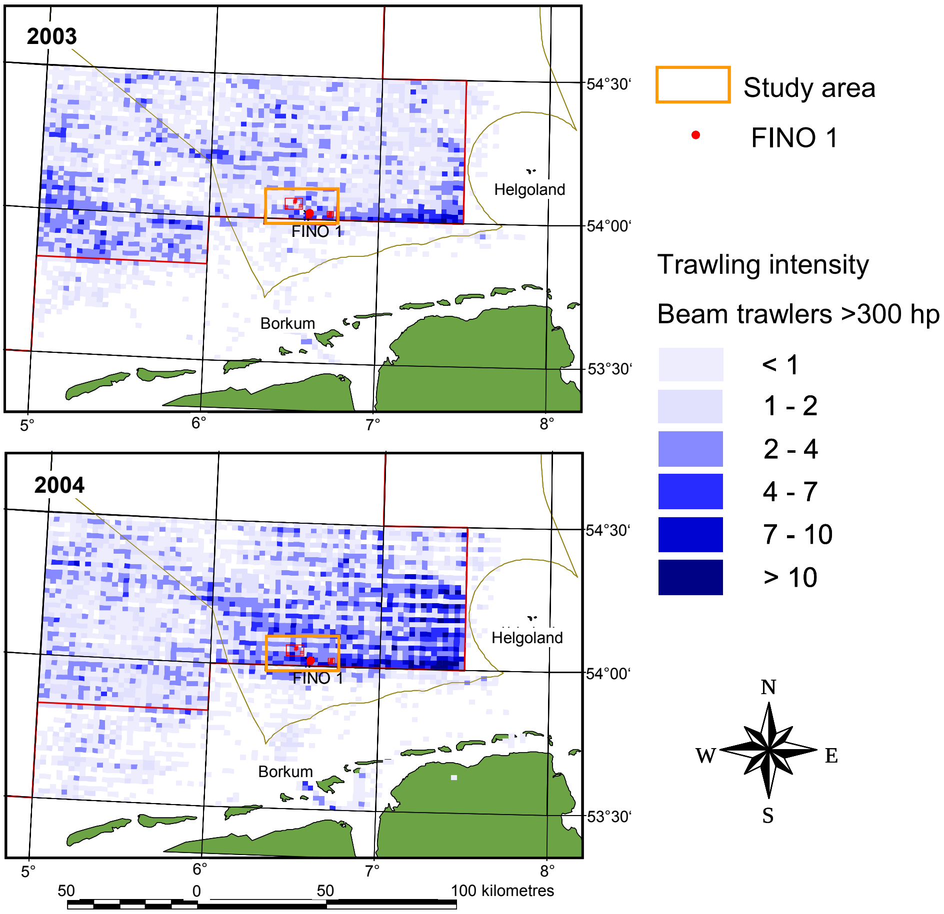


Figure 4: Trawling intensity of large beamtrawlers (>300 hp) in 2003 (upper figure) and 2004 (lower figure) in the study area (times trawled month^{-1}, VMS-data). Modified after Schröder & Dannheim 2006.

In the North Sea, Graham (1955) was the first to report on the effects of fishing on non-target species. Specific studies of bottom-trawling impact on the seabed and its fauna did not start before the 70s and 80s (reviewed inArntz & Weber 1970, De Groot 1984, De Groot & Lindeboom 1994, Lindeboom & de Groot 1998, Hall 1999).

Bottom trawling affects the benthic ecosystem in different ways, but in the first instance it simplifies the ecosystem by (i) levelling habitat structure (e.g. Riesen & Reise 1982, Auster & Langton 1999, Freese et al. 1999, Thrush et al. 2001, Thrush & Dayton 2002) and by (ii) reducing biodiversity (e.g. Jennings & Kaiser 1998, McConnaughey et al. 2000, Jennings & Reynolds 2000, Blanchard et al. 2004). Gear impact strength depends on the gear used, its weight and structure (e.g. number of tickler chains) on the one hand and on the habitat or sediment composition (e.g. Bergman et al. 1990, Eleftheriou & Robertson 1992, Collie et al. 2000) on the other hand.

Besides the removal of fish and bycatch, a loss in species number (e.g. Prena et al. 1999, Bergmann et al. 2001) and particularly of top predators (e.g. Pauly et al. 1998, Pauly & Palomares 2005), bottom trawling has two mayor impacts on the benthic communities. On the one hand, there is the direct physical impact of the gear: it causes sediment resuspension and an alteration of the sediment biogeochemical composition (e.g. Churchill 1989, Werner et al. 1990, Schwinghamer et al. 1998, Watling et al. 2001, De Madron et al. 2005, Trimmer et al. 2005).

Moreover, the physical impact causes dislocation, damage and mortality of benthic organisms within the trawl tracks (Arntz & Weber 1970, Rumohr & Krost 1991, Kaiser 1996, Bergman & van Santbrink 2000, Mensink et al. 2000, Piet et al. 2000, Ramsay et al. 2000). This effect is species specific, depending for example on size, mobility, and burrowing depth (Bergman & Hup 1992, Gilkinson et al. 1998). On the other hand, trawling has indirect effects, too, in particular a distortion of the trophic base through bycatch, discards and gear-induced mortality which attracts and favours predators and scavengers (Ramsay et al. 1998, Fonds & Groenewold 2000, Groenewold & Fonds 2000, Rumohr & Kujawski 2000, Bergmann et al. 2002).

In the long run, trawling effects become manifest as shifts in the species inventory and thus community structure: from long-lived to short-lived, from large sized to small sized, and from slow growing to fast growing species (e.g. Bergman & Hup 1992, Dayton et al. 1995, Kaiser & Spencer 1995, Tuck et al. 1998, Frid & Clark 2000, Bradshaw et al. 2002). Almost one century of trawling (Lindeboom & de Groot 1998, Lindeboom 2000, Rumohr & Kujawski 2000) has shifted the benthic community towards a low biomass/high productivity system (Duplisea et al. 2002, Jennings et al. 2002a, Hiddink et al. 2006a, Queirós et al. 2006).

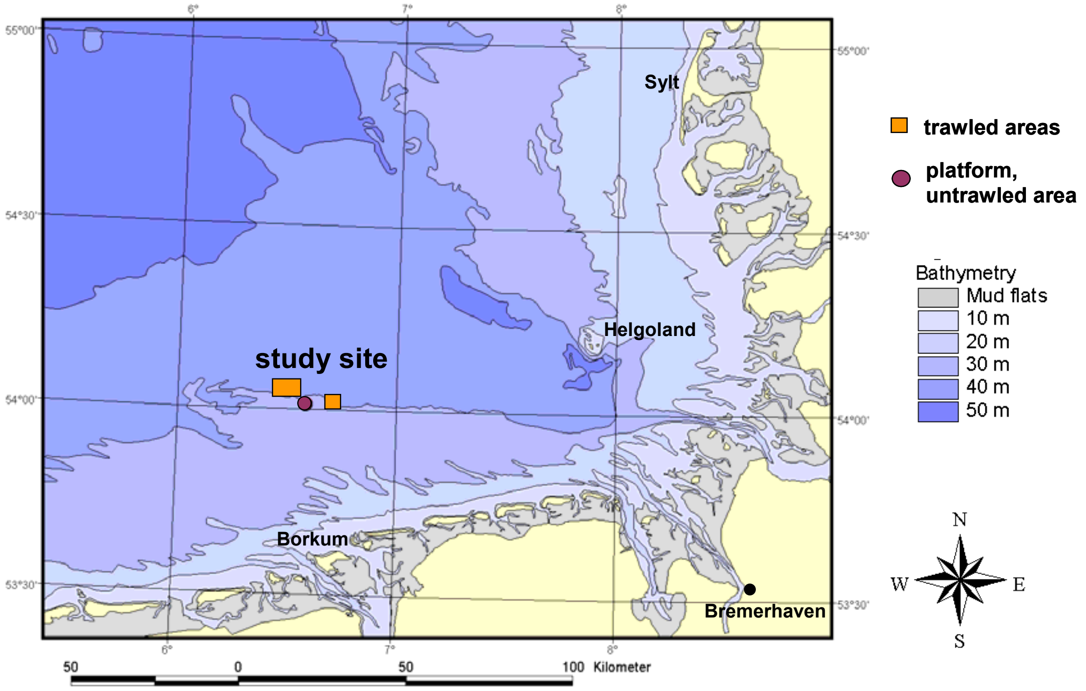
Experimental studies of short-term fishing impacts or comparisons of sites with different trawling intensities (reviewed in e.g. Collie et al. 2000, Kaiser et al. 2006) are the principial source of today’s understanding on trawling effects. Scientifically sound studies of long-term as well as indirect effects of bottom trawling, however, require the comparison of trawled with truly untrawled sites (Ball et al. 2000). This is difficult since pristine sites of comparable environmental settings are lacking in most European coastal waters (shifting baseline phenomena, e.g. Pauly 1995, Pauly & MacLean 2003, Lotze et al. 2005). This is, by the way, the focus of a lively discussion between scientists and the FAO (Food and Agriculture Organisation of the United Nations) on appropriate design of trawling impact studies (Gray et al. 2006, Sheppard 2006, Gray et al. 2007a, 2007b, Lokkeborg 2007, Valdimarsson 2007). Gray et al. (2006) stated that commonly "…*the onus is on the disturber to prove that they will not affect the environment before a potential disturbance is allowed…*" and that "…*marine ecologists* (are only able) *to prove damaging effects…*".

So far, only four studies looked at post-impact recovery by comparing untrawled and trawled sites (Collie et al. 2005, Smith et al. 2006, De Juan et al. 2007, Duineveld et al. 2007), but only the latter two were carried out in the North Sea. Recovery times and pathways of benthic communities were already determined in the 70s and 80s (see Pearson & Rosenberg 1978, Arntz & Rumohr 1982), but most data on bottom-trawling recovery are still estimates derived from models (e.g. Collie et al. 2000, Hiddink et al. 2006b).

System response depends to a great extent on species life spans and life-history traits (Collie et al. 2005, Tillin et al. 2006), whereas the nature of trawling effects are particularly trophic ones. Recent studies try to account for these interconnections by focussing either on changes in size spectra or trophic level (Jennings et al. 2001a, Duplisea et al. 2002, Jennings et al. 2002a, 2002b, Hiddink et al. 2006a, Queirós et al. 2006) or on effects at the level of biological trait entities (Blanchard et al. 2004, Tillin et al. 2006) to infer changes in trophic flow and trophic structure. Thus, "high resolution" studies at the species level, i.e. the evolutionarily derived basic unit of ecosystem functioning, are missing so far.

3 Methods and study site

3.1 Study site and sampling scheme



Map 1: Map of the study site located in the German Bight with the untrawled area (red circle) and the two trawled areas (orange squares), one situated north-west and one east of the untrawled area.

The study site is situated in the German Bight (North Sea) 30 nm off the island Borkum at 30 m water depth (North Sea, Map 1). The sediment consists of homogenous fine sands (median grain size of 177 µm). Hydrographically, the study site is homogenous. The water column is not stratified and characterised by wind and tidally driven strong currents. On a regional scale, North Sea waters are subjected to a wind driven anticlockwise circulation (see Becker et al. 1992, Ducrotoy et al. 2000). Tidally caused currents run east – west along the East Frisian coast and north – south along the North Frisian coast during flood tide and ebb tide, respectively. Thus the main netto water transport by wind and tides in the North Sea is west to north. At the study site, the main current direction is east and west between 0.2 and 0.4 m s^{-1} at the bottom. Due to the mostly north-westerly winds, the surface currents are slightly stronger in eastern direction (over 1 m s^{-1}) (unpubl. data of the Federal Maritime and Hydrographic Agency, BSH). Salinity ranges between 33 and 35, whereas the annual temperature amplitude is about 15°C (Figure 5).

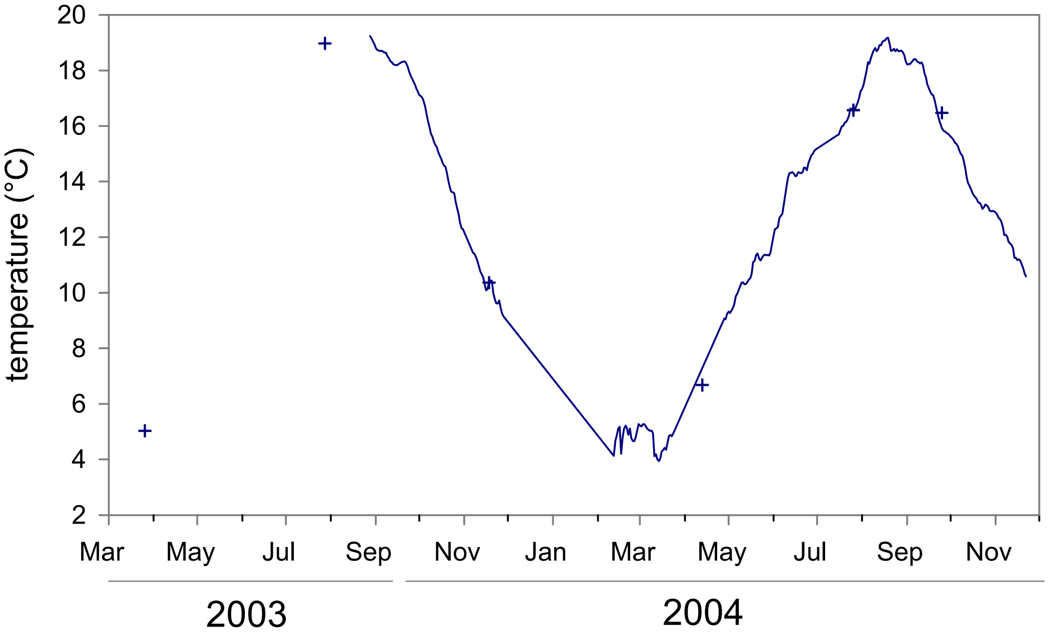


Figure 5: Annual temperature regime (°C) at the research platform FINO 1 (August 2003 – December 2004). Data provided by the Federal Maritime and Hydrographic Agency (BSH, Bundesamt für Seeschifffahrt und Hydrographie). Crosses mark mean temperature measured with the CTD during the cruises of this study.

Figure 6: Research platform FINO

Hitherto, no soft-bottom areas were closed permanently for bottom fishing in the German EEZ (Exclusive Economic Zone). The construction of the research platform FINO 1 (Figure 6, completed on the 14th July 2003) provided the unique opportunity to study the post-impact recovery of benthos after cessation of trawling. For safety reasons the surrounding of the research platform is closed to all shipping activities and consequently also for bottom trawling within a radius of 500 m (see Schröder & Dannheim 2006 for evidence of non-trawled status).

For sampling, the untrawled area was defined as the zone between an inner circle of 150 m radius and an outer circle of 400 m radius from the platform (Figure 7). These distances from the platform itself and from the border of the untrawled area were kept to minimize the effect of the platform (Knust et al. 2001, PUBLICATION III) and edge effects from the surrounding trawled area. The untrawled area was compared to two areas nearby exposed to “normal” trawling (Map 1).

In the untrawled area 5 stations were established, grab stations (north of the platform) apart from the 5 beamtrawl stations (south) to avoid self-made disturbance (Figure 7). Stations were compared to the 5 (only the north-westerly trawled area, Cruise C1, C2; see Table 1) respectively 9 stations (4 additional stations in the easterly trawled area, cruise C3 onwards) in the trawled areas.

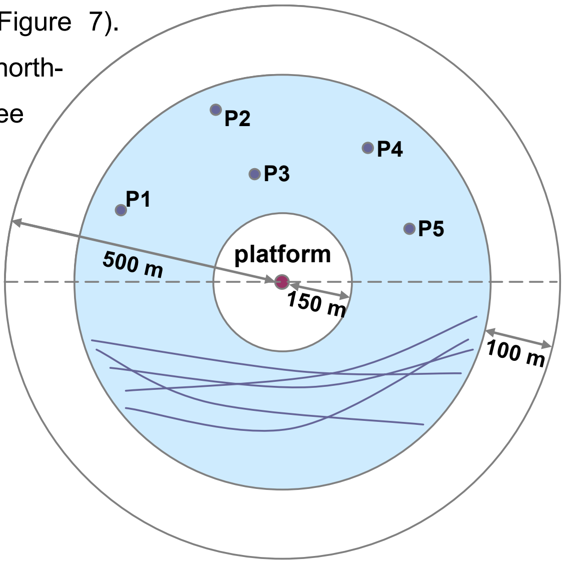


Figure 7: Sampling design for the untrawled area (blue area). In the northern part, grab samples were taken (stations P1 – P5), in the southern part the blue lines in the circle indicates exemplary beamtrawl tracks.

The timing of the sampling scheme was adjusted to the date of platform construction (Table 1). All cruises were carried out with the RV *Heincke*. Five different types of gear were used to analyse the community structure and to detect changes related to bottom trawling (Table 1). Infauna was sampled by van Veen grabs (0.1 m^2, 95 kg; Figure 8 upper left photo) and subsamples (sediment cores) were taken for further analyses of the sediment. Epifauna was studied by beamtrawls (3 m width, towed with 3 kn; Figure 8, upper right photo), and underwater photo- and videography (Figure 8, lower photos). For trophic analyses, once a year in autumn (C3, C6) infaunal and epifaunal specimens were sampled from additional grabs and beamtrawls.

Table 1: Cruise number (No.), date of cruise and month related to cessation of fishing respectively platform construction (“-“ means before construction). ✓ indicates samples taken for trawling intensity (TR) by side-scan sonar, for community and trophic analyses by several gears: van Veen grab (vV), beamtrawl (BT), underwater photography (P) and videography (V).

No.	Date	Month	TR	Community analysis				Trophic analysis	
				vV	BT	P	V	vV	BT
C1	17.03. – 04.04.03	-3		✓	✓	✓	✓		
C2	22.07. – 02.08.03	0	✓	✓	✓	✓	✓		
C3	14.11. – 21.11.03	4		✓	✓	✓	✓	✓	✓
C4	05.04. – 20.04.04	8		✓	✓	✓	✓		
C5	17.07. – 03.08.04	12	✓	✓	✓	✓	✓		
C6	18.09. – 02.10.04	14		✓	✓		✓	✓	✓

To estimate local trawling intensity once a year (C2, C5) in summer, side-scan surveys were carried out. Additional data on trawling intensity for the Dutch and German fleet were calculated from the **V**essel **M**onitoring **S**ystem (VMS) throughout both years (unpubl. data provided by S. Ehrich, Federal Research Centre for Fisheries, and G. Piet and F. Quirins, Netherlands Institute for Fisheries Research).

For Publication III additional grab samples were taken in the direct vicinity of the platform (see Publication III for sampling dates). Van Veen (0.1 m²) grab samples were collected monthly directly from the research platform FINO 1, up to 17 m away from the construction. Samples were used for identifying infaunal species and subsamples for sediment analysis.

For further details of sampling and of sample treatment see Publications I – V.

Figure 8: Main sampling gears used in this thesis: van Veen grab (upper left), beam-trawl (upper right), photo swing (lower left) and video camera (lower right).

3.2 Stable isotope ratios

The ratios of stable isotopes of nitrogen (^{15}N: $^{14}N \triangleq \delta^{15}N$) and carbon ($^{13}C$:$^{12}C \triangleq \delta^{13}C$) are proxies of an organism's position within the trophic hierarchy of an ecosystem (e.g. Wada et al. 1987, Fry 1988, Hobson & Welch 1992, Post 2002b). The underlying principle is the enzymatic selection of the heavier isotope (^{15}N and ^{13}C) with each assimilation step and hence a progressive enrichment within the body tissue along the trophic continuum (e.g. Peterson & Fry 1987). Fractionation is variable with an increase of consumer nitrogen isotopic ratio of about 1.4 – 3.4 ‰ per trophic step relative to their prey and up to 1 ‰ for carbon isotopic ratios (De Niro & Epstein 1978, De Niro & Epstein 1981, Minagawa & Wada 1984, Adams & Sterner 2000, Post 2002b, McCutchan et al. 2003).

Isotopic ratios and C/N-ratios were measured in an isotope-mass spectrometer (Thermo/Finnigan Delta Plus at GeoBioCenter^{LMU}, University of Munich). Both parameters were sensitive to environmental and physiological patterns and to sample treatment (Publication I). Carbon isotopes, which are primarily helpful to distinguish different food sources at the base of trophic systems (Fry 1988, Fry & Sherr 1984), correlate positively with lipid content of organisms (McConnaughey & McRoy 1979, Sweeting et al. 2006, Post et al. 2007). Since lipids were not measured but known to vary greatly with tissue, gender and size (e.g. Focken & Becker 1998, Schmidt et al. 2003), and since subtidal benthic food webs are based on one food source (detritus, e.g. Frid 2006), carbon isotopic ratios are neglected in Publication II and Publication V of this thesis.

In contrast, tissue nitrogen isotopic ratio is a robust proxy for organism trophic elevation in relation to the primary food source. That is $\delta^{15}N$ can be used to reconstruct the trophic hierarchy within an ecosystem, but also to infer inter- and intra-population diet variability (France et al. 1998, Jennings et al. 2002b, 2002c), ontogenetic diet shifts (De la Morinière et al. 2003, Post 2003, Rossi et al. 2004), and seasonal and spatial patterns in alimentation (Lorrain et al. 2002, Persic et al. 2004, Matthews & Mazumder 2005). Hence, nitrogen isotopic ratios describe and discriminate trophic niches to a certain extent (Genner et al. 1999, Davenport & Bax 2002, Bearhop et al. 2004, Matthews & Mazumder 2004, Jacob et al. in prep.). Particularly in systems that consist of small sized organisms and/or are characterised by many species that feed from a "storage pool" of matter that is difficult to differentiate (e.g. dead leaves in woodlands or detritus in aquatic systems), they provide a powerful tool to investigate trophic functioning.

4 Publications

Each publication, its connection to the broader scope of the dissertation and my share thereof are listed below. This chapter presents the five publications that constitute my thesis.

PUBLICATION I

Dannheim J, Struck U, Brey T (2007). Does sample bulk freezing affect stable isotope ratios of infaunal macrozoobenthos? Journal of Expermental Marine Biology and Ecology, 351: 37-41.

Division of work: I developed the initial idea and carried out all practical work (except isotope measurements, done by the second author), the statistical analysis (together with the 3rd author) and had the lead in writing the manuscript.

Context: Stable isotope ratios are an indispensable tool in food web studies but still imply certain uncertainties regarding pre-sample treatment. We tested here whether bulk freezing of complete grab samples onboard is an acceptable bias-free sample treatment.

PUBLICATION II

Dannheim J, Jacob U, Schroeder A, Brey T (manuscript). Two-dimensional trophic complexity of German Bight soft-bottom macrozoobenthos.

Division of work: I developed the idea and did the sampling and analyses, the latter with support from the 2nd and later with the 3rd author. I wrote the manuscript in discussion with the 2nd author and later with both other co-authors.

Context: PUBLICATION II deals with the trophic complexity of the subtidal benthic community of sandy bottoms in the German Bight. Trophic interactions are an important determinant of ecological functioning (May 1974, Cohen 1978, Pimm 1982), and combined with species richness, they are a central issue in studies of natural communities, particularly regarding the consequences of human impact (McCann 2000, Loreau et al. 2001, Dunne et al. 2002). Moreover, PUBLICATION II provides insights in trophic niche width of benthic species (e.g. omnivory, generalism, diet shifting, specialisation). These trophic patterns are essential for understanding community dynamics and ecological functioning.

PUBLICATION III

Joschko T, **Dannheim J**, Niehoff B, Schroeder A, Orejas C, Knust R (submitted). The effect of an artificial hard substrate on the loacal soft-bottom macrozoobenthos in the German Bight: A first step to understand the impact of future offshore wind turbines. ICES Journal of Marine Science.

Division of work: The 1st author and I developed the idea and concept of this manuscript. Sampling, sorting and data analysis were carried out by the 1st author, the 4th author and myself. The manuscript was written by the 1st author, the 3rd author and me and discussed with all other co-authors.

Context: We evaluate whether the presence of the research platform FINO 1 has a detectable effect on the surrounding benthic community that is distinguishable from the effect related to cessation of trawling.

PUBLICATION IV

Dannheim J, Finger K, Schroeder A (in press). Response of macrozoobenthic community to cessation of fishing activity in the North Sea. In: Demestre M (ed). Response of Benthic Communities and Sediment to Different Regimens of Fishing Disturbance in European Coastal Waters (RESPONSE). Final Report of the EU project Q5RS-2002-00787. ICM-CSIC, Barcelona: 238-303.

Division of work: The publication is part of the Final Report of the EU-project RESPONSE. The 3rd author led the project and developed its main objective together with the other EU partners. Sampling was carried out by all three authors. The 2nd author carried out the photo and video analyses. I did all the laboratory work and the major part of the data analysis, supported by the 3rd author. I wrote the report chapter, supported by the 2nd and in particular the 3rd author.

Context: The RESPONSE project (Response of benthic communities and sediment to different regimes of fishing disturbance in European Coastal waters, No: QRLT-2001-00787) focused on the recovery of benthic communities after cessation or different levels of trawling disturbance in the Irish Sea, the Mediterranean Sea (Catalan Sea and Adriatic Sea) and the North Sea. Thus it represents a central part of my PhD studies. For further informations see http://www.icm.csic.es/rec/projectes/response/. The PUBLICATION IV is part of the project final report. Fishing effects on benthic community structure were investigated by common community analyses, based on grab and beamtrawl samples. The observed recovery after fishing closure is compared to known trawling effects on macrozoobenthos (reviewed in Jennings & Kaiser 1998, Hall 1999, Fonteyne 2000, Kaiser et al. 2002, Kaiser et al. 2006).

PUBLICATION V

Dannheim J, Brey T, Schroeder A, Mintenbeck K, Knust R, Arntz W (submitted). Trophic look at soft-bottom communities – the long way of recovery from trawling. Marine Ecology Progress Series.

Division of work: I conducted the sampling together with the 3rd author and carried out most of the laboratory work, except stable isotope measurements. I did the data analysis supported by the 2nd and 3rd author. Some data were provided by the 4th author. I had the lead in drafting and writing the manuscript which was discussed with all co-authors.

Context: PUBLICATION V focuses on post-impact recovery phenomena that are detectable in trophic properties of the benthic community. We take (for the first time) a synoptic view on changes in species trophic position and changes in species mediated trophic flow. We discuss the relevance of the observed patterns for ecosystem trophic functioning and community resilience (e.g. McCann et al. 1998, McCann 2000, Dunne et al. 2002) with respect to trawling impact.

PUBLICATIONS RELATED TO MY THESIS

Schröder A, **Dannheim J** (in press). Estimation of fishing effort in the ASA of the North Sea. In: Demestre M (ed). Response of Benthic Communities and Sediment to Different Regimens of Fishing Disturbance in European Coastal Waters (RESPONSE). Final Report of the EU project Q5RS-2002-00787. ICM-CSIC, Barcelona: 107-129.

Finger K, **Dannheim J**, Suck I, Schröder A (in prep.). Imaging optical methods as a non-invasive method to detect trawling disturbance?.

Does sample bulk freezing affect stable isotope ratios of infaunal macrozoobenthos?

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Abstract

Macrobenthic infaunal sampling campaigns that aim at unpreserved "fresh" animals for later biochemical analysis follow one of two strategies: either samples are sieved and sorted on board and individual specimens are frozen, or grab/corer samples are frozen completely and animals are separated from sediments later in the laboratory. This study demonstrates that deep freezing of complete grab samples causes a significant bias in stable isotope ratios of nitrogen ($^{15}N/^{14}N$ or $\delta^{15}N$ vs. AIR) and carbon ($^{13}C/^{12}C$ or $\delta^{13}C$ vs. PDB) as well as in the C/N ratio of nine infaunal species from the German Bight. On average, molar C/N ratio increases by 0.93, $\delta^{13}C$ decreases by 1.87 ‰, and $\delta^{15}N$ decreases by 1.01 ‰. Mechanical cell destruction and subsequent loss of cytosol as well as metabolic degradation by free enzymes and by microorganisms are discussed as major causes for the observed effects. We recommend to abstain from using bulk frozen grab samples for the analysis of C/N ratio or stable isotope ratios.

Keywords: Freezing storage; Infaunal macrozoobenthos; Sample processing; Stable isotopes

1. Introduction

Analysis of tissue stable isotope ratios in nitrogen ($^{15}N/^{14}N$ or $\delta^{15}N$ vs. AIR) and carbon ($^{13}C/^{12}C$ or $\delta^{13}C$ vs. PDB) are an essential part of modern food web studies in marine benthic communities (e.g. Fry 1988, Hobson & Welch 1992, Herman et al. 2000, Jennings et al. 2002). The underlying principle is the enrichment of the heavier isotope ^{15}N and ^{13}C with each assimilation step in the food chain owing to the selective metabolic loss of the lighter isotopes during food assimilation and growth. On average, fractionation per trophic level amounts to 2.5 – 5 ‰ in $\delta^{15}N$ and to 0 – 1 ‰ in $\delta^{13}C$ (De Niro & Epstein 1978, 1981, Minagawa & Wada 1984, Post 2002).

There are many natural sources of variability in stable isotope ratios, but bias owing to sample treatment has drawn a considerable amount of attention recently. Besides sample acidification (Bosley & Wainright 1999, Jacob et al. 2005, Carabel et al. 2006) and sample lipid extraction (Sweeting et al. 2006), sample storage and preservation appears to be a crucial point. There is a general agreement that oven drying, freezing and freeze drying show little or no effects, whereas formalin and ethanol fixation cause significant bias (Bosley & Wainright 1999, Ponsard & Amlou 1999, Kaehler & Pakhomov 2001, Feuchtmayr & Grey 2003, Lorrain et al. 2003, Sweeting et al. 2004)

In studies on infaunal macrozoobenthic species, the bulk freezing of complete grab/corer samples directly after collection is an appealing approach (e.g. Lovvorn et al. 2005). Separating tiny animals from the sediment and identifying them is a time consuming and laborious task, which can be handled much better in the laboratory than on board of a research vessel with tight restraints on time and space. Here we evaluate whether bulk freezing of complete grab/corer samples and defrosting them again in the laboratory causes bias in stable isotope ratio determinations in animals collected from this sample, and whether such bias is species specific.

2. Material and Methods

Infaunal macrozoobenthos was collected with a 0.1 m^2 van Veen grab at one site in the German Bight (54°03.83 – 54°00.96N and 006°27.30 – 006° 43.13E, autumn 2004, *RV Heincke*). Thirteen samples were frozen directly after collection, i.e. the bulk content of the grab was transferred into a polyethylene box and stored at -20°C (bulk freezing, BF). From another 25 samples, we handpicked 91 individuals belonging to nine dominant infaunal species (*Echinocardium cordatum*, *Euspira pulchella*, *Lanice conchilega*, *Nephtys* sp., *Poecilochaetus serpens*, *Scolelepis bonnieri*, *Tellimya ferruginosa*, *Tellina fabula* and *Urothoe poseidonis*). Each individual was stored separately in a plastic jar at -20°C (individual freezing, IF). After 13 months storage, BF samples were slowly defrosted at 8°C, and the sediment was removed layer-by-layer following the thawing horizon down into the sample. 77 infaunal specimens were handpicked from the sediment and transferred to cooled seawater (3-4°C) where they remained for a maximum of 20 min before further processing. Subsequently, both BF and IF treated samples were lyphilised for 24 hours (Finn-Aqua Lyovac GT2E), homogenized in a ball mill, treated with 1 mol l^{-1} hydrochloric acid (HCL) to eliminate calcium carbonates following the procedure of Jacob et al. (2005), redried at 55°C and ground to powder in a mortar.

Stable isotope ratios $\delta^{13}C$ and $\delta^{15}N$ were determined by an isotope-ratio mass spectrometer (Thermo/Finnigan Delta Plus at GeoBioCenter^{LMU}, University of Munich). Gaseous standards (N_2 and CO_2 respectively) were calibrated against atmospheric nitrogen (AIR) for nitrogen and the PeeDee Belemite standard (PDB) for carbon. An internal standard (Peptone with known isotope composition) was used for every 6th sample. Experimental precision was less than ≤ ±0.2 ‰. Both isotopes ratios were expressed in δ notation:

δX (‰) = $[(R_{sample}/\ R_{standard})-1]\ x10^3$

where δX is ^{13}C or ^{15}N, and R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio.

All samples with < 5 µg nitrogen content were excluded from further analysis because of insufficient measurement precision (10 individuals). Multivariate outliers in the sample space [C/N, $\delta^{15}N$, $\delta^{13}C$] were identified by Mahalanobis distances (Barnett & Lewis1994) and excluded, too (1 individual). Delta^{13}C data were multiplied by -1 to obtain positive values, and all three data series (C/N, $\delta^{15}N$, $-\delta^{13}C$) were Box-Cox transformed (Sokal & Rohlf 1995) in order to achieve normality and equality of variances. Full interaction 2-way analysis of variance (ANOVA) followed by post-hoc Turkey HSD tests on differences between means was applied to check for effects of treatment (IF, BF) and of species on the three parameters.

3. Results

Compared to individual freezing (IF), bulk freezing (BF) caused a significant ($p<0.001$) increase in C/N (on average 0.93, Fig. 1a.), and a decrease in both $\delta^{13}C$ (on average 1.87 ‰, Fig. 1b.) and $\delta^{15}N$ (on average 1.01 ‰, Fig. 1c.). In C/N ratio and $\delta^{15}N$ ANOVA detected significant interactions between treatment and species (Table 1). On the species level, BF treatment effects were significant in seven (C/N, Fig. 1a.), nine ($\delta^{13}C$, Fig. 1b.), and three species ($\delta^{15}N$, Fig. 1c.), respectively.

4. Discussion

Freezing by itself, i.e. the exposure of organic matter to below zero temperature, has no effect on C/N ratio and stable isotope ratios (Bosley & Wainright 1999, Ponsard & Amlou 1999, Kaehler & Pakhomov 2001, Sweeting et al. 2004). There are, however, several distinct differences between the IF and the BF treatment procedure which may affect tissue condition and biochemical properties: (i) The freezing process of a bulk sample takes much longer owing to its larger mass and smaller surface/volume ratio compared to single animals. Slower freezing allows for the formation of more ice crystals inside tissues which can destroy cells mechanically and lead to cell content leakage (Salonen & Sarvala 1980, Feuchtmayr & Grey 2003). (ii) Tissues may be damaged further by mechanical stress caused by the antagonistic forces of liquid volume expansion during freezing against sample mass. (iii) Tissue components may be metabolized by free enzymes or by microorganism inhabiting the sediment (e.g. Ponsard & Amlou 1999), in particular during freezing and thawing of the sample and following mechanical tissue destruction. (iv) Certain macromolecules, in particular fatty acids can be oxidized chemically at temperatures as low as -30°C (E. Brodte, pers. comm.).

The observed increase in C/N ratio may be due to either an increase in C content or a decrease in N content. Salonen & Sarvala (1980) report a significant leakage of carbon during freezing but do not provide information on the corresponding loss in nitrogen. We presume that mechanical cell destruction during BF treatment leads to a loss of cytosol when thawing. Cytosol has a higher protein content – and thus nitrogen content – than organelles and membranes which are comparatively richer in carbohydrates and in fatty acids (Alberts 2002).

May cytosol loss following mechanical cell destruction cause the observed decrease in $\delta^{13}C$ and $\delta^{15}N$, too? Feuchtmayr & Grey (2003) compared the effects of various preservation techniques on $\delta^{13}C$ and $\delta^{15}N$ of zooplankton. They relate the observed depletion in the lighter isotopes ^{12}C and ^{14}N in normally frozen samples (-20°C) compared to shock frozen (liquid nitrogen) samples to leaching of cell material, too. This would, however, premise that the leached components are lower in $\delta^{13}C$ and $\delta^{15}N$. Distinct molecule groups are known to differ in their isotopic ratios from the average stable isotope composition of the bulk individual (e.g. Peterson & Fry 1987, Kelly 2000) but there is no direct evidence yet that e.g. cytosol components are isotopically lighter indeed.

Besides the physical processes discussed so far, chemical and biochemical activities may play an important role, too, in particular if cells have been damaged mechanically during freezing. Unfortunately, there are numerous potentially significant parameters such as molecule specific isotopic ratios (e.g. Peterson & Fry 1987, Kelly 2000), biochemical processes with specific effects on isotopic ratios (Smejkal et al. 1971, Owens 1987), and decomposition rates specific for certain substrates as well as metabolic pathways (Abraham et al. 1998, Fang et al. 2002, Lyons et al. 2003, Somsamak et al. 2006). Above all, both concentration and composition of sediment microorganisms and free enzymes may change from sample to sample. More sophisticated approaches, e.g. inhibition of free enzymes and/or of microorganisms, or monitoring of dissolved nitrogen and carbon components during sample storage and processing, will enhance our understanding of these processes.

For the time being we can only conclude that sample bulk freezing causes a significant and intolerable bias in the measurements of C/N, $\delta^{13}C$ and $\delta^{15}N$.

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Table

Table 1: 2-way analysis of variance testing the effects of treatment (IF, BF) and species on δ^{13}C, δ^{15}N and C/N ratio. Df: degrees of freedom, MS: mean square; * significant effect with p<=0.001.

		δ^{13}C		δ^{15}N		C/N ratio	
source	*df*	MS	*F*-value	MS	*F*-value	MS	*F*-value
treatment	1	1.98^{e-4}	309.34*	28.69	31.50*	0.001	215.82*
species	8	2.71^{e-5}	42.36*	178.19	195.62*	3.73^{e-4}	81.01*
interaction	8	7.47^{e-7}	1.17	10.22	11.22*	1.96^{e-5}	4.26*

Figure

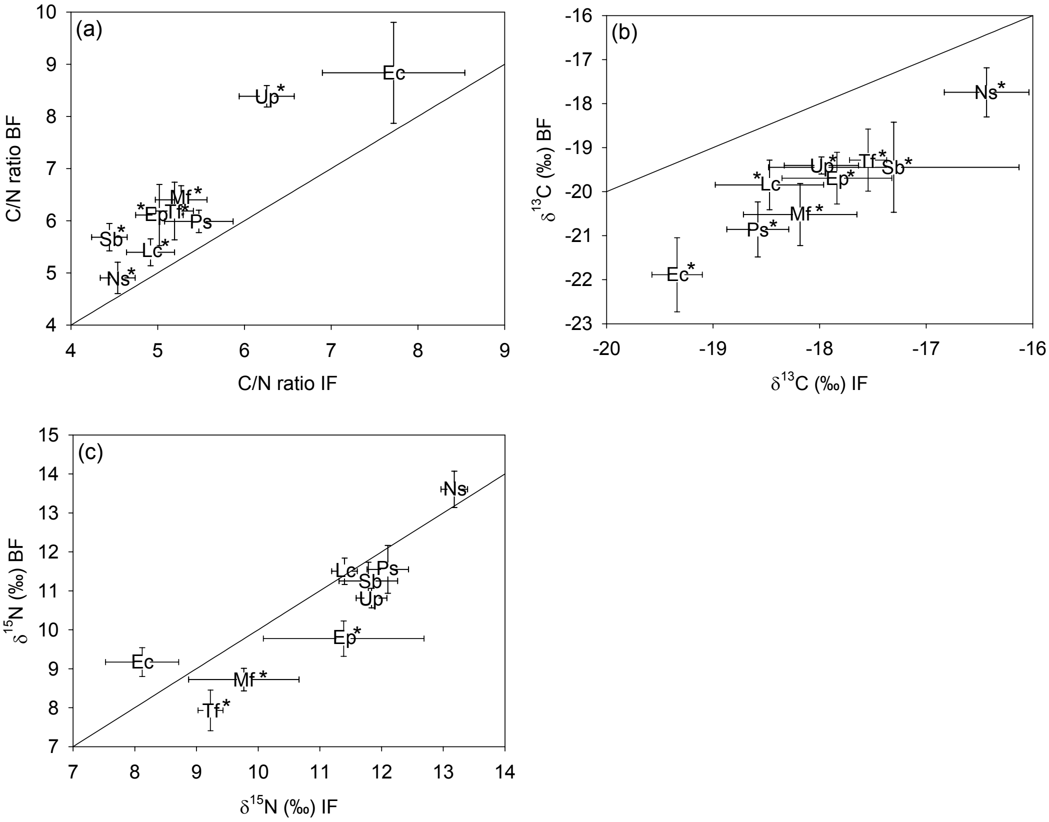

Fig. 1. Plots of (a) C/N ratio, (b) $\delta^{13}C$ and (c) $\delta^{15}N$ ratio in bulk treatment (BF) versus individual treatment (IF) samples. Horizontal and vertical bars represent standard deviation of x and y variable for *Echinocardium cordatum* (Ec), *Euspira pulchella* (Ep), *Lanice conchilega* (Lc), *Nephtys* sp. (Ns), *Poecilochaetus serpens* (Ps), *Scolelepis bonnieri* (Sb), *Tellimya ferruginosa* (Mf), *Tellina fabula* (Tf). Line indicates 1:1 ratio. *: significant difference between IF and BF in this species as indicated by post-hoc test ($p<0.05$).

Two-dimensional trophic complexity of highly dynamic coastal soft-bottom macrozoobenthos

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ABSTRACT

We study trophic complexity of a highly dynamic coastal soft-bottom community (German Bight, North Sea), using stable nitrogen isotope ratios ($\delta^{15}N$) as proxies of species trophic elevation and species trophic niche width.

At the community level, the relationship between horizontal (within trophic elevation) and vertical (across trophic elevation) dimension of trophic complexity was explored. Both measures indicate a moderate variety in traits, but particularly a high level of trophic redundancy. At the species level (i.e. the 20 most abundant species), vertical niche width (approximated by inter-individual variation in $\delta^{15}N$) and horizontal niche width (approximated by the number of potential prey species, PPI) were determined. Most dominant benthic species are generalists, indicating rather weak overall trophic interactions. Horizontal and vertical niche width is related to trophic compartments (basal, intermediate, and top). There appears to be an ecological trade-off between vertical niche width and ontogenetic shift in diet: species with distinct ontogenetic shift show only intermediate vertical niche width.

The applied two-dimensional proxy approach cannot substitute a high resolution food web study, but it constitutes an efficient, robust and standardised measure of community and species basic trophic properties. That is, within its inherent limits, it allows for scientifically sound comparisons of particular trophic properties and ecosystems on a rough scale.

Keywords: trophic complexity, trophic niche width, trophic structure, ontogenetic diet shifts, trophic functioning, stable isotopes, macrozoobenthos, North Sea

INTRODUCTION

In order to withstand the steadily increasing demand for services and goods, the sustainable management of aquatic resources must be based upon an ecosystem approach (e.g. Pauly et al. 2002, Worm et al. 2006). Trophic interactions constitute the major part of organism-organism interactions in living communities and thus are a significant determinant of ecological functioning (May 1974, Pimm 1982, Cohen 1978). Correspondingly, the relationship between biodiversity and trophic functioning became a central issue of ecology during recent years (e.g. Yachi & Loreau 1999, Loreau et al. 2001, Ives et al. 2005) with regard to natural community dynamics (Paine 1992, Polis & Strong 1996), but particularly concerning the consequences of human impacts on ecosystems. This encompasses e.g. the loss or extinction of species (e.g. Dunne et al. 2002, Christianou & Ebenman 2005) or the response of communities to perturbations (e.g. McCann 2000, Dunne et al. 2004, Montoya et al. 2006).

Key trophic features of a system may persist despite a change in species inventory (De Ruiter et al. 2005). Nevertheless, food web structure relies on species inventory, i.e. the trophic role of each species and its interaction with other species (e.g. MacArthur 1955, Paine 1992, McCann 2000, Cardinale et al. 2006).

Community trophic complexity can be tackled by adding a trophic dimension to taxonomically defined biodiversity (*sensu* Duffy et al. 2007), generating a ‘complexity space’ with the dimensions ‘horizontal diversity’, i.e. community species richness within each trophic level and ‘vertical diversity’, i.e. the number of trophic levels within a system. Accordingly, at the species level the within-species trophic variability is composed of ‘vertical niche width’, i.e. the extension of feeding across trophic levels and ‘horizontal niche width’, i.e. resource generalism (Duffy et al. 2007).

Purchasing diet information from benthic organisms is difficult since they are usually small in size, and many feed on the bulk litter of detritus (e.g. Eggers & Jones 2000, Polunin & Pinnegar 2002). Species are, therefore, commonly lumped into functional groups or feeding guilds (Briand & Cohen 1984, Martinez 1991) and/or structured by size and trophic position (e.g. Jennings et al. 2002, Brose et al. 2006). Stable isotope ratios provide a versatile lever to tackle this problem: On the one hand, nitrogen stable isotope ratios ($\delta^{15}N$) are a proxy for an organism’s position in relation to the base of the food web within the trophic hierarchy of an ecosystem, i.e. the species trophic elevation (Post 2002, McCutchan et al. 2003). On the other hand, variability in $\delta^{15}N$ can be used as an indicator for inter-individual variability in trophic elevation of food assimilated, i.e. intra-population diet variability (Bolnick et al. 2003, Bearhop et al. 2004, Matthews & Mazumder 2004), indicative of seasonal (e.g. Matthews & Mazumder 2005), spatial (e.g. Davenport & Bax 2002), and ontogenetic shifts (e.g. De la Morinière et al. 2003, Post 2003).

It seems impossible to capture all parameters that define community complexity and species niche width, but a subset may provide a sufficiently accurate and reliable approximation. Here, we approach community trophic complexity and trophic niche of the dominant species of a German Bight soft-bottom system by means of a two-dimensional approach that follows the concept of Duffy et al. (2007). We explore whether such a rather simple approach that depends on a limited number of parameters can provide feasible insights into community trophic structure and dynamics.

MATERIALS AND METHODS

Study area. The study area is situated in the German Bight (54°00.96' – 54°03.83' N and 006°27.30' – 006°43.13' E) at 30 m depth 45 km off the island Borkum. Hydrographical conditions are homogenous within the study area, as the prevailing strong tidal currents (up to 1 m s^{-1}) displace the water masses over far larger scales than the study area. Accordingly, sediments are quite uniform within the study area (homogenous fine sand; median grain size: 177 µm), shaping a consistent macrozoobenthic community in terms of species composition (Schröder & Dannheim unpubl. data).

Sampling and sample treatment. Sampling proceeded during two cruises with *RV Heincke* (November 2003, September/October 2004). The infauna was sampled with a 0.1 m^2 van Veen grab (95 kg) at 14 stations with 3 replicates on each station. Grab contents were sieved on 1 mm mesh size and fixed in 4 % buffered formalin. Epifauna was collected with a beam-trawl (3 m width) at the same 14 stations (haul duration <=10 min at 3 knots). Trawled distance was determined by Differential Global Positioning System (DGPS). Epifaunal subsamples from each catch were stored frozen until further treatment. Specimens were identified to the lowest possible taxonomic level. For each species, the abundance (m^{-2}), the biomass (wet weight, mg m^{-2}) and the mean body mass (M, mg) was determined and converted to dry mass after Brey (2001).

With additional grab and beam-trawl samples, 421 samples of the 21 most dominant species (see table 1) were collected for stable isotope analysis. All individuals were sorted alive on board and samples were stored at –20°C until further treatment. In small bodied species (*Euspira pulchella*, *Poecilochaetus serpens*, *Spiophanes bombyx*, *Urothoe poseidonis*) several individuals were pooled to achieve the minimum sample size (>5 µg nitrogen), required for sufficient precision in isotopic measurements. In large bodied species, only muscle tissue served as samples (*Liocarcinus holsatus*, *Asterias rubens*, *Astropecten irregularis*). All samples were lyophilised for 24 h (Finn-Aqua Lyovac GT2E) and subsequently weighted (DW, mg) to obtain the body mass (M) of specimens. Afterwards, samples were homogenized in a ball mill, treated with hydrochloric acid (HCl) to eliminate calcareous shells (Jacob et al. 2005), dried again at 55°C and ground to powder in a mortar. Stable isotope ratios were analysed with an isotope-ratio mass spectrometer

(Thermo/Finnigan Delta Plus) at GeoBioCenter^{LMU}, University of Munich. Common gaseous standards were used for calibration. Experimental precision was better than ±0.2 ‰.

Species trophic elevation. Nitrogen stable isotope ratios ($\delta^{15}N$) are a proxy of an organism's position within the trophic hierarchy of an ecosystem. In principle, the heavier isotope ^{15}N is enriched by an enzymatic selection with each assimilation step in the food chain. The fractionation of ^{15}N is variable ranging between 1.4 – 3.4 ‰ per trophic level for marine invertebrates (e.g. Post 2002, McCutchan et al. 2003). According to Yodzis (1984) and Cohen et al. (2003), we define trophic elevation TE_i of species *i* by

$$TE_i = \delta^{15}N_i \qquad (‰) \qquad (1)$$

Trophic elevations were determined for 21 species. For the remaining 137 species encountered in the study area, trophic elevations were inferred indirectly from various published and unpublished sources: For $\delta^{15}N$ values, we referred to species which were functionally, taxonomically and geographically as close as possible (for $\delta^{15}N$ data sources see ANNEX). To make $\delta^{15}N$ data from other ecosystems comparable to our data, we adjusted $\delta^{15}N$ values by the difference in $\delta^{15}N$ value of the primary food source (POM, particulate organic matter) between the German Bight (our data) and the corresponding ecosystem, i.e.:

$$TE_i = \delta^{15}N_i + (\delta^{15}N_{POM,GB} - \delta^{15}N_{POM,OS}) \qquad (‰) \qquad (2)$$

where TE_i is the corrected trophic elevation ($\delta^{15}N$) of species i, GB is German Bight and OS is other system. When $\delta^{15}N$ of primary consumers (PC) and not of POM was given as a baseline we used:

$$TE_i = \delta^{15}N_i + (\delta^{15}N_{PC,GB} - \delta^{15}N_{PC,OS}) \qquad (‰) \qquad (3)$$

where PC,GB is the average of directly measured $\delta^{15}N$ of primary consumers (see ANNEX, species marked with asterisk).

Individual trophic elevation was computed from data using these equations. As a last step, to species without equivalent trophic elevation data, we assigned the average value of their feeding guild (for feeding guilds and corresponding literature see ANNEX). The parasite *Vitreolina philippi* was excluded from analyses (1 individual).

Horizontal and vertical trophic diversity. At the community level, we define trophic complexity by two dimensions: the vertical trophic diversity (VTD), i.e. the trophic range of the system as defined by the range in $\delta^{15}N$ across all species

$$VTD = \delta^{15}N_{max} - \delta^{15}N_{min} \qquad (‰) \qquad (4)$$

Horizontal trophic diversity (HTD) was defined as the average number of species within a defined range of trophic elevation. This range was set to 1 ‰ $\delta^{15}N$, about 1/3 of the average trophic step size in marine systems (e.g. Post 2002, McCutchan et al. 2003). A window of size 1 ‰ $\delta^{15}N$ was moved stepwise (increment 0.1 ‰) across the trophic elevation frequency distribution of the community and the number of species S_i within this window was computed at each step i. The median of all S_i was taken as a representative estimate for HTD.

$$\text{HTD} = \text{Median}\ (S_i) \qquad (S/1\ ‰) \qquad (5)$$

Horizontal and vertical trophic niche width. At the species level, we evaluated trophic niche width in a similar analysis. We derived an index of vertical niche width (DV) from the inter-individual variability in $\delta^{15}N$ according to Bearhop et al. (2004), i.e.

$$DV_i = \delta^{15}N_{i,max} - \delta^{15}N_{i,min} \qquad (‰) \qquad (6)$$

where $\delta^{15}N_{max}$ and $\delta^{15}N_{min}$ were highest and lowest value of species i.

The number of potential prey items (PPI) of consumer i were used as an index of potential horizontal trophic niche width. Nemertini were excluded from this and further analysis owing to insufficient numbers. A prey species was assigned to PPI_i if (i) it was, on average, of equal or smaller size than consumer i (acc. to Cohen et al. 1993, Brose et al. 2006, see table 1 for mean body mass of consumers), and (ii) if its average $\delta^{15}N$ was within the presumed range (R_i) of prey $\delta^{15}N$ of consumer i. R_i was computed by

$$R_i = (\delta^{15}N_{i,min} - X) \text{ to } (\delta^{15}N_{i,max} - X) \qquad (‰) \qquad (7)$$

where X is fractionation per trophic step. Since fractionation is highly variable in marine invertebrates (1.4 – 3.4 ‰, see Post 2002, McCutchan et al. 2003), we choose a statistical approach to estimate PPI_i: X was set to 1.4 ‰ initially and PPI_i was computed. Subsequently, X was increased stepwise by 0.1 ‰ until 3.4 ‰, and PPI_i was computed for each step. The median of the 20 values computed was used as a representative PPI for consumer i.

According to trophic elevation rank order and the PPI_i, the 20 species formed three trophically distinct groups (cluster analysis and discriminant analysis, see results table 1). Consequently, we grouped the species into the three compartments 'TOP' (TC), 'INTERMEDIATE' (IC) and 'BASAL' (BC). The relation between vertical and horizontal trophic niche width was analysed by ANCOVA (DV versus trophic compartment and covariate PPI). Subsequently, we checked whether trophic elevation was related to body mass (ANCOVA; TE versus trophic compartment and covariate body mass). Data were checked for normality and homogeneity of variances (Barlett test) prior to statistical analysis. If differences in variance were detected, we increased the significance level for the subsequent test from $\alpha = 0.05$ to $\alpha = 0.01$.

Effects of inter-annual and ontogenetic shifts on vertical trophic niche width. To identify ontogenetic shifts in diet $\delta^{15}N$, we correlated TE with body mass (log M). The variation coefficient (R^2) of this relationship was used as the measure DS_i of ontogenetic diet shift in species i. We attempted to capture a sufficient size spectrum of the 20 species and evaluated the sampled size range as percentage data of species' potential maximal body mass (see table 1). Vertical trophic niche width (DV_i) was tested for inter-annual differences

(2003, 2004) and for ontogenetic shifts by ANCOVA (DV versus year and covariate body mass (log M)) or for ontogenetic shift only (ANOVA of DV versus body mass), if there were less than five data points in one year. Data were tested for normality and homogeneity of variances (Barlett test). If variances were different, we increased the significance level for the subsequent test from α = 0.1 to α = 0.01.

RESULTS

Horizontal and vertical trophic diversity. Vertical trophic diversity amounts to 12.3 ‰ δ^{15}N (range 5.87 ‰ to 18.17 ‰) (Fig. 1). Horizontal trophic diversity shows a bell shaped distribution with a maximum of 25 species in the interval 11.8-11.9 ‰. Median horizontal trophic diversity is 13 species /1 ‰.

Horizontal and vertical niche width. Potential horizontal trophic niche width was smallest for *Phaxas pellucidus* (2 PPI) and widest for *Crangon crangon* (93 PPI) (Fig. 2, table 1). Vertical trophic niche width varied between 0.72 ‰ (*U. poseidonis*) and 5.11 ‰ (*G. maculata*) (Fig. 2, table 1).

The plot of vertical niche width index DV versus horizontal niche width index PPI indicates of the trophic compartments ‘TOP’ (TC), ‘INTERMEDIATE’ (IC) and ‘BASAL’ (BC) (Fig. 2). The corresponding ANCOVA indicated a significant effect of PPI, compartment and their interaction on vertical niche width index DV (see table 2a). There was a distinct difference in PPI between compartments at the same DV (BC < IC < TC), albeit not vice versa.

Trophic elevation TE was significantly affected by trophic compartment and the interaction of trophic compartment*body mass (log M) (see table 2b).

Effects of inter-annual and ontogenetic shifts on vertical trophic niche width. 5 out of 20 species showed significant inter-annual differences in trophic elevations TE ($p<0.1$, Fig. 3). Trophic elevation was lower in 2004 in *E. cordatum* (- 1.47 ‰), *Lanice conchilega* (- 0.27 ‰) and *A. irregularis* (- 0.18 ‰), while it was higher in *L. holsatus* (+ 0.31 ‰) and *Tellina fabula* (+ 0.38 ‰). A significant ($p<0.1$) ontogenetic shift in diet δ^{15}N was found in 5 species: Anthozoa spp. (DS=0.48), *L. holsatus* (DS=0.07), *Nephtys* spp. (DS=0.18), *O. albida* (DS=0.27) and *T. ferruginosa* (DS=0.40). All significant diet shifters had a rather small vertical niche width (DV<2.6 ‰). Accordingly, the plot of vertical niche width index DV versus diet shift index DS results in a triangular plot limited by the three species with lowest DV, highest DV, and highest DS (Fig. 3).

DISCUSSION

The first part of the discussion will focus on general methodical problems of evaluating ecosystem trophic functioning and the suitability of our rather simple proxy-based approach for describing ecosystem trophic complexity. In the second part, we examine the patterns of trophic characteristics identified in our example system and discuss their implications for food web structure and ecological functioning.

Studies of ecosystem trophic functioning face two basic methodical problems, taxonomic resolution and diet resolution. Usually, limited resources of manpower and time forestall a high resolution on both axes, especially when dealing with species rich systems. More often than not species are grouped into larger taxonomic units (e.g. Martinez 1991, Morris et al. 2005) or into functional (trophic) groups or guilds (e.g. Eggers & Jones 2000, Davenport & Bax 2002). I.e. species specific trophic features are neglected on the consumer as well as on the diet side (e.g. Hall & Raffaelli 1993, Pinnegar et al. 2005). Diet analysis becomes particularly demanding in small-sized consumers and in those feeding on ‘storage pools’ such as detritus (e.g. Ponsard & Arditi 2000). Here, highly advanced biochemical or genetic approaches may be required to identify single prey items (e.g. Iverson et al. 2004, Blankenship & Yayanos 2005).

Our study is an attempt to maximise efficiency by combining high resolution in consumer taxonomy, i.e. species level, with low resolution in diet analysis, i.e. individual nitrogen stable isotope ratio. We use $\delta^{15}N$ to approximate consumer trophic elevation within the food-web hierarchy (e.g. De Niro & Epstein 1981, Davenport & Bax 2002, Winemiller et al. 2007) as well as consumer trophic niche width (Bearhop et al. 2004). Basically, this approach is inferior to conventional niche width measurements based on multiple variables (e.g. Hutchinson 1959, Matthews & Mazumder 2004), owing to limits of resolution as well as to potential methodical pitfalls (e.g. Frazer et al. 1997, Jacob et al. 2005, Sweeting et al. 2005, Dannheim et al. 2007).

However, the transformation of our ‘simple’ measurements taxon and $\delta^{15}N$ into a two-dimensional niche space creates a new quality, we obtain an objective measure of basic trophic properties at the species and community level. There are intrinsic shortcomings, obviously, mainly the neglect of intra-guild predation and cannibalism (see Polis et al. 1989), the fact that species $\delta^{15}N$ is a poor proxy of horizontal niche overlap, the positive correlation between horizontal and vertical niche width, and the insufficient taxonomic resolution at the base of the food web, i.e. regarding primary producers and detritus (see Moore et al. 2004). Nevertheless, these drawbacks may be outweighted by the fact that we have a practical tool that allows for standardized between-system comparisons of trophic structure.

In the following, we will evaluate the information provided by this tool on the trophic complexity of the benthic community analysed here, and whether this is in accordance with our *a priori* knowledge of the system and in the light of ecological theory.

The evolutionarily derived basic unit of ecological functioning is the species within a food web. Seemingly trophically ‘similar’ species may play quite different roles owing to differences in the strength of specific trophic links (e.g. Pimm & Lawton 1978, Paine 1992, Polis & Strong 1996, De Ruiter et al. 2005). Particularly, ‘weak interactions’ (trophic links between otherwise highly connected species) enhances trophic redundancy (e.g. Eggers &

Jones 2000) and are therefore crucial for community resistance (e.g. McCann et al. 1998, Berlow 1999, McCann 2000). Trophic niche width indicates trophic interaction strength to a certain extent, as a narrow niche points towards specialists or ontogenetic diet shifters with few prey items and thus, few, comparatively strong trophic links, and a wide niche indicates generalists or omnivores with many prey species and many links (Polis & Strong 1996, McCann & Hastings 1997, Post et al. 2000, McCann et al. 2005).

Ecological theory claims that the horizontal and vertical diversity define the variety of species derived trophic traits within a community, and thus the potential trophic flexibility in case of changing conditions (Duffy et al. 2007). Theoretical ecology predicts further that in particular trophic redundancy, i.e. replacement of lost species by others which are capable to trophically compensating them, constitute a buffering effect and thus enhances community resistance (insurance hypothesis, Naeem & Shibin 1997, Yachi & Loreau 1999). Accordingly, trophic complexity, redundancy and finally ecological functioning in terms of resistance are positively related to both diversity measures (e.g. Yachi & Loreau 1999, Duffy et al. 2007, Ives & Carpenter 2007, May et al. 2007).

At the species level, our two-dimensional approach indicates a linear relationship between vertical and horizontal niche width index, albeit with different slope in different compartments (compare Fig. 2 and table 2 for statistical results). On the one hand, this is a function of consumer trophic elevation: the higher the trophic position within the trophic hierarchy, the larger becomes the variety of potential food items it can select from (e.g. Pimm & Lawton 1978, Cohen et al. 1993, Davenport & Bax 2002). On the other hand, this relationship depends on distribution of species along the trophic elevation axis in the system under investigation, i.e. on the food-web structure.

Both theory and applied studies indicate that body size is one structuring factor in food webs (e.g. Jennings et al. 2002, Brose et al. 2006). Trophic elevation tends to increase with body size, but this relationship weakens in very large species, i.e. some of the largest organisms feed on small prey (e.g. Jennings 2005). Within a species, individual trophic niche may change significantly with increasing body size (ontogenetic diet shift, e.g. De la Morinière et al. 2003, Post 2003). Our approach indicates a particular relationship between species vertical trophic niche width and ontogenetic diet shift that resembles a ‘trophic niche triangle’ (see Fig. 3). The corners of the triangle represent (i) distinct specialists (narrow vertical trophic niche width DV, no ontogenetic diet shift DS), (ii) distinct generalists (wide DV, no DS) and (iii) pronounced ontogenetic diet shifters (intermediate DV, DS). Interestingly, the range of species vertical niche width decreases with increasing tendency towards ontogenetic diet shift. This is obvious for the lower limit of DV, because a stronger ontogenetic shift in diet shift implies a higher number of prey items for the species as a whole. The decrease of the upper limit of DV with increasing DS may indicate an evolutionary constraint. Apparently, trophic strategies above this line, i.e. ‘high DV-high DS’, just do not pay off (*sensu* optimal foraging theory, e.g. Begon et al. 1996).

Among the dominant benthic species of our German Bight system are no typical specialists and only a few ontogenetic diet shifters (Fig. 3). I.e., we deal with a system dominated by trophic generalists. Accordingly, the trophic structure is characterised by a high proportion of weak links and thus high trophic redundancy (e.g. Naeem & Shibin 1997, Yachi & Loreau 1999, Eggers & Jones 2000) which both point towards enhanced community resistance (McCann et al. 1998, Berlow 1999, McCann 2000).

Ecological theory predicts exactly such a structure for a system subjected to continuous disturbance (e.g. Menge & Sutherland 1987, Dunne et al. 2004), as manifest in terms of hydrodynamics and particularly long-term bottom trawling in the German Bight (see Clark & Frid 2001, Kaiser et al. 2002, Callaway et al. 2007, Dannheim et al. submitted). This has indications for the whole ecosystem and its basic trophic features as follows:

So far, our German Bight example system is the only one for which δ15N based measures of vertical (VTD) and horizontal trophic diversity (HTD) are available. Further data will put our concept to the test: If we take our continuously disturbed system as a reference point for a typical resistant system, i.e. comparably moderate to low biodiversity (e.g. Jennings & Kaiser 1998) and the system trophic properties moderate VTD (12.3 ‰) and high HTD (13 species/1 ‰), then we can make predictions of how VTD and HTD should measure in systems of different settings. ‘Persistent’ systems characterised by low levels of disturbance, long-term stability, and consequently high biodiversity (e.g. the Antarctic system, coral reefs, kelp forests, see Vitousek et al. 1997, Jackson et al. 2001, Jacob et al. 2006) should display higher VTD but lower HTD. ‘Resilient’ systems that experience regularly albeit ‘random’ catastrophic disturbance events and subsequent recolonisation (e.g. the Baltic Sea, see Arntz & Rumohr 1982, Nilsson & Rosenberg 2000, Bonsdorff 2006), should have lower VTD and lower HTD.

Regarding the German Bight system, the price for enhanced resistance is less efficiency. Niche models indicate that efficiency of nutrient processing increases with the share of trophic specialists in total species number and enhanced trophic complexity of a system (Thébault & Loreau 2003, Ives et al. 2005). A trophic specialist is evolutionary adapted to handle one and only one particular food source, and in this task it is more efficient than any generalist that must be able to deal with a variety of food sources (e.g. Tilman et al. 1996, Cardinale et al. 2006). Hence, overall efficiency will increase with the share of specialists in the food web.

Obviously, our relatively ‘quick-and-dirty’ proxy based approach towards trophic functioning cannot substitute a high resolution food web study. But it constitutes an efficient, robust and standardised measure of basic trophic properties of communities as well as of species. That is, within its inherent limits, this tool allows for scientifically sound comparisons of particular trophic properties, as well as of ecosystems on a rough scale.

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TABLES

Table 1. Species ordered by trophic elevation (TE$_i$) and number of potential prey items (PPI$_i$) within trophic compartments: 'TOP', 'INTERMEDIATE' and 'BASAL' according to the cluster and discriminant analysis. N: number of specimen (N) collected (2003/2004), TE: mean trophic elevation (δ^{15}N, ‰ ± standard deviation), PPI: index of potential horizontal niche width (median no. of potential prey items), DV: index of vertical niche width (δ^{15}N range in ‰), M: mean body mass (mg DM ± standard deviation). Size range covered as percentage of maximum recorded body mass (equals 100 %) in the study area over investigation time. Feeding guilds are given in parenthesis: DF = deposit feeder, IF = interface feeder, PS = predator and scavenger, SF = suspension feeder, SL = sandlicker. n.c. means not calculated.

Species	**N ('03/'04)**	**TE (δ^{15}N, ‰)**	**PPI**	**DV (δ^{15}N, ‰)**	**M (mg DM)**	**size range covered (% of max. size)**
TOP compartment						
Pomatoschistus minutus (PS)	11/19	15.19 ± 0.65	76	3.44	444.0 ± 207.9	8 – 48
Goniada maculata (PS)	10/9	14.93 ± 1.05	75	5.11	20.6 ± 8.8	18 – 100
Crangon crangon (PS)	10/0	14.69 ± 1.40	93	4.90	568.0 ± 204.0	24 – 93
Asterias rubens (PS)	10/19	14.10 ± 0.39	56	1.88	1936.1 ± 1091.1	6 – 72
Anthozoa spp. (PS)	0/8	13.92 ± 0.86	57	2.12	331.3 ± 376.5	1 – 100
Scolelepis bonnieri (PS)	2/6	13.90 ± 1.51	78	4.78	6.4 ± 3.7	11 – 51
Astropecten irregularis (PS)	10/20	13.63 ± 0.45	51	1.70	2449.6 ± 1710.1	5 – 100
Liocarcinus holsatus (PS)	10/20	13.33 ± 0.58	65	2.59	3436.7 ± 1766.3	13 – 90
INTERMEDIATE compartment						
Ophiura albida (PS)	10/10	13.47 ± 0.41	23	1.32	233.3 ± 53.5	33 – 73
Nephtys spp. (PS)	10/19	13.29 ± 0.38	29	1.60	122.5 ± 94.2	3 – 99
Spiophanes bombyx (IF)	6/21	12.30 ± 0.52	35	2.77	1.8 ± 0.7	16 – 83
Urothoe poseidonis (SL)	3/17	11.82 ± 0.22	13	0.72	1.2 ± 0.2	45 – 88
Euspira pulchella (PS)	6/5	11.82 ± 1.20	38	3.56	23.5 ± 21.1	9 – 100
Poecilochaetus serpens (IF)	1/20	11.77 ± 0.50	23	1.52	1.2 ± 0.4	28 – 100
Lanice conchilega (IF)	10/20	11.41 ± 0.28	18	0.98	52.2 ± 26.1	12 – 100
BASAL compartment						
Phaxas pellucidus (SF)	16/13	10.01 ± 0.32	2	1.36	90.9 ± 77.4	6 – 100
Pectinaria koreni (DF)	0/12	9.92 ± 0.60	3	1.79	43.3 ± 28.4	15 – 100
Tellimya ferruginosa (DF)	1/9	9.77 ± 0.80	4	2.38	6.5 ± 4.0	15 – 100
Echinocardium cordatum (DF)	10/9	9.42 ± 1.03	5	3.60	1998.6 ± 1809.2	2 – 74
Tellina fabula (SF)	10/16	9.08 ± 0.30	3	1.47	129.6 ± 82.8	14 – 100
omitted owing to insufficient N						
Nemertini spp. (PS)	0/3	15.14 ± 0.35	n.c.	0.60	114.3 ± 239.2	29 – 63

Table 2. Full interaction ANCOVA of (a) diet variability (DV) versus number of potential prey items (PPI) and trophic compartments (BC, IC, TC) and (b) trophic elevation (TE) versus species body size (log M) and trophic compartments. DV was optimum box cox transformed according to Sokal & Rohlf (1995). df: degrees of freedom.

(a)			**DV**	
source	**df**	**Sum of squares**	***F*-value**	**p-value**
PPI	1	4.48	47.35	<0.01
trophic compartment	2	5.95	31.43	<0.01
interaction	2	5.31	28.06	<0.01
(b)			**TE**	
source	**df**	**Sum of squares**	***F*-value**	**p-value**
log M	1	0.14	0.19	0.66
trophic compartment	2	1107.80	768.09	<0.01
interaction	2	44.17	30.63	<0.01

FIGURES

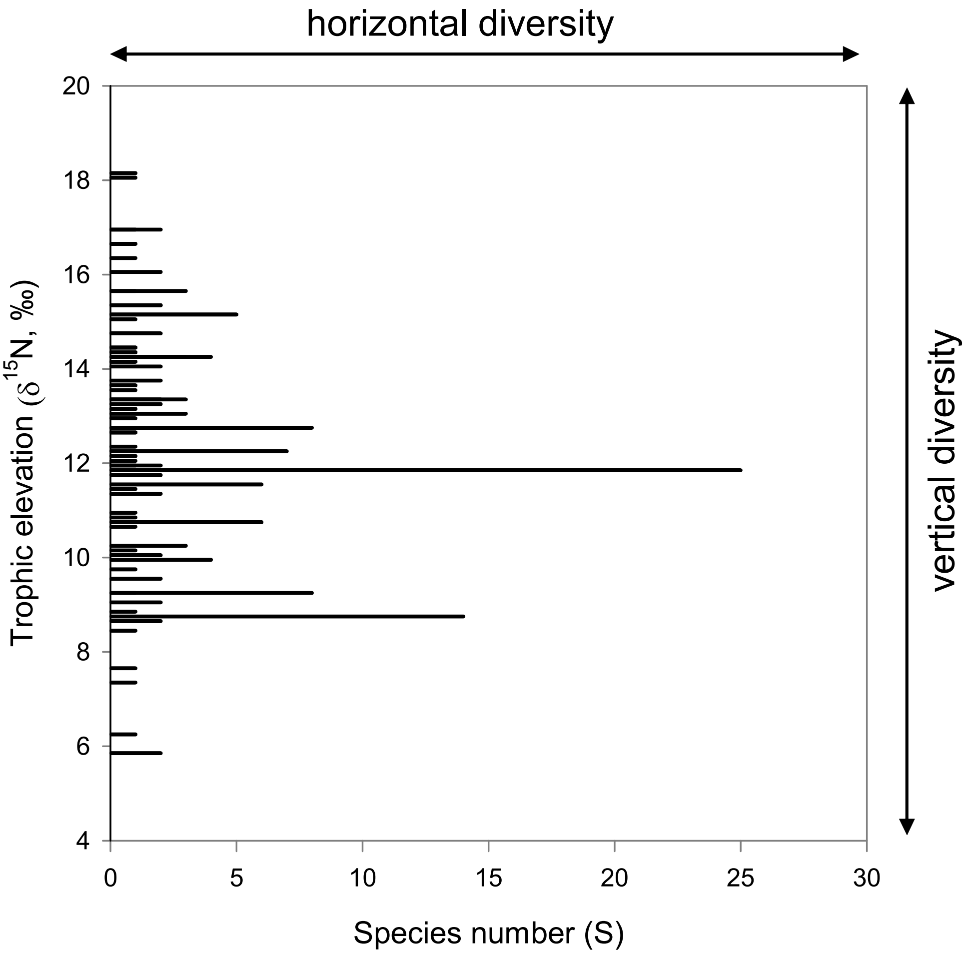

Fig. 1: Trophic elevation frequency distribution of the benthic community (158 species).

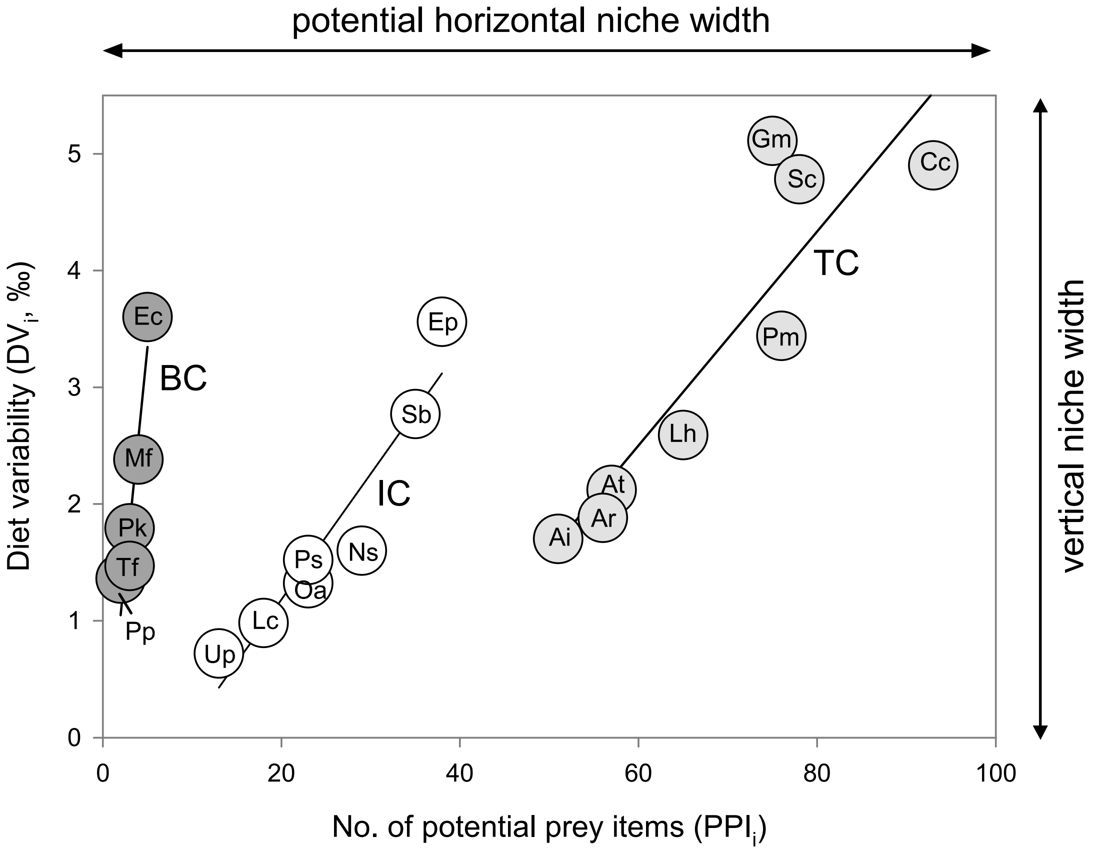

Fig. 2: Relation between vertical niche width index (DV_i ‰; diet variability) and potential horizontal niche width index (median number of potential prey items, PPI_i) depending on trophic compartments (BC= basal compartment, IC = intermediate compartment, TC = top compartment): At= Anthozoa spp., Ar = *Asterias rubens*, Ai = *Astropecten irregularis*, Cc = *Crangon crangon*, Ec = *Echinocardium cordatum*, Ep = *Euspira pulchella*, Gm = *Goniada maculata*, Lc = *Lanice conchilega*, Lh = *Liocarcinus holsatus*, Ns = *Nephtys* spp., Oa = *Ophiura albida*, Pk = *Pectinaria koreni*, Pp = *Phaxas pellucidus*, Ps = *Poecilochaetus serpens*, Pm = *Pomatoschistus minutus*, Sc = *Scolelepis bonnieri*, Sb = *Spiophanes bombyx*, Mf = *Tellimya ferruginosa*; Tf = *Tellina fabula*, Up = *Urothoe poseidonis*.

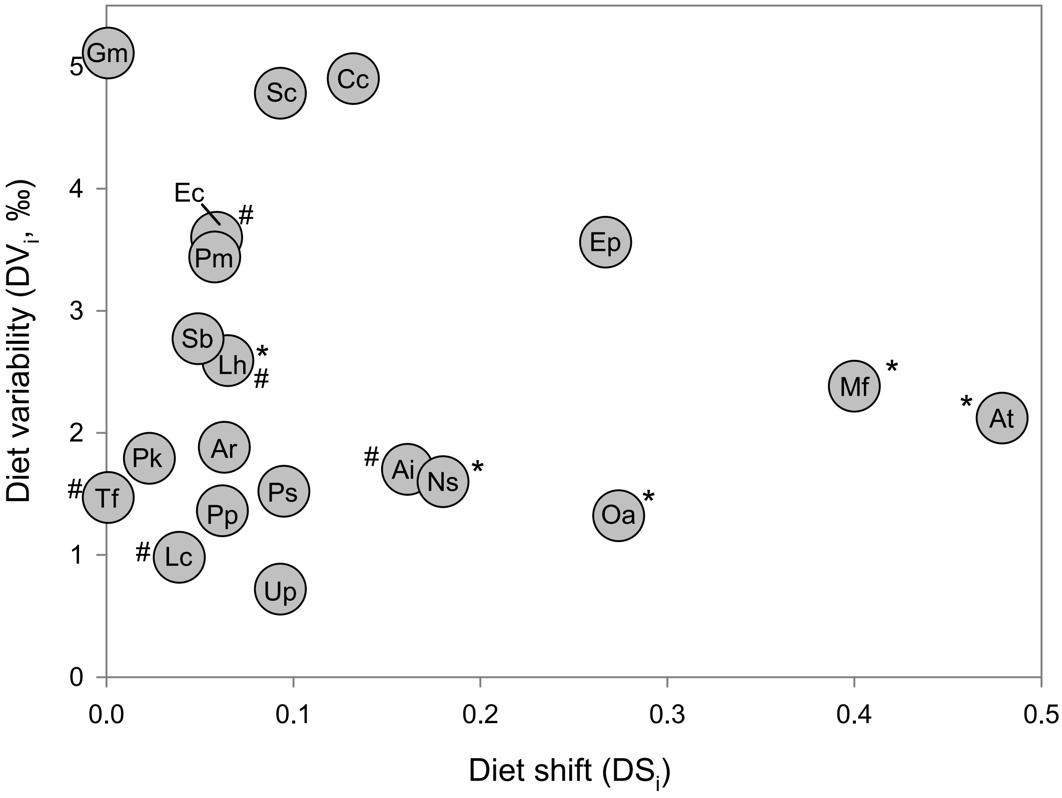

Fig. 3. Relation between diet variability (DV_i, ‰) and ontogenetic diet shift (DS_i) for species: At= Anthozoa spp., Ar = *Asterias rubens*, Ai = *Astropecten irregularis*, Cc = *Crangon crangon*, Ec = *Echinocardium cordatum*, Ep = *Euspira pulchella*, Gm = *Goniada maculata*, Lc = *Lanice conchilega*, Lh = *Liocarcinus holsatus*, Ns = *Nephtys* spp., Oa = *Ophiura albida*, Pk = *Pectinaria koreni*, Pp = *Phaxas pellucidus*, Ps = *Poecilochaetus serpens*, Pm = *Pomatoschistus minutus*, Sc = *Scolelepis bonnieri*, Sb = *Spiophanes bombyx*, Mf = *Tellimya ferruginosa*, Tf = *Tellina fabula*, Up = *Urothoe poseidonis*. * significant ontogenetic diet shift ($p<0.1$), $^{\#}$ significant inter-annual diet variability ($p<0.1$).

The effect of an artificial hard substrate on the local soft-bottom macrozoobenthos in the German Bight: A first step to understand the impact of future offshore wind turbines

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Abstract

To estimate the impact of the foundations of wind turbines, the habitat structure and the macrozoobenthic community were studied at a research platform, similar in size and shape to wind turbines planned in the German Bight. Sampling started prior to the platform construction and continued for 17 months after construction. The macrozoobenthos at the platform shifted from an assemblage dominated by sessile and sedentary species to one characterised by mobile and often predatory species. This modification of the community composition is likely to be caused by increased erosion as this process probably removed sedentary species from the sediment. In addition, shell fragments accumulated in the vicinity of the platform, which are an unsuitable habitat for soft bottom species. The decrease of total abundance and species number was most pronounced close to the platform but also the community at least to 17 m distance changed. To date, it can not be predicted if extensive wind farming will cause cumulative or indirect effects. Nevertheless, our results are a first step to an understanding of the ecological implications of offshore wind turbines in the German Bight, showing that the macrozoobenthic community structure may change considerably in the vicinity of a wind turbine.

Key-words: artificial hard substrate, environmental changes, North Sea, offshore wind energy, research platform, soft-bottom community, wind turbine

Introduction

Pioneered by the construction of the wind farm “Horns Rev” in 2002 (North Sea, Denmark) many European countries plan to install offshore wind turbines along their coastline during the next years (Petersen and Malm, 2006). Also in the German Exclusive Economic Zone (EEZ) of the North Sea, large offshore wind farms with hundreds of wind turbines are planned. Our knowledge about the environmental impacts of wind farms, however, is generally limited (Gill, 2005) and it is not clear yet whether these wind farms will have significant impacts on the marine ecosystem (see reviews by Merck and Nordheim, 2000; Petersen and Malm, 2006).

Previous studies on artificial reefs, wrecks or oil platforms identified ecological impacts of artificial hard substrates. These studies show that such substrates in natural soft sediments often induce changes of hydrographical conditions which modify the grain size of the adjacent sediment (e.g. Davis *et al*., 1982; Ambrose and Anderson, 1990; Nelson *et al*., 1994). Changes in sediment structure may affect the soft bottom community as its composition is largely determined by sediment characteristics (e.g. Duineveld *et al*., 1991; Künitzer, *et al*. 1992). In addition, artificial hard substrates are quickly colonised by a characteristic hard bottom fauna of considerable biomass (e.g. Forteath *et al*., 1982; Whomersley and Picken, 2003; Stachowitsch *et al*., 2002). The additional biomass may attract predators that do not only feed on the fouling community but may also increase the predatory pressure on the surrounding soft bottom fauna. As a consequence, the abundance of certain taxa, and thus the benthic community composition, changes in the vicinity of artificial reefs (Ambrose and Anderson, 1990; Nelson *et al*., 1994; Posey *et al*., 1994; Fabi *et al*., 2002). Likely, similar changes will occur at the underwater structures of the wind turbines. At present, however, comparable studies on the impact of complex underwater structures of wind turbines are lacking, and hence the consequences on the marine environment of the German Bight can only be estimated theoretically on the basis of investigations on other artificial hard substrates. Therefore, prior to the construction of wind farms in the German Bight, a research platform FINO 1 (**F**orschungsplatformen **i**n **N**ord- und **O**stsee; research platforms in the North and Baltic Sea) similar in size and shape to planned wind turbines was installed in order to investigate not only the feasibility and profitability of offshore wind farming but also its prospective impact on the marine environment.

This study examines the characteristics of the associated soft bottom macrozoobenthic community and the sediments prior to until one and a half years after the construction of FINO 1. Sediment and benthic community composition at four distances from the research platform are compared to a reference area to determine the spatial extend and temporal development of changes after the construction of the artificial hard substrate.

Material and methods

Study site

The research platform FINO 1 was deployed in the German Bight in July 2003 at 54°0.86'N 06°35.26'E at a water depth of 28 m, about 45 km north of the Island of Borkum (Fig. 1). The fundament of the platform is a steel made jacket structure with four braced piles, spreading from a square of 7.5 x 7.5 m at the surface to one of 26 x 26 m at the sea bed.

The sediment of the study area consists of homogenous sand inhabited by a macrozoobenthos community characterised as *Tellina-fabula*-association (*sensu* Salzwedel *et al.*, 1985). During the investigation period, salinity ranged from 32.9 in spring 2004 to 34.7 in winter 2004. Seawater temperature varied from 3.1°C in spring 2004 to 19°C in summer 2004. Main current directions were east-southeast and west-northwest depending on the tidal currents and reached up to 1 m s^{-1} at the surface and 0.4 m s^{-1} near the bottom twice a day (unpublished data provided by the German Federal Maritime and Hydrographic Agency, BSH).

Sampling

Preliminary study

To estimate the spatial variability of sediment structure and macrozoobenthic infauna abundance in the study area, 17 van Veen grab samples were taken (0.1 m^2, 95 kg) onboard RV "Heincke" in March 2003 four months prior to the installation of the underwater construction of FINO 1. The stations were spread over the entire future study area by drifting from north-east to south-west over the prospective position of the research platform (Fig. 2).

Sampling procedure

Since the construction of the platform in July 2003, sediment and infauna were sampled at 4 stations in a distance of 2, 5, 10 and 15 m from the underwater structure of the platform. Samples were taken monthly with a van Veen grab from August 2003 through December 2004 (see Table 1). The grab was operated from a crane installed on the platform covering a maximum distance of 15 m in one direction. Due to strong currents, it was not possible to always hit exactly the same sampling position and thus, the grab sampled with an estimated inaccuracy of ± 2 m. In order to keep disturbances due to sampling procedure at minimum, only one sample was taken at each distance per month.

The effects of artificial underwater structures are usually restricted to 50 – 100 m distance from the hard substrate (see e.g. Knust *et al.*, 2003 for review). Hence, a reference area, which allows to compare the sediment and benthic community structure at the platform with that of sea bottom unaffected by artificial hard substrate, needs to be located in at least 200 m distance. For safety reasons all shipping activities, including bottom trawling, are prohibited at the platform within a radius of 500 m. Therefore, as bottom trawling considerably changes the benthic community structure (e.g. Jennings *et al*., 1999), also the reference area must not be exposed to fishery. To fulfil both requirements, we established reference stations in 200 -400 m distance from the platform to exclude the effects of both, the artificial hard substrate and bottom trawling.

Samples of the reference stations were taken onboard RV “Heincke” in approx. three months intervals. The sampling period started shortly after the platform construction (July 2003) and was continued for 17 months (December 2004; see Table 1). During each survey, at each of five reference stations (R1 – R5) three replicate samples were taken (see Fig. 2).

Sub-samples for sediment analysis were taken randomly from each grab from the platform and from one grab per reference station with a 5 cm² PVC corer from the 5 cm top layer. These sub-samples were analysed by wet and dry sieving over a Wenthworth scaled standard filter set (Wenthworth, 1922). The sediment fractions were weighed and proportions [%] of the total sub-sample were calculated. The silt and clay fraction [%; < 63 µm] (SCC), median grain size [µm] (MGS) and the sorting of the sediment (Graphic Standard Deviation, GSD; Folk 1974) were determined after Buchanan (1984). To analyse the total organic carbon content [%] (TOC), an additional sub-sample was taken randomly from the 2 cm top layer of the sediment. After freeze-drying, the inorganic carbon was removed by adding hydrochlorid acid (HCl) and samples were analysed by an autoanalyser (LECO CS-125 Analyser).

In addition to the sediment analysis in the laboratory, general habitat structure was examined visually during sampling: Onboard, the shell content of the sediment (SCS) was roughly estimated by distinguishing five categories (1) no shell content; (2) minor shell content; (3) sediment mixed with shell; (4) more shell than sediment and (5) only shell. Unpublished data on the erosion of sediment were provided by the Research and Technology Centre (FTZ), Büsum (Germany) to identify scour development around the research platform. These data were confirmed by scientific divers.

The sampling procedure for macrozoobenthic infauna followed the ICES and HELCOM recommendations (Rumohr, 1999). The grab samples were sieved (1000 µm) and preserved in 4 % formalin buffered with Borax in seawater. In the laboratory, the macrozoobenthic infauna was sorted, identified to species level if possible and counted. To avoid assumptions of homogenous spatial pattern, species abundance was not extrapolated to 1 m^2 but results are presented as individuals per sample (0.1 m^{-2}).

Data processing and statistical analysis

Community structure was described by total abundance (ind. 0.1m^{-2}), species density (spp. 0.1 m^{-2}), Shannon-Wiener diversity (H’ based on ln) (Shannon and Weaver, 1963) and evenness (J) (Pielou, 1966). Multivariate analyses were performed using PRIMER 6 software (Clarke and Gorley, 2006, Clarke and Warwick, 2001). Bray-Curtis similarities were calculated after 4th root-transformation of the benthic abundance (Field *et al.*, 1982) to reduce the effect of dominant species. Similarities in species compositions between different samples were visualized by non-metric Multidimensional Scaling (MDS) (Kruskal, 1964). Significant differences between the reference area and the platform stations were detected by ANOSIM (Analysis Of SIMilarities). Results were accepted as statistically significant at alpha < 0.05. Taxa that contributed most to the community structure and the differences between areas were determined by SIMPER (SIMilarity PERcentages).

Relationships among the benthic communities and environmental parameters were explored with the BIOENV routine (Clarke and Warwick, 2001). Parameters which have been tested were: (1) median grain size (MdGS) [µm], (2) silt and clay content (SCC) [%], sorting of the sediment (GSD), total organic carbon (TOC) [%] and shell content (SCS) [categories].

Results

Preliminary study

Samples taken four months before platform construction were widespread over the study area (see Fig. 2). Benthic community compositions of all samples were similar to approx. 62 %. Hence, the benthic community composition before platform construction was similar in the entire study area before platform construction.

Habitat structure

The sediment characteristics at the reference stations were similar to those before the implementation of the platform and varied only slightly over the investigation period (Fig. 3). The sediment consisted of well sorted fine sands, with 1.2 to 5.2 % silt and clay content and low organic carbon content (TOC: 0.06 to 0.15 %). The sediment at the 10 and 15 m stations were comparable to that of the reference stations during the course of the study. At the 2 and 5 m stations the sediment characteristics were slightly higher and more variable in terms of GSD (2 m: 0.51 to 1.54; 5 m: 0.42 to 1.01), silt and clay content (2 m: 0.86 to 28.55 %; 5 m: 0.72 to 17.93 %) and the total organic carbon content only at the 2 m station respectively (0.003 to 1.12 %).

Most pronounced changes were found in the general habitat structure, i.e. the shell content of the sediment. At the reference stations, shell content remained low (category 1 – 2) during the entire study period. At the 5, 10 and 15 m stations, the shell content increased slightly until the end of the investigation period up to category 4 – 5. At the 2 m station, it increased considerably. Here, the habitat structure was regularly classified as category 5, which characterizes grab samples containing only shells but no sediment.

Results from a multi beam investigation (FTZ) and observations by scientific divers indicated the development of scours of approx. 1.5 to 0.6 m depth in the surrounding of the underwater structure. In easterly direction from the North pile where the crane for sampling is operated, the scours were about 1.5 m deep close to the underwater structure. In the further course scours diminished to a depth of 0.6 m in 16 m distance.

Benthic community

Temporal development of total abundances of the macrozoobenthos differed only slightly between the five reference stations (Fig. 4a). Abundance was highest at all stations in summer 2003 due to extremely high numbers of the phoronid *Phoronis mülleri*. Afterwards it levelled off until the end of the investigation period. Generally, total abundance was lower at the four platform stations than at the reference stations over the whole study period (Fig. 4b). The differences were most prominent in summer 2003, one to two months after platform construction.

Species number at the reference stations was highest at all stations in summer 2003. Thereafter, it decreased continuously until spring 2004 and slightly increased again until the end of the investigation period (Fig. 5a). At the platform, species number was lower at the 2 m station than at the 5, 10 and 15 m stations and in the reference area from summer 2003 until spring 2004. In summer 2004, it increased at the 2 m station and reached equally high values as at the 5, 10 and 15 m stations. Thereafter, species number at the four platform stations decreased and was again lower than at the reference stations.

In the reference area, temporal development of species diversity index (H’) and evenness (J) was similar at all five stations. Both indices were low in July 2003 caused by the high dominance of *P. mülleri* (Fig. 5b, c). Due to the decreasing dominance of *P. mülleri*, diversity and evenness increased continuously from July 2003 until the end of the investigation period in September 2004. At the platform, both indices in summer 2003 (one to two months after platform construction) were higher than at the reference stations. Thereafter, species diversity was lower at the 2 m than at all other stations until spring 2004 (Fig. 5b). Evenness was lowest at the 2 and 5 m stations as compared to all other distances including the reference area (Fig. 5c). In summer 2004, values of both indices were similar at the platform stations. Afterwards they decreased and were lower than at the reference stations.

The MDS-plot shows a separation of platform and reference stations with regard to the community composition over the entire study period (Fig. 6). Samples taken at the 5, 10 and 15 m stations were more clumped than samples from the 2 m station, indicating higher variation in the community composition of the latter samples.

Results from ANOSIM showed that communities significantly differed between the reference stations and the four platform stations (Table 2). Comparing the platform stations only, the analysis did not detect significant differences between the infauna composition at the 5, 10 and 15 m stations. At the 2 m station, community composition differed significantly but only slightly from all other platform stations.

The results from the BIOENV indicated that the silt and clay content (SCC), GSD and total organic carbon content (TOC) in the reference area showed the best correlation with the benthic community similarity matrix (abundance-data, 4th root transformed) ($r = 0.301$; Table 3). In contrast, the shell content (SCS) together with the GSD, TOC explained most of the benthic community similarity at the platform ($r = 0.465$).

Since the analyses of community composition showed that all five reference stations were homogenous (see ANOSIM-results, Table 2), they were pooled to compare temporal development of community structure between the reference area and the four platform stations.

The species which contributed most to the dissimilarities between the communities (SIMPER-analysis, Table 4) were sedentary tube building worms such as *P. mülleri*, *Spiophanes bombyx* and *Lanice conchilega* with high abundances in the reference area and crustacean such as *Atylus swammerdami* (Amphipoda) and Nemertini with high densities at the platform.

Integrated over time, the macrozoobenthic community in the reference area was characterised by *P. mülleri* (36 %), the polychaete *S. bombyx* (10 %), Nemertini (9 %), the polychaetes *L. conchilega* (7 %) and *Poeciloceatus serpens* (5 %) and the amphipod *Urothoe poseidonis* (5 %) (Table 5). With exception of *S. bombyx*, the sedentary species *P. mülleri*, *L. conchilega* and *P. serpens* were less abundant at the platform. In contrast, mobile taxa contributed most to community compositions at the platform: *A. swammerdami*, *U. poseidonis*, *B. elegans*, *Bathyporeia guilliamsoniana* and the polychaete *Nepthys* spp.. This trend was most pronounced at the 2 m station where the benthic community consisted almost completely of mobile species including larger decapods such as *Liocarcinus holsatus*.

The change in community composition developed over time (Fig. 7). Prior to the construction of the platform in March 2003 the infauna of the entire investigation area was dominated by polychaetes. Here, *S. bombyx* contributed the largest proportion (Table 5).

In the reference area, the phoronid *P. mülleri* dominated the community from summer 2003 to spring 2004 (Fig. 7). In July and September 2004, the community was again dominated by polychaetes, mainly *S. bombyx*, *L. conchilega* and *Chaetozone* cf. *setosa*, and *P. mülleri*.

In summer 2003, immediately after platform construction, *P. mülleri* had disappeared at all platform stations and remain absent until the end of our study. During the first months after construction, abundance of most polychaetes at the platform was relatively similar to the reference area but some species i.e. *L. conchilega* and *Owenia fusiformis* disappeared immediately. The abundance of spionid polychaetes, including *S. bombyx* at first decreased only at the 2 m station whereas at the 5, 10 and 15 m stations it decreased not until five months after construction.

Polychaetes at all platform stations were dominated by *Nepthys* spp.. At the 2 m station also *Scoloplos armiger* and *Eunereis longissima* occurred sporadically in high densities. The polychaetes at the 5, 10 and 15 m stations consisted of mobile species such as *Goniada maculata*, *Magelona johnstoni* and *P*. *serpens*. The abundances of amphipods increased at the platform, most pronounced at the 2 m station, with highest densities in summer 2004 (eleven to thirteen months after platform construction). The amphipods were dominated by the species *A. swammerdami*, *Urothoe poseidonsis*, *B. elegans* and *B. guilliamsoniana*. During the investigation period, decapods (especially *Processa* spp. and *L. holsatus*) were more abundant at the 2 m station than at the other platform and reference stations (Fig. 7).

Discussion

The implementation of the artificial underwater structures has a significant impact on the surrounding soft bottom community, changing the community composition particularly in the vicinity of the research platform FINO 1. Four months prior to the construction of the platform, the benthic community determined at 17 stations covering the entire study area revealed a similarity of approx. 62 % between single grabs. This is in the typical range, comparing benthic community compositions at different locations in the German Bight (Schröder 2003), and indicates a homogeneous distribution of the fauna between the 16 stations. During the following months, the communities at the five reference stations developed similarly with respect to abundance, diversity and species number over the next 1.5-year sampling period. In contrast, the stations close to the platform developed differently in all these parameters, and we conclude that the physical presence of the underwater structure of the platform is responsible for the observed differences in the community structure of the reference and platform area.

At the platform, abundance of sedentary and sessile soft bottom species decreased whereas abundance of mobile species increased. Thus, community structure at the platform changed from an assemblage dominated by sedentary and sessile soft bottom species to one of mainly mobile species. The decrease of species may be explained as follows: On a small temporal and spatial scale, the physical forces during the deployment of the underwater structure have certainly caused relocation and erosion of sediment and consequently the reduction of sedentary and sessile species. Immediately after platform construction, diversity was low and only a few species dominated the benthic community especially at the 2 m station pointing to a heavily disturbed area (Odum, 1985). However, low abundance of sedentary and sessile species was detected in up to 17 m distance and persisted over time. Hence, additional effects must have contributed to the changes in community structure.

Artificial hard substrates alter the hydrographical regime and often lead to increasing bottom current velocities and development of turbulences in variable directions (Richwien and Lesny, 2004). Horizontal flow across the bottom creates hydrodynamic shear stress that lifts sediment into suspension, thus eroding sediment patches which accumulate elsewhere (Nowell and Jumas, 1984). At FINO 1, erosion of sediments led to the development of scours in the vicinity of the platform as also described e.g. in the surrounding of artificial reefs (e.g. Davis *et al*., 1982). During scour development, it is likely that the resident small sessile and sedentary organisms were displaced. Since scours can develop in fine sands within a few days (Richwien and Lesny, 2004), the abundance of sessile and sedentary soft bottom species may decrease rapidly as observed at the platform after construction. An example of a species, which responded very sensitive to the habitat changes at the platform, is *Phoronis mülleri*. This species occurred in extremely high numbers in the reference area. Such high abundances are frequently observed in the German Bight (e.g. Rachor and Gerlach, 1978; Rehm and Rachor, 2007). Likely, this is due to the fact that the study area is closed for fishing and in particular tube building worms profit from the absence of the impact of bottom trawling (A. Schröder and J. Dannheim, unp. Data). Similar distribution patterns were found in the sessile and sedentary polychaetes *L. conchilega, S. bombyx* and *Owenia fusiformis*. Such decrease in abundance of tube-building worms in the sediments probably affects other benthic species and, consequently the whole community. In sediments around patches of polychaetes tubes benthic species diversity and abundance are usually increased (Woodin, 1978; Callaway, 2006). The tubes influence the recruitment pattern of other species (Trueblood, 1991), and alter the meiofaunal community (Phillips and Lovell, 1999).

Especially close to the underwater structure (2 m station) the resuspension of sediment in the vicinity of the platform not only caused a washout of sedentary species but also a distinct change in habitat structure since the heavier shell fragments remained on the ground and formed a thick layer. Such a process has been previously reported from the vicinity of artificial reefs (Davis *et al*., 1982; Ambrose and Anderson, 1990; Barros *et al*., 2001). The BIOENV analysis indicated that the shell content of the sediment, besides the sorting of the sediment and the total organic carbon content, is the main factor explaining macrofaunal distribution at the platform. The total organic carbon content of the sediment might be increased and accumulated at the platform by organic components (e.g. faces, dead animals) from the settled hard bottom fauna on the underwater structure (Orejas *et al*., 2005). Additionally, the shell layer might trap sediment particles resulting in a more heterogeneously sorted sediment than in the reference area.

The accumulated shell fragments apparently provide shelter and a suitable foraging habitat for small mobile species such as amphipods and predatory polychaetes, which accumulated particularly nearest to the platform. Moreover, the amphipods, dominating at the platform (e.g. *A. swammerdami* and *Bathyporeia* spp.) are well adapted to sediment disturbances or even unstable sediments (Wieking and Kröncke, 2003; Lackschewitz and Reise, 1998). The large amount of shells might enhance oxygen supply in the habitat, which enables the amphipods to dig and feed in their typical way (Nicolaisen and Kanneworff, 1969).

With the changes in species inventory, the trophic structure of the macrozoobenthic community at the platform modified. Here, abundances of mobile and carnivorous infaunal organisms such as the polychaetes *Nepthys* spp., *E. longissima* and *Goniada maculata* increased. These predators/scavengers may have been attracted by the amphipods and also by the hard bottom fauna on the underwater construction (Orejas *et al*., 2005). Also larger predators and scavengers, mainly the decapods *Cancer pagurus*, *L. holsatus* and *Pagurus bernhardus*, were more frequently observed in the close vicinity of the platform. It has to be noted that the van Veen grab does not sample the larger individuals of theses species quantitatively. We found, however, more small individuals of these decapods in the grab samples close to the platform than at the 10 and 15 m stations and in the reference area. In addition to invertebrate predators, fish species are often attracted by artificial structures (Posey and Ambrose, 1994; Nelson *et al*., 1994; Wilhelmsson *et al*., 2006). During our study, we did not obtain abundance data of pelagic and demersal fishes, but an underwater camera attached to the piles observed species such as *Pholis gunellus*, *Trisopterus luscus* and *Taurulus bubalis* (C. Orejas *et al*., unp. Data) at the platform, which are known to feed on infaunal species too (e.g. Knust, 1996). Thus it seems likely that the predation pressure on the surrounding macrozoobenthos community increased due to an increase in invertebrate and vertebrate predator abundance.

While our study shows a significant impact of the underwater structure of the platform on habitat structure and benthic community composition, an investigation at the wind farm at Horns Rev (Denmark) did not (Bech, 2005). However, the two installations differ in several aspects, and the results are therefore not comparable. (1) Other than FINO 1, Horns Rev is situated in shallow water (14 m), and the area is characterised by coarser sands inhabited by a *Goniadella*-*Spisula*-association (Bech, 2005). This community comprises mainly mobile species which are better adapted to frequently disturbed sediments than the *Tellina-fabula*-association prevailing in the study area (Rachor and Nehmer, 2003). (2) The underwater constructions of the wind turbines at Horns Rev are monopiles whereas the fundament of the FINO 1 is a jacket structure. The concepts for wind turbine structures varied from monopiles to tripod- and jacket-structures depending on water depth and economical considerations. However, at the moment, most of the planned underwater structures of the wind turbines be installed in the German EEZ seem to have a tripod structure which is more comparable in size and shape to the jacket structure than to a monopile. (3) Contrary to the FINO 1, a scour protection (gravel boulders) was installed in the surrounding of the wind turbines at Horns Rev. The use of such a protection at the planned wind farms in the German Bight is not decided yet.

The magnitude of the ecological impact of wind farms on the soft bottom community is thus linked to the environmental conditions and the local fauna in the respective construction areas as well as to the size and structure of the underwater construction. Therefore, the impact needs to be estimated specifically for different habitats and/or communities. The planned wind farms in the German Bight will be mainly constructed in areas of fine sediments which are mainly inhabited by sedentary species (Rachor and Nehmer, 2003). Likely, the impairments of the habitat structure and community composition in such areas might therefore be similar to our study results. Consequently, intensive wind farming in the German Bight, i.e. the installation of several hundreds of wind turbines, might lead to cumulative effects on a spatial scale and to indirect effects on ecological functioning such as the trophic structure of the benthic system.

At the moment, we can neither predict if the changed benthic community composition of up to 17 m around a wind turbine really constitute a main environmental or a management problem nor if extensive wind farming caused cumulative or indirect effects (e.g. in the trophic system). Nevertheless, our results are the first step to understand the ecological implications of offshore wind turbines in the German Bight, showing that the macrozoobenthic community structure may change considerably in the vicinity of a wind turbine.

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Tables

Table 1: Dates of sampling for the preliminary study (P), the reference stations (200 – 400 m distance) and the platform stations (2, 5, 10 and 15 m) including months after platform construction.

Year	Date	Sampling at Reference stations	Sampling at Platform stations	Months before (-) and after platform construction
2003	18 Mar	•	•	-4 (P)
	28 Jul	•		0
	21 Aug		•	1
	24 Sep		•	2
	14 Nov	•		4
	27 Nov		•	4
	11 Dec		•	5
2004	28 Jan		•*	6
	30 Mar		•	8
	07 Apr	•		9
	28 Apr		•	9
	30 Jun		•	11
	23 Jul	•		12
	05 Aug		•	13
	02 Sep		•	14
	26 Sep	•		14
	27 Oct		•	15
	23 Nov		•	16
	15 Dec		•	17

* sampling only at the 2 m station

Table 2: Results of the pairwise one-way ANOSIM (*R* values) between the community structures of the reference area © and the platform stations (2, 5, 10 and 15 m). Bold numbers indicate statistically significance.

Stations	**R**	**15 m**	**10 m**	**5 m**
R	**-**	**-**	**-**	**-**
15 m	**0.976**	**-**	**-**	**-**
10 m	**0.978**	0.087	**-**	**-**
5 m	**0.981**	0.057	0.161	**-**
2 m	**0.973**	**0.387**	**0.343**	**0.267**

Table 3: Best two results of the multiple correlations between abundance of macrozoobenthic species and habitat parameters (BIOENV analysis). Habitat parameters were: silt and clay content (SCC), sorting of the sediment (GSD), total organic carbon content (TOC), shell content of the sediment (SCS), median grain size (MdGS). Preliminary study was excluded.

	Number of variables	***R* values**	**Variable implicated**
Reference area	3	0.301	SCC, GSD, TOC
	2	0.292	SCC, TOC
Platform stations	3	0.465	GSD, TOC, SCS
	3	0.464	SCC, TOC, SCS

Table 4: Results of SIMPER analysis: percentage contribution of the main discriminating taxa to the average dissimilarities between macrozoobenthic communities of the reference area I and at the platform stations (2, 5, 10 and 15 m).

Taxa	**Contribution [%]**			
	R *vs*			
	15 m	**10 m**	**5 m**	**2 m**
Nemertini	5.2	5.1	5.2	4.9
Polychaeta				
Lanice conchilega	6.4	6.2	6.2	5.7
Spiophanes bombyx	6.4	6.4	6.5	6.3
Owenia fusiformis	4.9	5.0	5.0	4.5
Crustacea				
Atylus swammerdami	0.6	0.3	0.6	5.7
Phoronida				
Phoronis mülleri	35.9	36.4	36.1	32.6

Table 5: Percentage contribution (integrated over the whole study time) of the main discriminating taxa sharing 75 % in abundance of the macrozoobenthic community composition of the preliminary study (P), reference area I and platform stations (2, 5, 10 and 15 m).

Station	**Taxa**	**Contribution [%]**
P	*Spiophanes bombyx*	54.9
	Urothoe poseidonsis	10.6
	Nepthys spp.	7.9
R	*Phoronis mülleri*	35.8
	Spiophanes bombyx	10.4
	Nemertini	9.2
	Lanice conchilega	7.1
	Poecilochaetus serpens	5.1
	Urothoe poseidonis	4.9
15 m	*Urothoe poseidonis*	18.6
	Nepthys spp.	16.1
	Spiophanes bombyx	14.0
	Bathyporeia guilliamsiniana	8.2
	Bathyporeia elegans	6.2
	Goniada maculata	3.9
	Pseudocuma longicornis	3.3
	Nemertini	2.9
10 m	*Nepthys* spp.	20.6
	Urothoe poseidonis	18.3
	Bathyporeia guilliamsiniana	11.7
	Spiophanes bombyx	10.5
	Bathyporeia elegans	6.5
	Nemertini	3.4
	Magelona johnstoni	3.0
5 m	*Urothoe poseidonis*	20.9
	Nepthys spp.	50.6
	Spiophanes bombyx	9.6
	Bathyporeia elegans	6.5
	Bathyporeia guilliamsiniana	6.8
	Nemertini	6.1
	Goniada maculata	3.8
2 m	*Atylus swammerdami*	40.9
	Urothoe poseidonis	7.4
	Nemertini	5.1
	Nepthys spp.	4.7
	Lanice conchilega	4.5
	Scoloplos amiger	4.0
	Liocarcinus holsatus	3.5
	Eunereis longissima	3.2

Figures

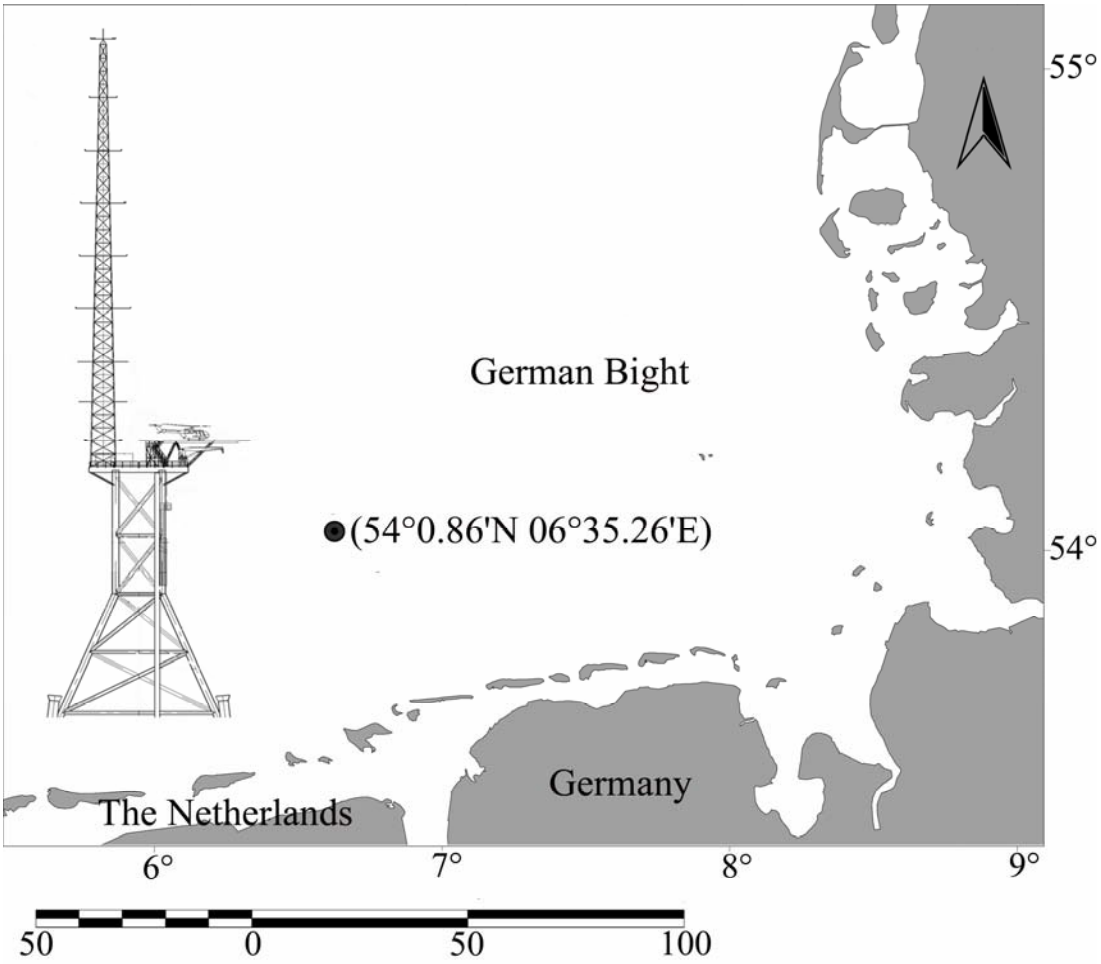

Figure 1: Location and construction design of the research platform FINO 1 including the navigational coordinates and engineering drawing (lateral view).

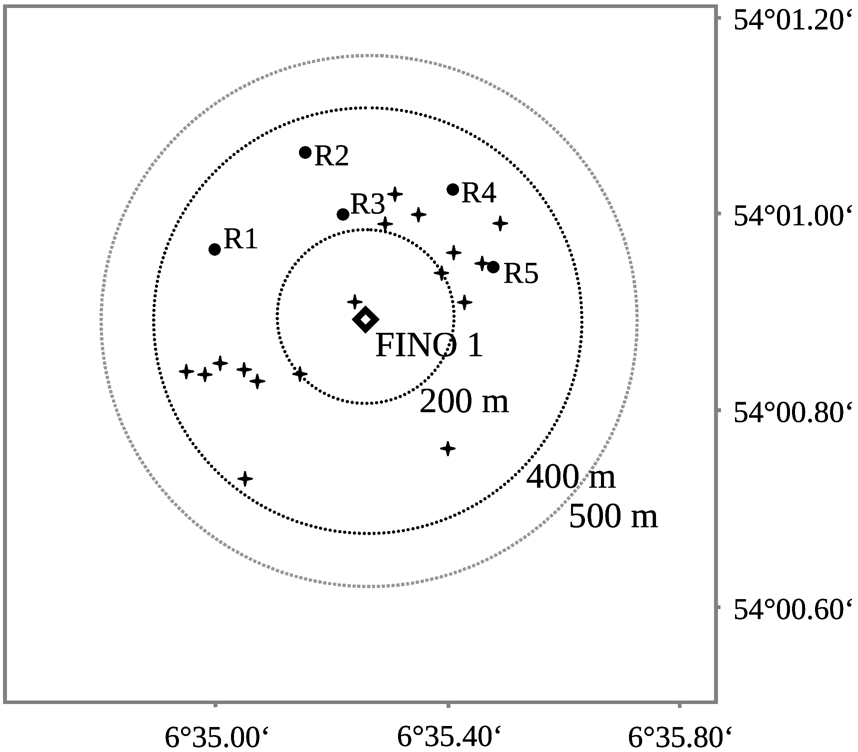

Figure 2: Sampling positions of the preliminary study (crosses) and of the reference stations after the platform construction (dots, R1 to R5) located in 200 – 400 m distance from the FINO 1 (diamond).

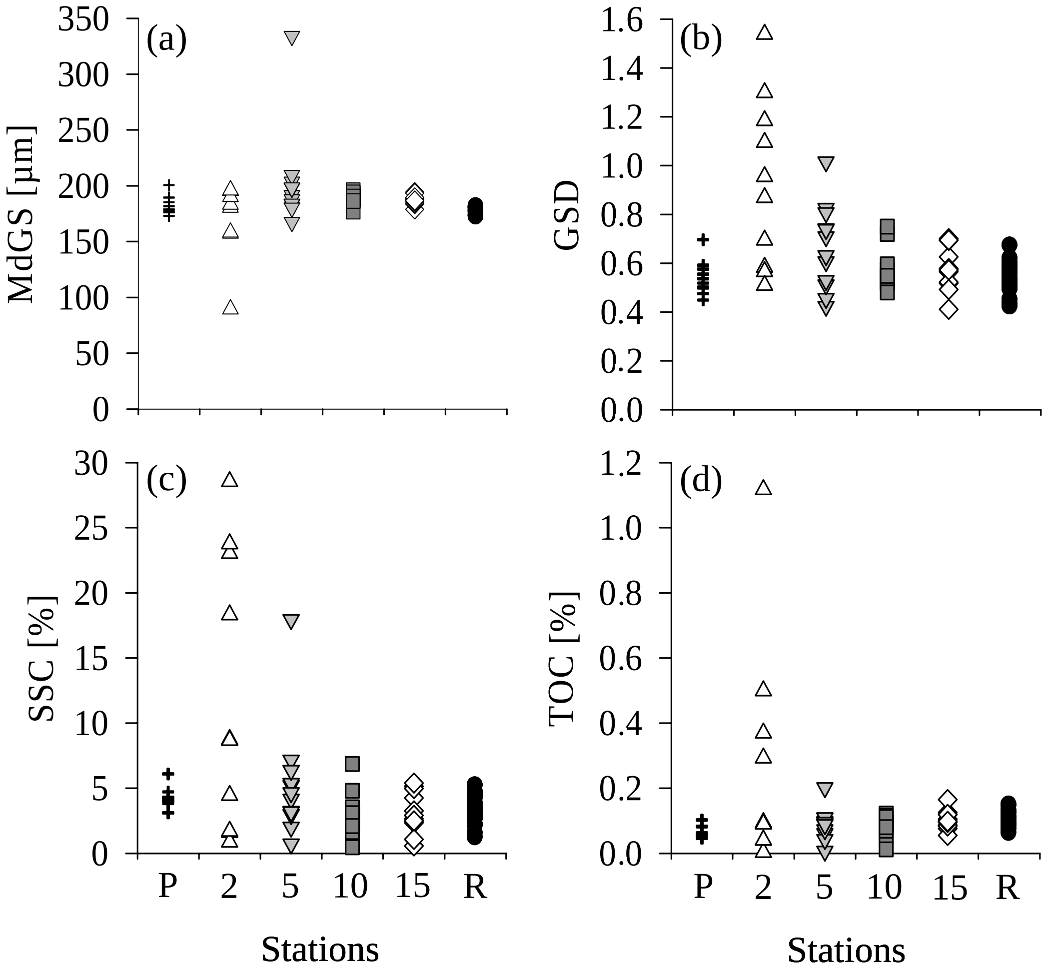

Figure 3: Sediment characteristics of the sediment sampled during the preliminary study (P) and after the implementation of the platform in 2, 5, 10, 15 m distance and in the reference area ©. (a) Median grain size (MdGs) [µm], (b) inclusive graphic standard deviation (GSD), (c) silt and clay content (SSC) [%] and (d) total organic carbon (TOC) [%]. Each symbol indicates one sample.

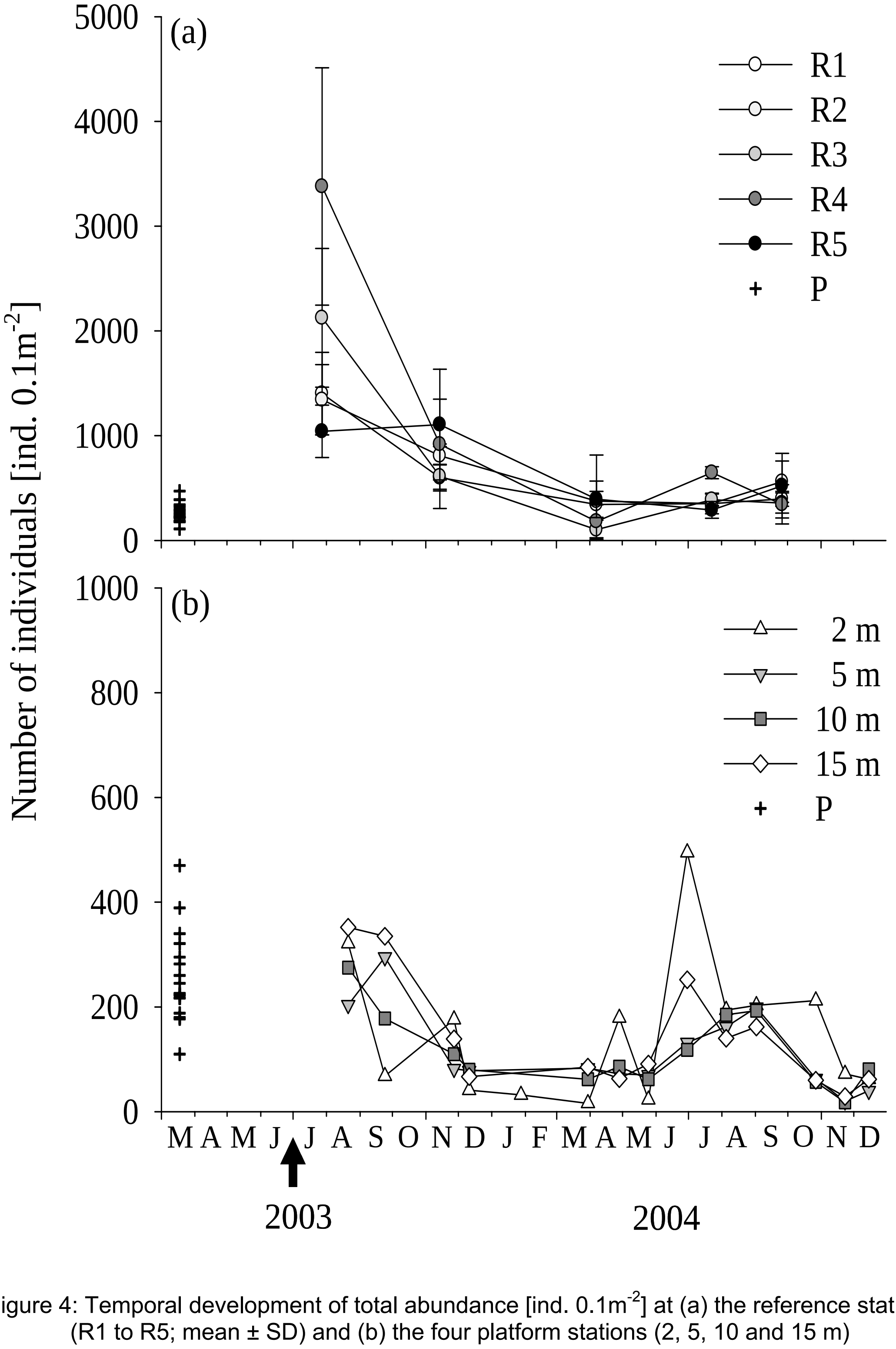

Figure 4: Temporal development of total abundance [ind. $0.1m^{-2}$] at (a) the reference stations (R1 to R5; mean ± SD) and (b) the four platform stations (2, 5, 10 and 15 m) including the preliminary study (P). Sampling period: March 2003 to December 2004. Arrow marks date of platform construction. Please note the different scales in abundance.

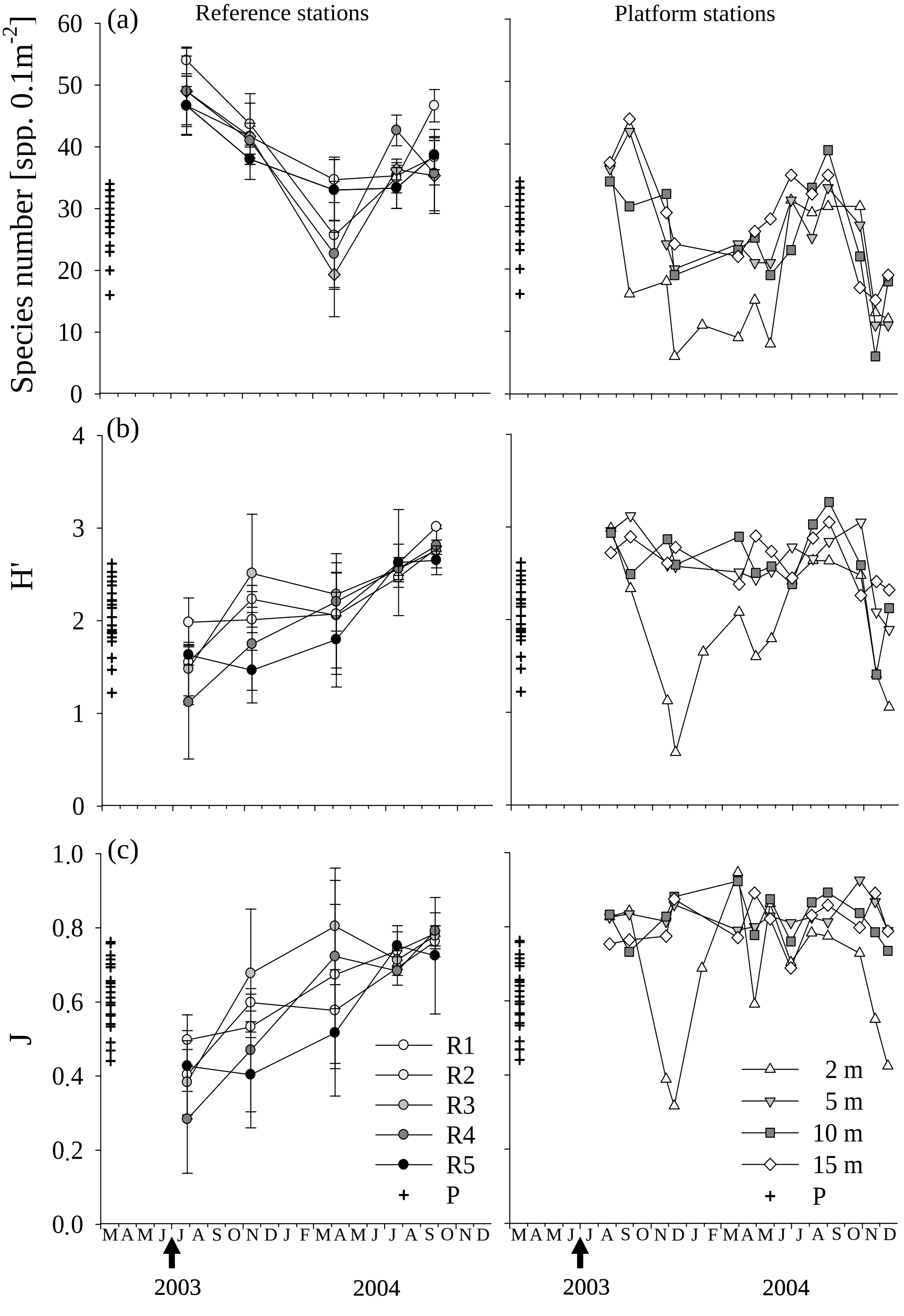

Figure 5: Temporal development of (a) species number [spp. 0.1m^{-2}], (b) diversity (H' Shannon-Wiener) and (c) evenness (J after Pielou) at the reference stations (left; mean ± SD) and (b) the four platform stations (right) including the preliminary study (P). Sampling period: March 2003 to December 2004. Arrow marks date of platform construction.

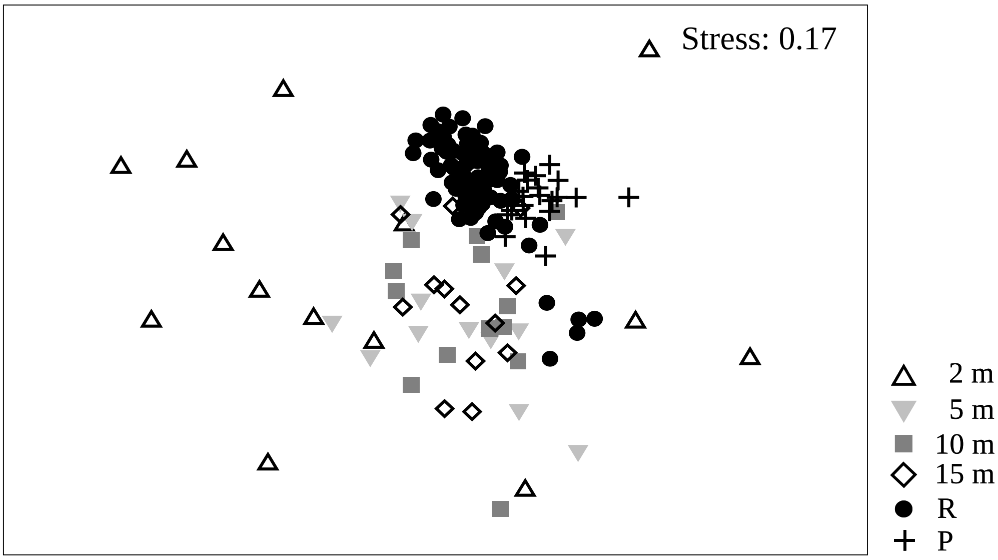

Figure 6: MDS ordination by abundance [ind. $0.1m^{-2}$] of the macrozoobenthos community structure (Bray-Curtis similarities, 4th root transformed). Symbols indicate all replicates of the preliminary study (P; crosses), the reference stations (R; dots) and the platform stations (2 m: triangle up; 5 m: triangle down; 10 m: square; 15 m: diamond) over the entire study period.

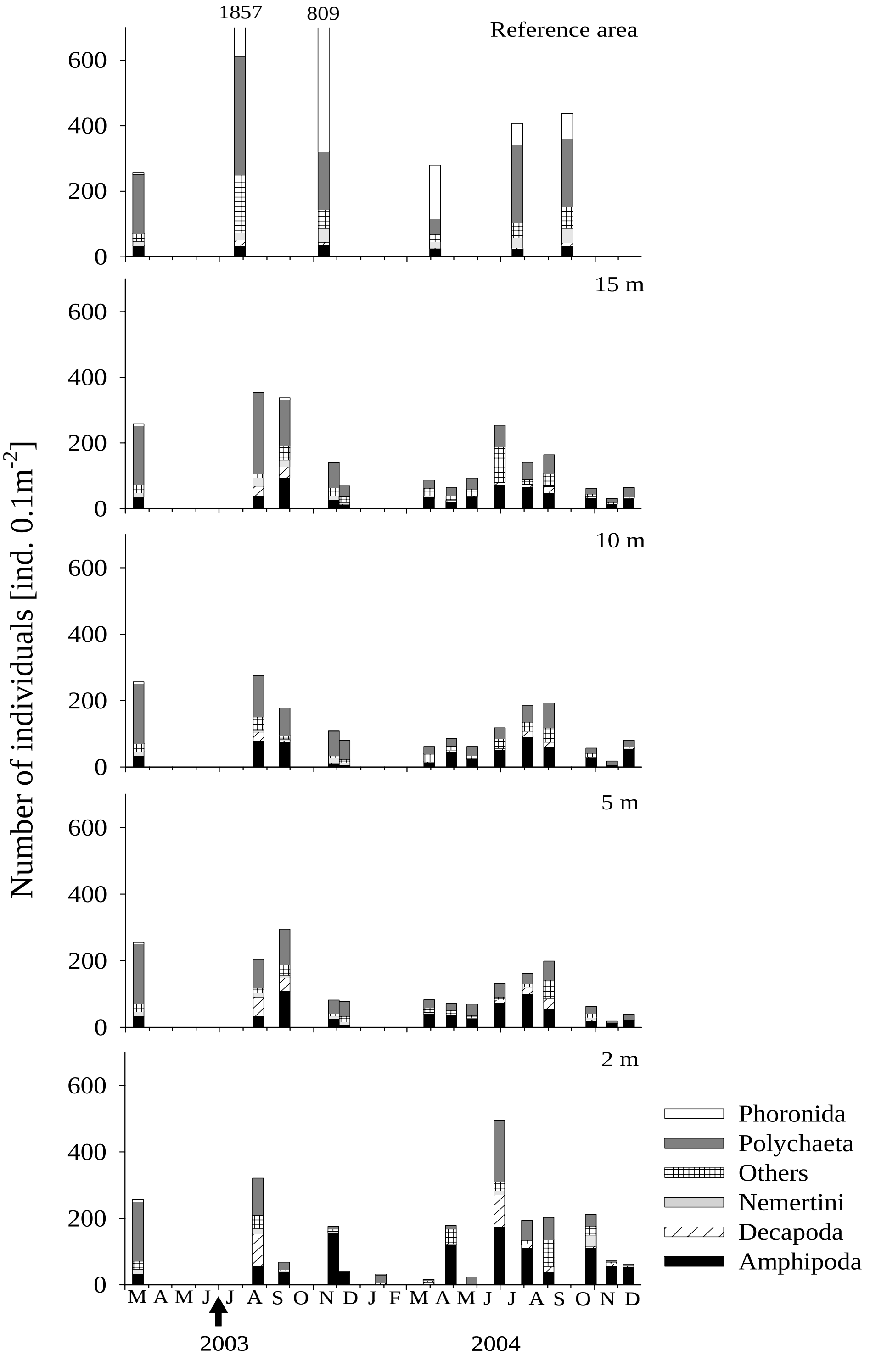

Figure 7: Temporal development of taxonomic group abundance [ind. 0.1m^{-2}] of the macrozoobenthos in the reference area and at the platform stations (2, 5, 10 and 15 m). Sampling period: March 2003 to December 2004. Arrow marks date of platform construction.

16. Response of macrozoobenthic community to cessation of fishing activity in the North Sea

Jennifer Dannheim, Kristin Finger & Alexander Schroeder

Introduction

The effects of fishing on benthic communities take centre stage of the scientific and public discussion (Malakoff 1998). As the short-term most effective catch stood in the foreground, the effort has risen worldwide during the last century with an increasing mechanisation and industrialisation of the fisheries (Pauly et al. 2003). Every form of fishing is an interference in the respective ecosystem, as parts of the system are removed. One of the heaviest disturbances is caused by bottom trawling.

The impact of the different gear types on benthic organisms has been investigated since the beginning of the 70ies (e.g. De Groot 1984). Several studies focusing on the trawling impact, especially in the North Sea followed in the last years (e.g De Groot & Lindeboom 1994, Jennings & Kaiser 1998, Lindeboom & De Groot 1998, Collie et al. 2000). These investigations showed a number of fishing effects on the benthic ecosystem. The intensity of the impact depends on the gear used, its weight and trawling speed, but also on the habitat respectively the sediment structure (Bergman & Hup 1992, Kaiser et al. 1998).

A direct consequence of bottom trawling is the mechanical disturbance on the bottom through fishing gears. Short-term effects comprise an alteration of the sediment structure and direct mortality of the benthic organisms (Rumohr & Krost 1991, Kaiser 1996, Bergman & Van Santbrink 2000, Ramsay et al. 2000). Continuous trawling may even permanently alter the structure and functioning of the benthic community (Jennings & Kaiser 1998, Hall 1999, Kaiser & De Groot 2000). Beneficiaries of the fishing disturbance are mainly scavengers and predators (e.g. crabs, fishes and star fishes). Besides the increased mortality of benthic animals within the trawl tracks, the discards become available as an additional food source (Ramsay et al. 1998, Groenewold & Fonds 2000, Rumohr & Kujawski 2000, Ramsay et al. 2001). Thereby scavengers and fast growing, opportunistic species profit of heavily fished areas (Gilkinson et al. 1998, Jennings et al. 2001), while long-living, relative large individuals are in disadvantage (Bergman & Van Santbrink 2000, Kaiser et al. 2000). Large individuals of macrofaunal species need about five years to recover from trawling (Dinmore et al. 2003) and recovery of the community is not considerable faster even considering immigration of species (Collie et al. 2000).

Bottom trawling is one of the heaviest impacts for marine environments all over the world (Dayton et al. 1995, Jennings & Kaiser 1998, Thrush et al. 2001) and the North Sea is one of the most intensively fished areas. The investigated area lies in one of the most heavily trawled areas in the North Sea (Rijnsdorp et al. 1998, Jennings et al. 1999). But fishing is not the only factor affecting the community. Water movements caused by strong storms and tidal currents may lead to sediment relocations, seasonal temperature variations of more than 15 °C and different water masses influence the ecosystem and created a fauna well adapted to these natural fluctuations. However, several anthropogenic impacts are superimposed on these natural variations and put further stress on the benthic communities. Over the 20th century an increase in biomass of the macrozoobenthos and a shift in community structure from large longliving to opportunistic short-living species were observed (Duineveld et al. 1991, Kroencke 1992, Kroencke 1995, Schröder 2003).

Due to the complicate interplay of numerous factors at various temporal and spatial scales, it remains unclear whether these shifts were induced by natural change or by an increase of arthropogenic effects (e.g. eutrophication, fishing). The present benthic fauna is in a way a “skipjack” reacting rapidly to any kind of disturbance which makes it difficult to identify the effects of single factors. However, the question nowadays is not whether trawling has an impact as more how huge it is (Malakoff 2002).

To supply evidence of long-term trawling induced changes and indirect influences, either long-term investigations or direct comparisons of fished and unfished areas are the only adequate methods (Ball et al. 2000). In the present study, we focused on the development of the macrozoobenthic communities after the local cessation of fishing in a soft bottom habitat. Up to now, no soft bottom areas have been permanently closed for fishing in the German EEZ (exclusive economic zone). In July 2003 the research platform “FINO 1” was installed for preliminary studies for offshore windfarms. The surrounding of the platform is closed to all shipping activities and consequently for bottom trawling. This provides the unique opportunity to study the development of the unfished area versus the heavily trawled area around it from the onset.

Material & Methods

Investigation area

After the start of the RESPONSE project the construction of the pilot wind farm which should have been used as an unfished area was delayed until 2006. Instead the construction of the research platform “FINO 1” in June 2003 adjacent to the area of the planned pilot wind farm was considered as unfished area. The surrounding of the research platform within a radius of 500 m is closed for safety reasons to all shipping activities and consequently also for bottom trawling. A map of the selected ASA (appropriate study area) is shown in figure 16.1.

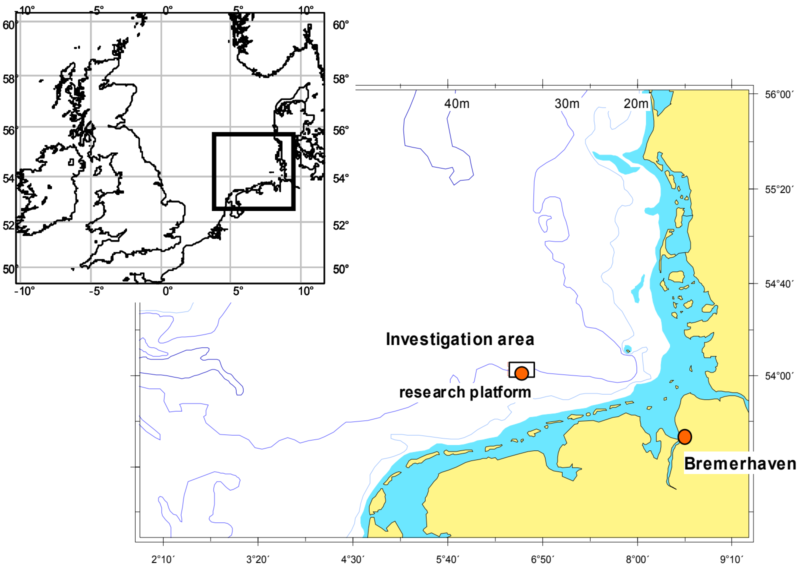

Fig. 16.1. Map of the selected ASA in the southern German Bight.

The direct effects of the artificial hard substrate provided by such constructions are usually restricted to the direct vicinity of such structures up to 50 – 100 m (Gray 1977). To exclude these direct effects, a minimum distance of 150 m was kept for all sampling for the RESPONSE-project. To exclude edge-effects and to be sure that no fishing occurs in the area, a maximum distance of 400 m from the platform was assured. The area between 150 and 400 m from the platform should thus be free from fishing effects as well as from direct effects from the platform.

According to previous results (Knust et al. 2001), a normally fished reference area was established north-west of the research platform (fished area 1; Figure 16.2). Preliminary analyses of the faunal data from the first RESPONSE cruise between the faunal community of the platform area and the reference area 1 showed that the species composition of both areas is the same but there are some differences in the abundances of the dominant species. This highlights the sensitivity of the applied methods to detect even small changes in benthic communities, which most likely are a result of natural spatial variability. To clearly distinguish the effects of this natural spatial variability from the effect of the closure of the platform area to bottom fisheries, a second reference area, fished area 2, was established east of the platform area (Figure 16.2) which has been sampled on all consecutive cruises since November 2003.

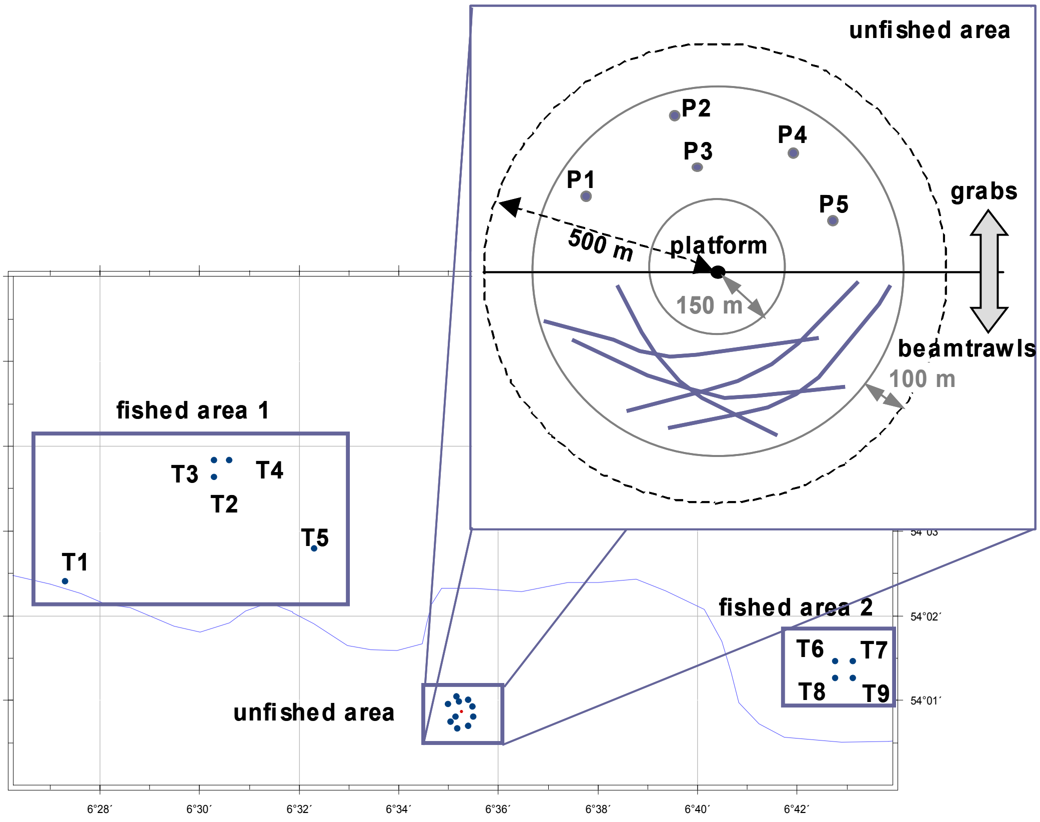

Figure 16.2. Position of sampling stations in the unfished and fished areas. The position of the area within the German Bight is indicated by the small frame in Figure 16.1.Figure 16.1 T: fished/reference station; P: unfished grab station, blue lines in the circle: exemplary beam-trawl tracks

The position of the reference stations for the RESPONSE project was chosen to achieve a maximum agreement in sediment composition and benthic community composition between the platform area and the reference areas according to previous studies in the area (Knust et al. 2001).

Sampling scheme for the North Sea ASA

According to the date of platform construction, the timing of the RESPONSE cruises was adjusted to the dates listed in Table 16.11. Cruise C1 in late March 2003 was intended to study the "*status quo ante*" when normal fishing took place in both the platform area and the reference area to assure the comparability of both areas. The following cruise C2 was conducted immediately after the construction of the platform, which was completed on 14.7.2003 with the associated closing of the surrounding area (± 500 m) for all fishing activities. Consequent cruises follow after 3, 8, 12 and 14 months without fishing.

Table 16.1. Cruises within the RESPONSE project

RESPONSE Cruise No.	Date		Cruise Code	Vessel
C1	before closing area	(17. Mar. – 04. Apr. 2003)	HE 185	RV Heincke
C2	directly after closing	(22. Jul. – 02. Aug. 2003)	HE 194	RV Heincke
C3	3 months after closing	(14. – 21. Nov. 2003)	HE 200	RV Heincke
C4	8 months after closing	(05. – 20. Apr. 2004)	HE 205	RV Heincke
C5	12 months after closing	(17. Jul. – 03. Aug. 2004)	HE 214	RV Heincke
C6	14 months after closing	(18. Sept. – 02. Oct. 2004)	HE 219	RV Heincke

The sampling scheme was nearly the same on each cruise. During the first two cruises an initial set of 5 stations in the platform area, which is closed for fishery since June 2003, and five stations in reference area 1 were sampled. This was complemented by four additional stations in reference area 2, which were sampled in cruises C3 – C6, adding up to a total of 9 reference stations from C3 onwards (Table 16.2).

General characteristics of the sea bed were identified by sidescan transects, UW-video (10 – 20 min at < 1 kn), UW-photography (1 m²), grab samples (0.1 m² van Veen grab), beam-trawl (3 m width) and otter-trawl (app. 15 m width) hauls. Grab samples were also used to generate a map of the sediment distribution in the area.

Table 16.2. Sampling scheme for the North Sea ASA

Samples	Sampling scheme Fished/reference area	Unfished area
Infauna	9 stations á 3 grabs	5 stations á 3 grabs
Epifauna	9 beam trawls	5 beam trawls
Sediment	9 samples superficial*	5 samples superficial*
Photo	4 stations á 20 photos	2 stations á 20 photos
Video	4 stations á 20 min video	2 stations á 20 min video

* sediment cores taken in march 2003 for analysing differences in vertical distribution showed no differences between surface and lower layers and are therefore no longer taken

Hydrography

CTD profiles for temperature, salinity and turbidity were taken approximately at high and low tide at the respective station. Distances between stations (~ 2 nm) are too small to expect regional differences betweens stations with the prevailing tidal current speed (up to 1 m/s and more), while temporal differences due to tidal influences or displacement of various water masses could be expected.

Hydrographic data from the research platform FINO1 and several other measuring stations were kindly supplied by the German Federal Maritime and Hydrographic Agency (BSH) and analysed as general forcing factors in the ASA.

Sediment

On each grab station, two superficial sediment samples were collected from the grab content for grain size analysis and organic carbon analysis. In addition to this, vertical sediment cores were taken in March 2003, which were divided in layers. The first five centimetres were analysed separately while the lower layers from 5 to 10 cm depth were pooled. The analysis of these samples showed no differences between the layers, as could be expected for a sediment consisting of homogeneous fine sand. Therefore the layered sampling was given up for further cruises.

Grabs

On each station three 0.1 m² van Veen grabs (95 kg) were taken for the analysis of macrozoobenthic infauna. The geographical position of each grab was determined with a DGPS. Samples were sifted on 1 mm mesh size screens and fixed in 4 % buffered formalin. In the laboratory, species were determined to the lowest possible taxonomic level, counted and wet weight was determined per species. Species abundance and wet weight were standardized to 1 m². For further analyses, pelagic species and fishes were excluded.

Beam trawls

For larger epifaunal organisms, one ten minute-haul was taken at a speed of app. 3 kn at each station with a 3 m beam-trawl. In the unfished area (platform ± 400 m), the beam-trawl hauls are positioned across the southern semi-circle of the untrawled area in a roughly W-E-direction avoiding the direct vicinity of the platform (± 150 m) (Figure 16.2). The geographical postitions of “gear on ground” and “gear off ground” were determined with a DGPS, in order to calculate the area trawled.

Samples are stored frozen for a later analysis in the laboratory. Species were determined to the lowest possible taxonomic level. Fishes were weighted (wet weight) and lengths were measured for every individual (standard length, total length), the same was done with swimming crabs and shrimps. Other species were counted and individuals were weighted per species. Abundance and biomass data were standardized to 1000 m². Pelagic fishes were excluded from further analyses.

Photo and Video

Photos and videos were taken on two stations in both reference area and two in the unfished area (one north of the platform, one south). Photos were taken by a photo sled (modified to the one from Gutt 1988), covering an area of 1 m² each, while drifting across the station (determination of position by DGPS). The sampling procedure was as described in Piepenburg & von Juterzenka (1994). Additionally, 20 min of video were recorded with a hand-guided video system while drifting across the central position of the station at a speed of less than 1 kn. The geographical position of the video was recorded by DGPS in 1 min intervals. The monitored area was calculated from the distance between marks and the analyzed transect’s width (0.25 m). Missing datasets are caused by bad visibility, too fast towing speeds or inconstant bottom contact. The analyses were restricted to sessile and free-living epifauna. Burrowing organisms could not be identified. Species were determined to the lowest possible taxonomic level, but identification beyond family or genus level was rarely achievable. Hence, several species had to be combined (e.g. sand gobies (*Pomatoschistus* spp.)

and dragonets (*Callionymus* spp.) or flatfishes (Soleidae and Bothidae)). Brittle stars weregrouped to class level Ophiuroidea.

Statistical analyses

For all analyses, abundance and biomass were standardized to 1 m² for infauna and 1000 m² for epifauna.

Univariate measures used to characterise the community structure were total abundance, biomass (g wet weight), species density (spp./ 0.3 m² for infauna and spp./per haul for epifauna), eveness (J) after Pielou (1966), diversity (H' based on loge) after Shannon & Weaver (1963).

To analyse the fishing impact on functional groups, four categories were fixed: Position of the individuals (surface, subsurface), vulnerability of the species (high, low and medium), mobility of the animals (sedentary, mobile and highly mobile) and the feeding type (filter feeder, detritus feeder, omnivorous species and predator/scavenger).

The percentage difference between the unfished and fished areas was calculated following the formula from Collie et al. 2000:

$$D = \frac{(A_t - A_c)}{A_c} * 100$$

where D = percentage difference

A_t = abundance in trawled/fished area

A_c = abundance in control/unfished area

Multivariate analyses were carried out using PRIMER software (Clarke & Warwick 994, Clarke & Gorley 2001). The infaunal and epifauna datasets were transformed with 4th root and Bray-Curtis similarity was used to construct a similarity matrix. Multidimensional scaling plots (MDS) were used to analyse differences in community composition and the multivariate dispersion index (MDI) was calculated to measure the variability within groups. The main discriminating species were identified by the SIMPER routine. Additionally, an ANOSIM analysis was performed (one way analyses for each cruise: factor fishing; two-way-crossed analyses: factor cruise/seasonality and fishing) and the R-value used as a measure of the distinction of the community in fished and unfished areas. These values can be interpreted as follows (Clarke & Gorley 2001):

> 0 (and around) = no differences; between groups and within group similarity is roughly equal
> 0.25 = groups barely separable
> 0.50 = separation of groups
> 0.75 = groups well separated
> 1.00 = groups totally separated

The dimension of the R-values is assisted by a monte carlo significance test (p in %). The identification of abiotic factors explaining most of the fauna variation was achieved using General Linear Modelling (GLM) and the BIOENV routine. Before the BIOENV was performed, highly correlated variables were eliminated (surface temperature). BIOENV was performed with the abiotic data fishing effort [times trawled], time [months], total organic carbon [%], median grain size [µm], mud content [%], turbidity [g/l] and bottom temperature [°C]. For the separate analyses of each cruise, a reduced dataset was used.

The significance of detected differences was tested by ANOVA (using Statview software). Equality of variances and normal distribution were tested before. Where necessary, data were log transformed to achieve homogeneity of variances.

Results

Sediment

Initially no clear differences in sediment composition between the fished and unfished areas were obvious (Figure 16.3). The spatial differences were not larger than the temporal variability. However, during the spring and summer cruises 2004 (C3 & C4) sediments in the eastern fished area (F2) were significantly smaller than in the other two areas (marked by *).

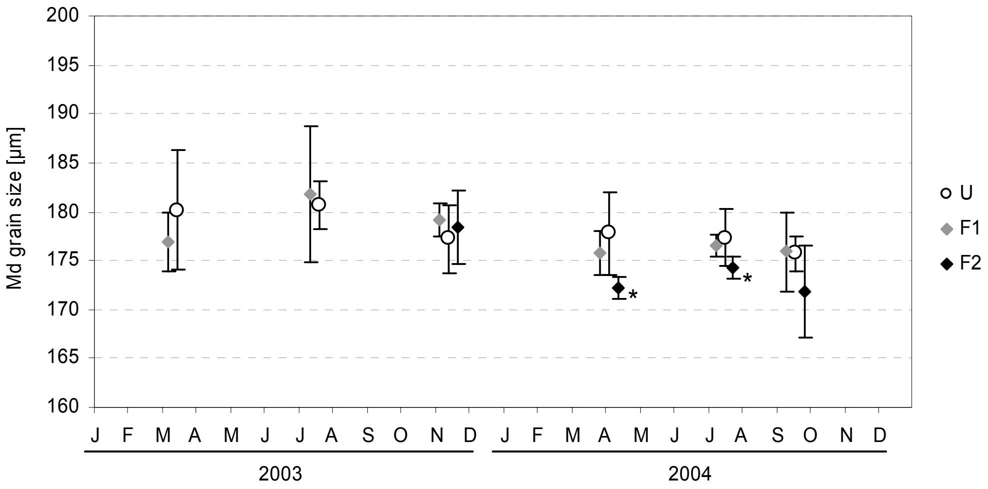

Figure 16.3. Mean median grain size (Md GS ± SD) from sediment analyses from Cruises C1 – C6; U = unfished area; F1, F2 = fished area 1 & 2; * = significantly smaller than in U.

Also in the total organic carbon content the values from the fished areas seemed to be slightly higher than in the unfished area in 2004 (Figure 16.4.). A seasonal difference was very small, as the carbon content seemed to be lowest in spring, highest in summer and decreasing again in autumn, but always on a very low level of less than 0.2 %.

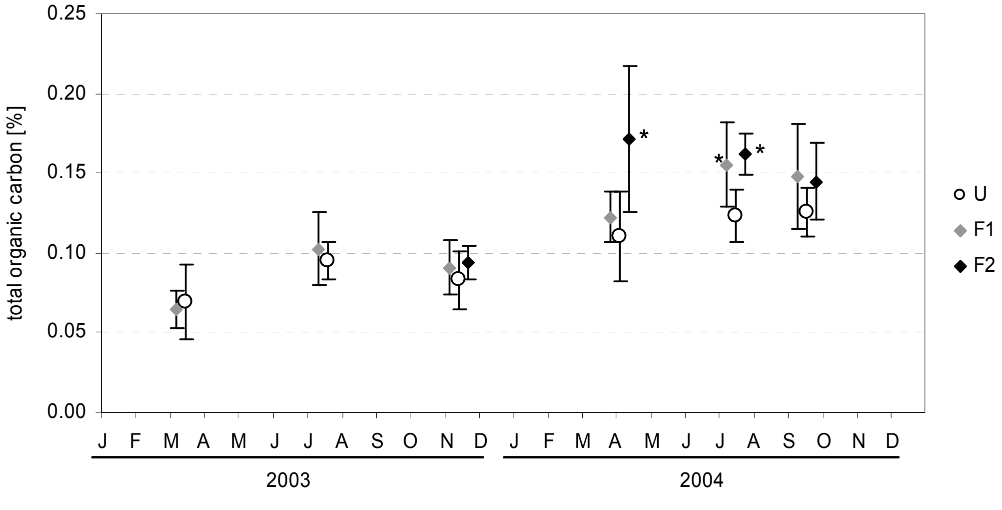

Figure 16.4. Mean total organic carbon content (TOC ± SD) from sediments from Cruises C1 – C6; U = unfished area; F1, F2 = fished area 1 & 2; * = significantly larger than in U.

Hydrography

The water column in the North Sea ASA was mostly mixed all year through and no clear stratification was observed. Due to high tidal current velocities of up to more than 1 m/s, there were also no visible differences between the fished and unfished areas.

Turbidity

No significant differences between the sampling areas in the concentration of suspended particle were detectable from the CTD-attenuation measurements. Some differences were observed over time as turbidity increased especially near the bottom after e.g. a strong storm during cruise C6 (Fig. 16.5 a, b). Another marked increase in turbidity near the bottom was observed after the onset of fishing on Monday morning (Fig. 16.5 b, c). Early that day we observed a number of vessels arriving in the area and starting to fish. As a response to that, the CTD-measurements during the afternoon showed a sharp peak in the near bottom layers (Fig. 16.5 c).

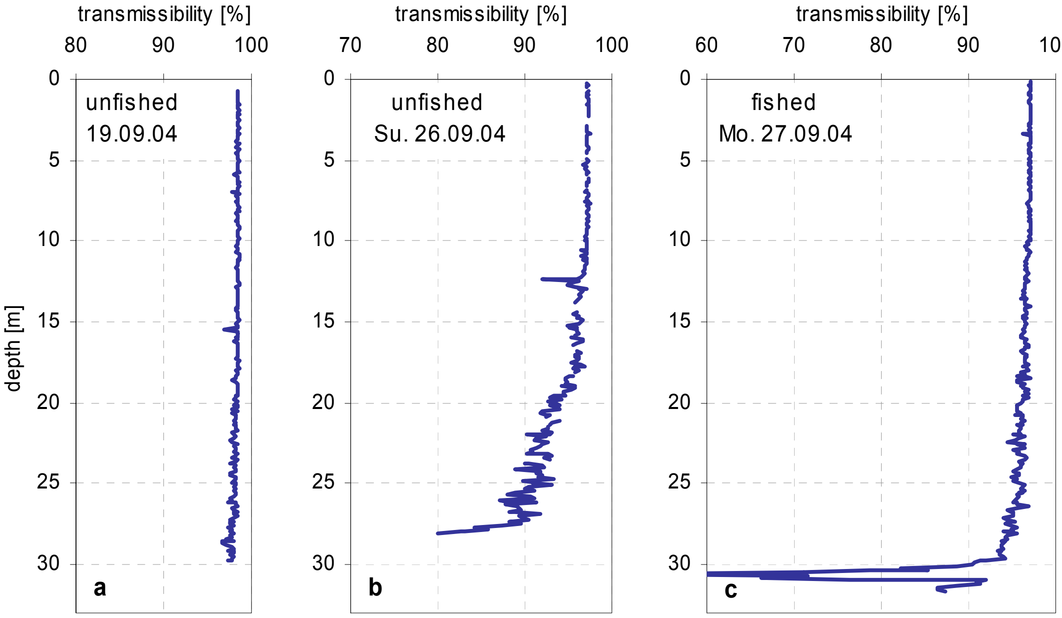

Figure 16. 5. Representative vertical CTD-profiles of transmissibility from fished and unfished areas during cruise C6.

Currents

The main current directions in the ASA are easterly (ESE) and westerly (WNW) tidal currents (Fig. 16.6). Twice daily, the water runs to the east until high tide and then turns anticlockwise to run off again to the west. Close to the surface the mostly northwesterly winds cause an on average stronger easterly current, leading to frequently measured currents of over 1 m/s. This influence has fewer effects in 26 m depth and maximum current speeds reached only 87 m/s.

A remarkable feature of the bottom currents is the absence of really slack water (Fig. 16.6 b). Even at high and low tide the minimum currents were on average about 15 cm/s, while average tidal currents reached almost 40 cm/s twice daily.

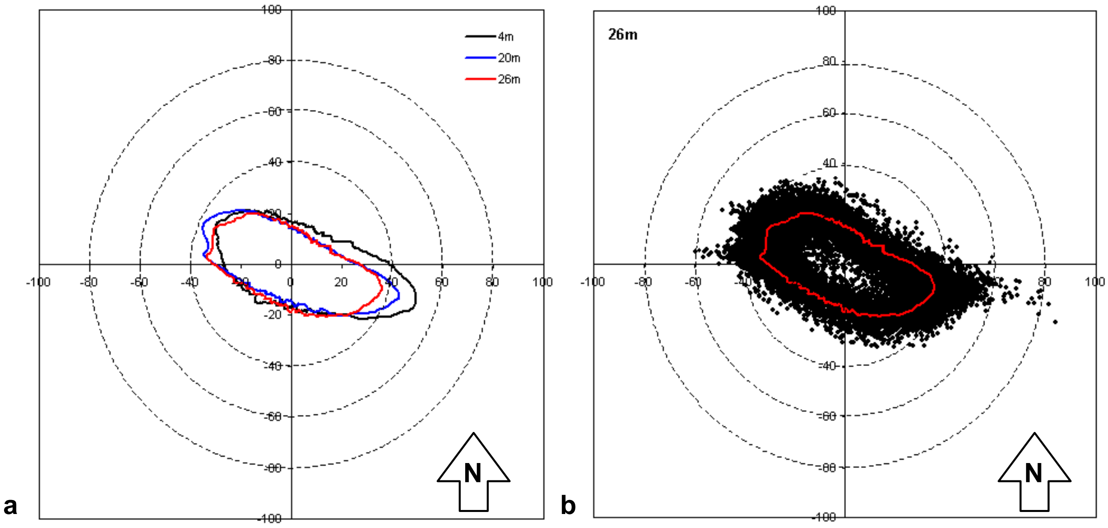

Figure 16.6. Current regime at the platform FINO1 in 2004: a) mean current strength [m/s] in 4, 20 & 26 m depth; b) absolute values and mean current in 26 m depth.

The strong currents correspond to a movement of the water app. 6 km to the west and to the east during each tide, explaining to lack of difference in hydrographical measurements between the investigated areas.

Termperature

Unfortunately, the system did not work for the whole period, but the existing data allow a good impression of the main temperature regime in the area. The temperature curves of all depths show a seasonal pattern, which is typical for this part of the North Sea (Figure 16.7). From the end of August 2003 the temperatures decreased until the end of November from app. 19°C to around 9°C. For December 2003, January and late March until the end of April 2004, no data are available as the measuring system was not working. For Febuary/March 2004 only data from 3 m and 20 m depth are available. During this period the temperature in 20 m depth was up to 2°C below the surface temperature and reached down to 3.1°C in March 2004. This difference between 3/6 m and 20/25 m was still recognisable at the onset of measuring in the end of April. With the increasing temperatures in spring, this difference decreased. The maximum temperatures were reached in August for all depths, slightly earlier at the surface than at the bottom. Only short term temperature stratifications of less than 2°C were found during the study period. Salinity in the ASA was constantly between 33 and 34 PSU and maximum differences between surface and bottom reached not more than 0.4 PSU for a few days only.

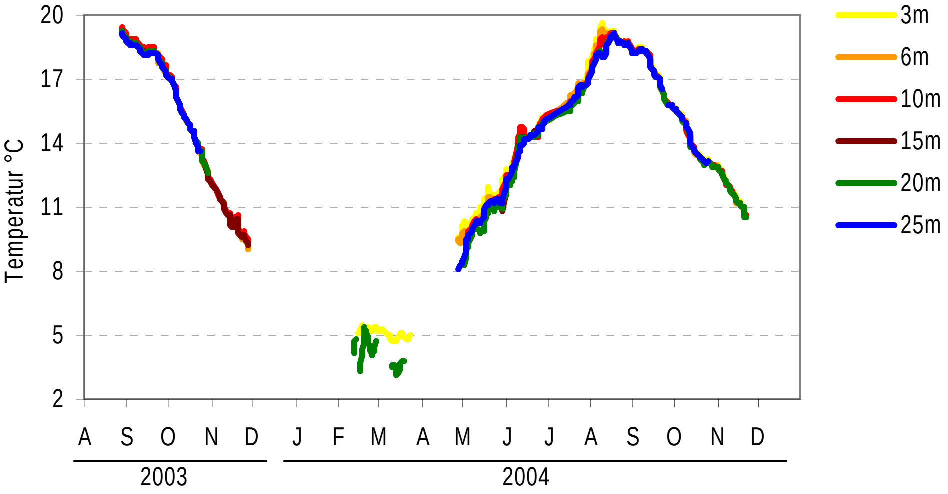

Figure 16.7. Annual temperature regime at the platform FINO1 from Sept. 2003 until Dec. 2004 in differentwater depths. Data from BSH.

Waves

Wave data from the FINO1 platform are rather sparse and do only start in Sept. 2003. Therefore we chose data from the offshore location of Helgoland, which should represent the same wave regime as in the ASA. Maximum wave highs of nearly 6 m were reached in spring 2004, but for most of the time the waves were between 1 and 3 m high (Figure 16. 8.).

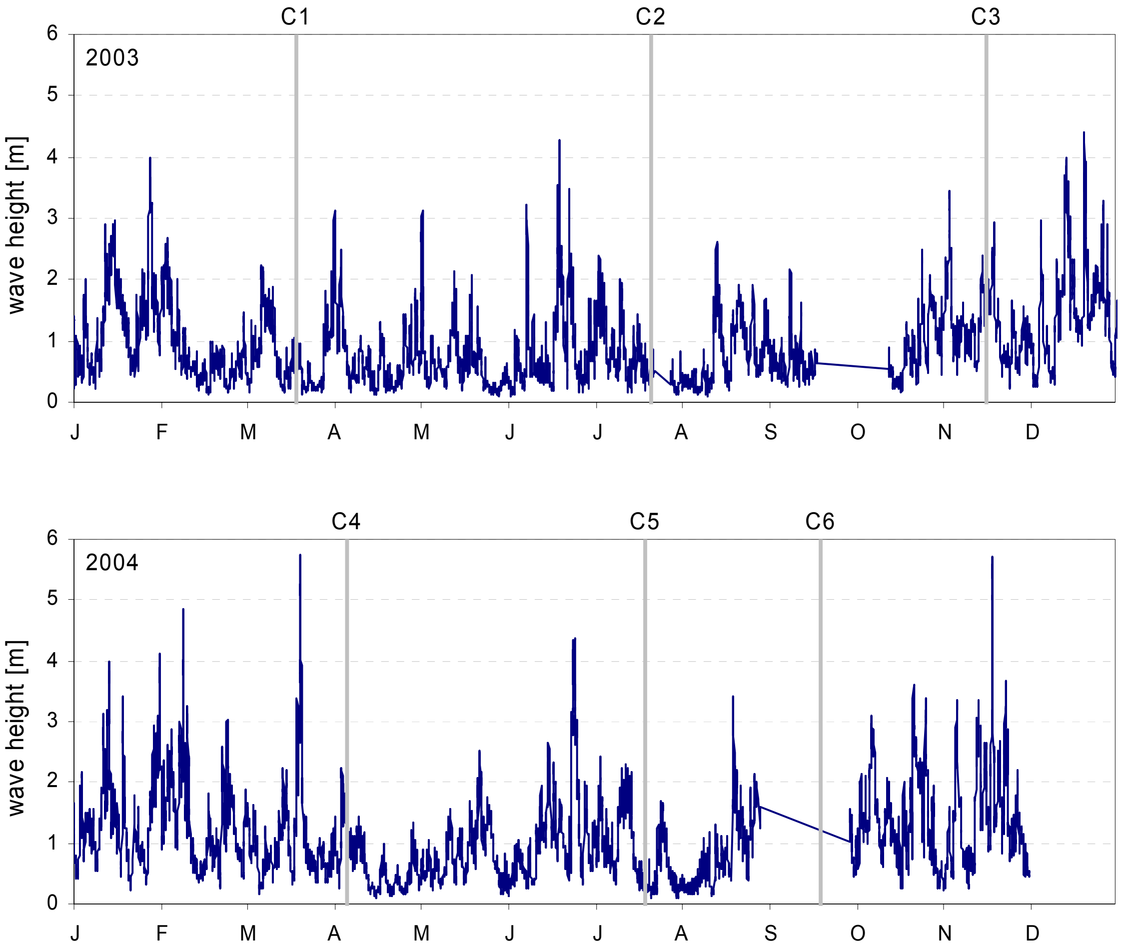

Figure 16. 8. Annual wave regime at Helgoland in 2003 & 2004. The beginning of the sampling cruises is indicated by grey lines. Data from BSH.

River run-off

Main peaks in run-off occur in spring every year, while during summer and autumn the values remain low (Figure 16.9.). The total run-off in 2003 was much higher than that in 2004.

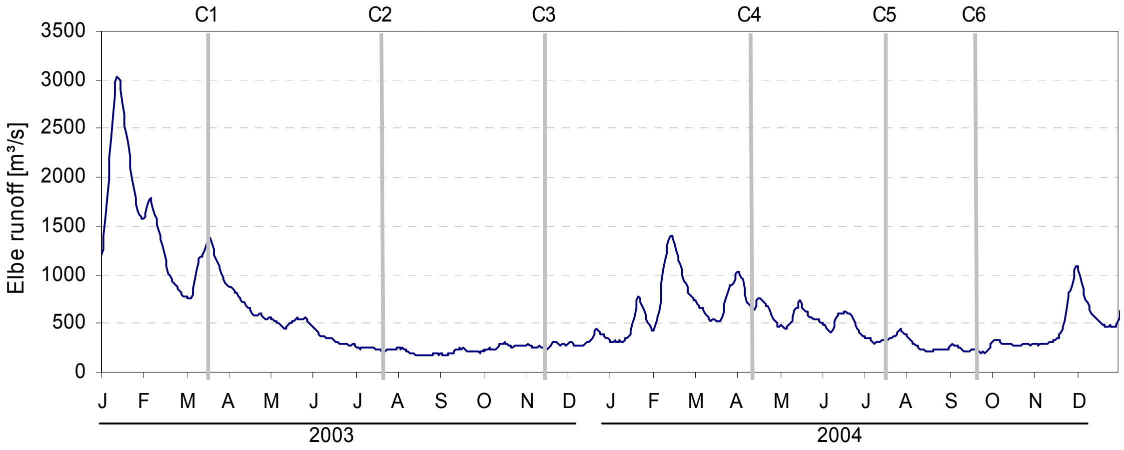

Figure 16.9. Elbe river run-off in 2003 & 2004. The beginning of the sampling cruises is indicated by grey lines.

Infauna

Description of community

The community represents a typical *Tellina-fabula*-community (sensu Salzwedel et al. 1985) common in shallower water areas with fine sandy bottoms. Some of the species which are listed in the annex I belong rather to the *Amphiura-filiformis*-community which inhabits fine sediments and slightly deeper waters (Salzwedel et al. 1985, Rachor & Nehmer 2003). All together, 146 taxa were identified in grab samples: 60 taxa of Arthrophoda, 8 Echinodermata, 24 Mollusca, 48 Polychaeta and 6 belonging to other phyla (Fig. 16.10).

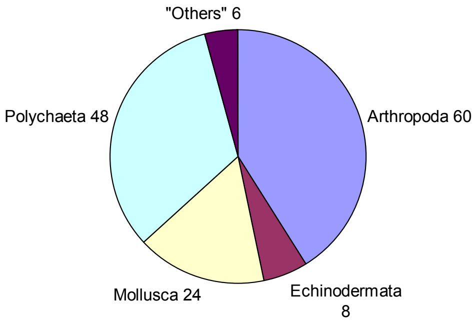

Figure 16.10. Total species number of main taxonomic groups in the investigation area

The fauna of the investigation area is characterised by some species which occurred very regularly over the whole study period (Table 16.3).

Table 16.3. Dominance, mean abundance (±SD) (N/m²) and presence of the most dominant infaunal species in the whole investigation area

Species	**dominance** [%]	**mean abundance (± SD)** [N/m²]	**presence** [%]
Phoronis spp.	37.41	1726 ± 3784	100
Spiophanes bombyx	9.89	456 ± 381	100
Lanice conchilega	8.61	397 ± 533	97
Nemertini indet.	5.33	246 ± 147	100
Ophiuridae spp.	4.71	217 ± 413	95
Poecilochaetus serpens	3.59	166 ± 115	98
Owenia fusiformis	3.44	158 ± 232	100
Urothoe poseidonis	3.26	151 ± 79	100
Montacuta ferruginosa	1.76	81 ± 52	98
Ophiura albida	1.64	75 ± 86	96
Chaetozone cf. *Setosa*	1.42	66 ± 90	91
Echinocardium cordatum	1.35	62 ± 84	98
Eumida sanguinea	1.18	55 ± 66	87
Magelona johnstoni	1.17	54 ± 32	100
Tellina fabula	1.15	53 ± 46	100
Spio decoratus	0.99	46 ± 89	75
Euspira pulchella	0.86	40 ± 19	100
Spio filicornis	0.65	30 ± 43	76
Malmgrenia marphysae	0.64	30 ± 49	84
Scoloplos armiger	0.53	25 ± 27	93

Eight species were recorded at every single station. Twenty species were registered on more than 90 % of the stations, but only a few species dominate the community. *Phoronis* spp. accounts for to 37 % of total individuals, *Spiophanes bombyx* 10 %, *Lanice conchilega* 9 %, Nemertini indet. 5 % and juvenile ophiuroids also 5 %.

Temporal variability

The infaunal community of the investigation area is strongly influenced by seasonal changes. Total abundances (Fig. 16.11) varied through the year. In March (cruise C1 and Cruise C4) the lowest abundances were found. In the first year, the abundances were generally higher with highest value in summer 2003 (cruise C2: 13092 ± 8776 N/m²) mainly caused by *Phoronis* spp. The mean abundance of the main groups changed between cruises (Fig. 16.11). During cruise C1, C5 and C6 the dominant group were Polychaeta. On the first cruise the polychaete *Spiophanes bombyx* was the most abundant species, while on the cruise C5 and C6 also *Lanice conchilega*, *Poecilochaetus serpens* and *Chaetozone cf. setosa* caused the dominance of the group Polychaeta. Cruises C2 – C4 were dominated by the genus *Phoronis* spp., while the densities of this massive settlement of *Phoronis* spp. and Polychaeta in summer ’03 were decreasing, in summer ’04 there was only a recruitment of Polychaeta.

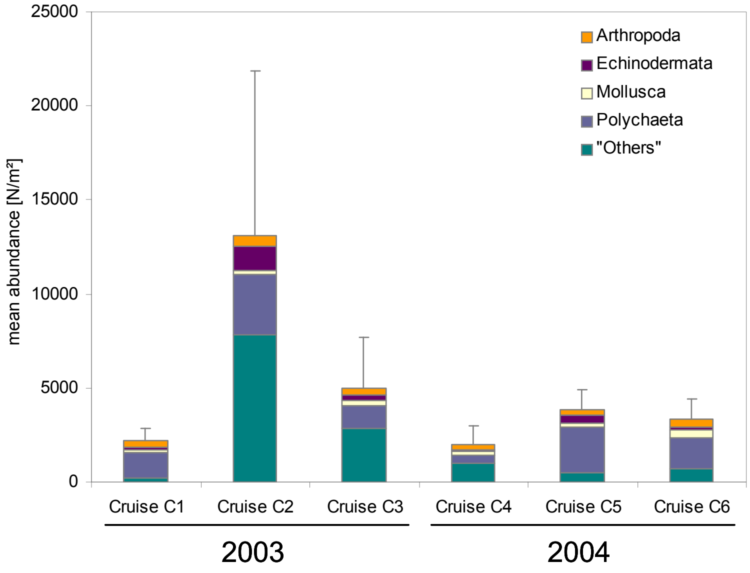

Figure 16.11. Mean abundance (± SD) [N/m²] split by the main groups of infauna

The mean biomass was higher in the year 2004 (Fig. 16.12) reaching its highest value in summer 2004 (328 ± 199 g/m²). The biomass of the main groups did not show large changes. Biomass is dominated by the heart urchin *Echinocardium cordatum* and changes in biomass during investigation time depended mostly on the number of individuals of this species caught in the grab.

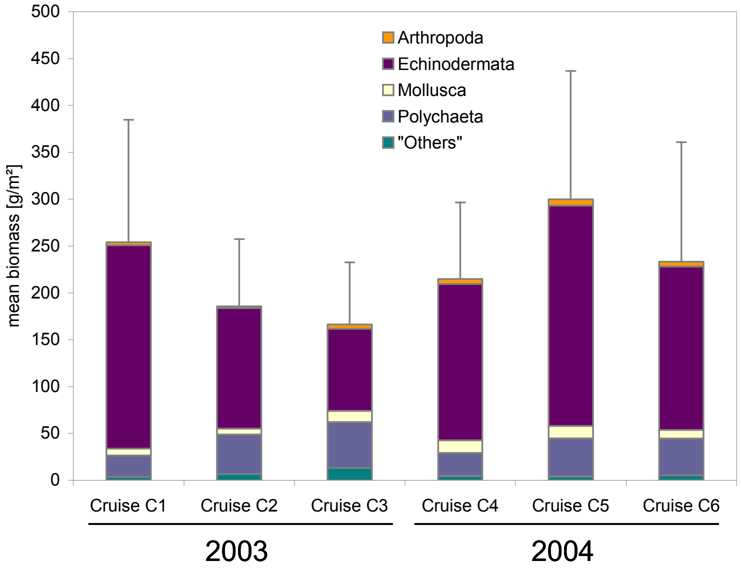

Figure 16.12. Mean biomass (± SD) as wet weight [g/m²] split by main groups of infauna

Species density, diversity and evenness changed considerably through the time of investigation (Figure 16.13.). Species density (Figure 16.13. a) was highest in summer 2003 (69 ± 5 spp/0.3 m²), lowest values have been recorded for springtime 2003 and 2004 (both 46 ± 5 resp. 46 ± 6 spp/0.3 m²).

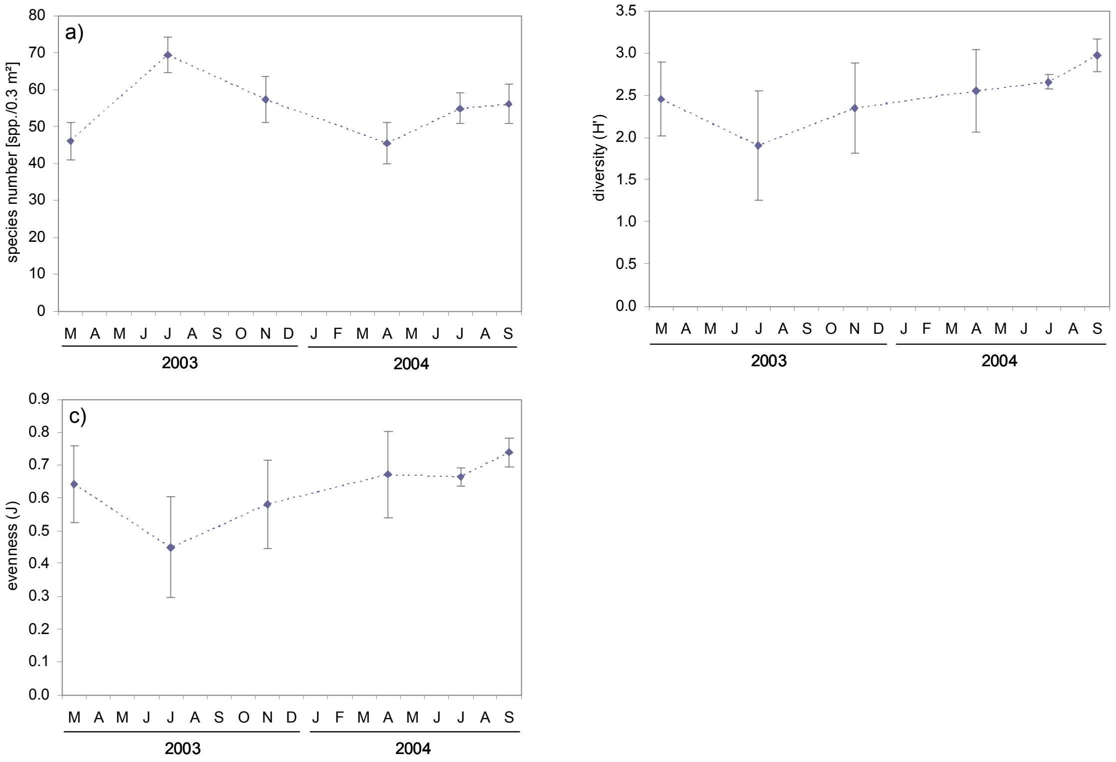

Figure 16.13. a) mean species number [spp./0.3 m²] (± SD), b) mean diversity (H'(loge)) (± SD) and c) mean evenness (J) (± SD) of the infauna over time

Diversity and evenness showed lowest values in summer 2003 (H': 1.9 ± 0.7; J: 0.5 ± 0.2), mainly caused by the strong dominance of Phoronis spp. and increased until the end of sampling time (H': 3.0 ± 0.2; J: 0.7 ± 0.04).

The community of the investigation area is strongly influenced by seasonality. The MDS-plot shows a distinction of mainly two groups (Figure 16.14.): the fauna of the spring cruises (yellow) and that of the late autumn cruise in 2003 (blue triangles) and the second group of the summer (red) and the early autumn cruise in 2004 (blue circles). Furthermore, the benthic community is more homogenous in summer, while the fauna in spring and the late autumn shows a higher variability (see also Table 16.6). Overall, the fauna of the different seasons can be well separated. (Global Rvalue = 0.95; p = 0.1 %).

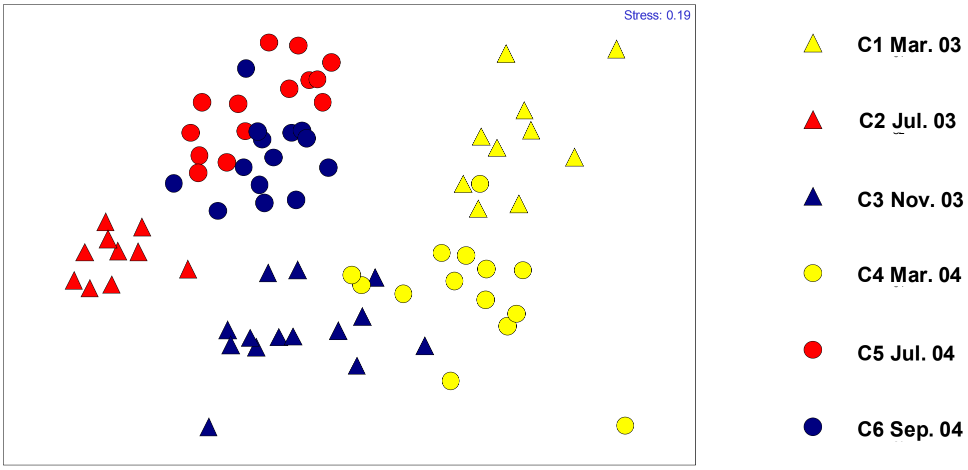

Figure 16.14. MDS-plot of all cruises of infauna abundance (Bray-Curtis-Index; transformation: 4th root)

The analysis with biotic and abiotic data over the time of investigation underlines the results of the community analyses. The main explaining factor for differences of the fauna is bottom temperature (Table 16.4), which showed the highest correlation value, coupled with abundance as well as biomass data of the infauna.

As a resume, it can be stated that the infaunal community of the investigation area is strongly influenced by seasonal changes. The dominant groups in numbers were the polychaetes *Spiophanes bombyx* and *Lanice conchilega*, as well as the group of “others” which reflects the strong dominance of *Phoronis* spp..

Table 16.4. Results of the BIOENV correlation I between abiotic data and the infauna community (abundance and biomass data). Selection of abiotic factors with the best correlation: 1: effort; 2: time; 3: total organic carbon (%); 4: median grain size (µm); 5: mud (%); 6: turbidity; 7: bottom temperature.

Abundance		**biomass**	
R	Selections	R	Selections
0.689	7	0.517	7
0.622	2,7	0.455	2,5,7
0.588	2,5,7	0.433	2,7
0.553	2,3,7	0.432	2,3,5,7
0.552	5,7	0.428	5,7
0.548	3,7	0.415	2,3,7

Effects on community composition

Plotting all data in one MDS-plot, no distinction due to fishing was visible (Figure 16.15.), as the influence of seasonality was larger than the impact of fishing activity.

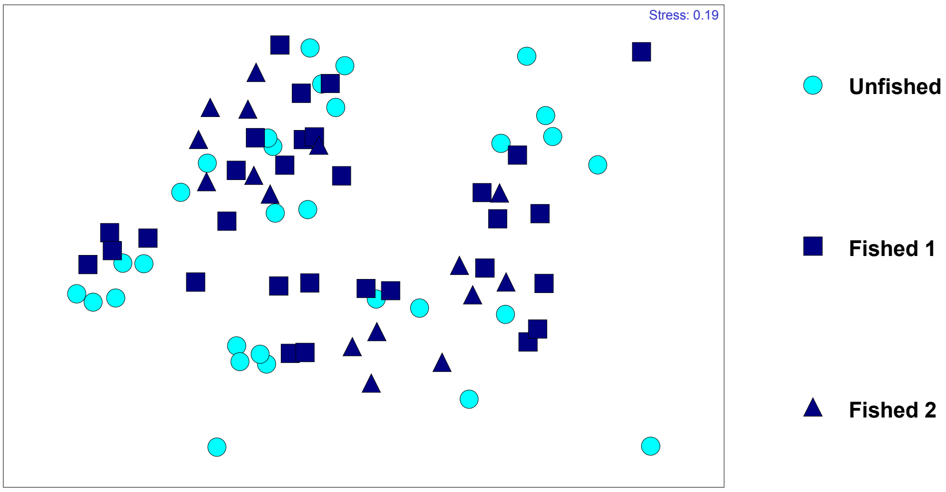

Figure 16.15. MDS-plot of all cruises of infauna abundance (Bray-Curtis-Index; transformation: 4th root)

A two way crossed ANOSIM (factors: cruise/seasonality and fishing impact) showed a significant separation of the unfished and fished areas in general (Table 16.5). The results become clearer looking at the pairwise tests.

Table 16.5. Results of two way crossed ANOSIM. R-values and significance level p [%] for the disctinction of unfished and fished areas with abundance and biomass data of the infauna

	Abundance		**Biomass**	
	R	**p [%]**	**R**	**p [%]**
Global	**0.56**	**0.1**	**0.47**	**0.1**
Unfished/Fished 1	0.51	0.1	0.44	0.1
Unfished/Fished 2	0.74	0.1	0.62	0.1
Fished 1/Fished 2	0.48	0.1	0.41	0.1

Abundance and biomass data show a larger distinction between the unfished area and both fished areas than between the two fished areas. The separation between fished area 2 and the unfished area was the highest between all areas, in biomass and abundance data.

To exclude seasonal effects, the data were analysed for each cruise separately to highlight the fishing effects.

The distinction of the unfished and fished areas had been noticeable before the construction of the platform (before closure, Figure 16.16.). This results mainly from the dominance of *Spiophanes bombyx* which occurred in higher numbers in the unfished area at the beginning of the investigation. Distinction directly after the closure is due to the high dominance of *Phoronis* spp. in the study area (see Table 16.3). Looking at the last cruise, the fauna of the unfished area is more similar than the fauna in the fished areas which is reflected in a greater spread of the stations of the fished fauna in the

MDS-plot. This result is supported by the higher MDI in the fished areas (Table 16.6, fishing 14 months after closure).

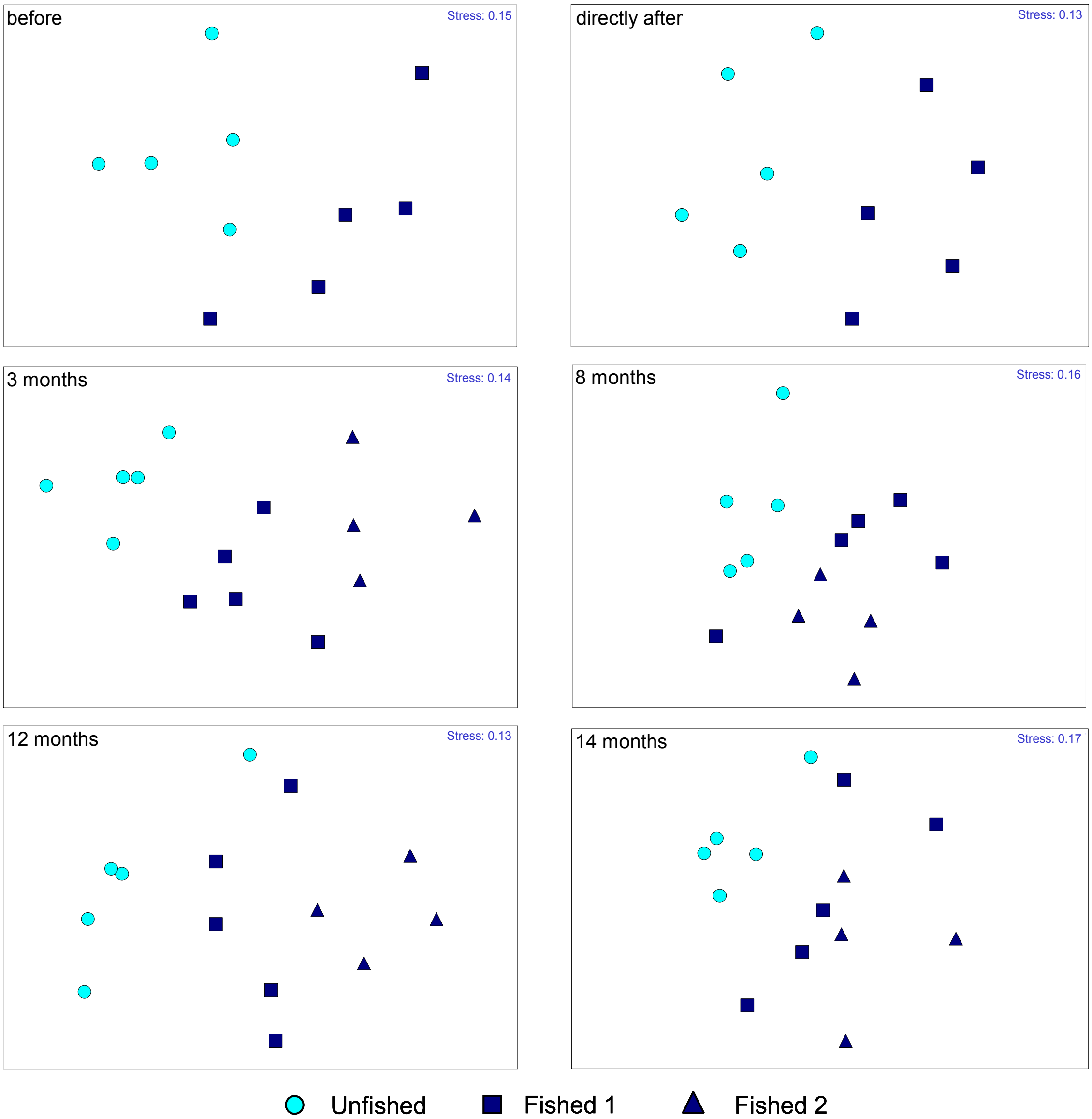

Figure 16.16. MDS-plots of infauna abundance (Bray-Curtis-Index; transformation 4th root) during the study period (before until 14 months after closure)

Table 16.6. Multivariate dispersion indices (MDI) for the infaunal community of the three areas, related to the factor fishing (both fished areas pooled) and the sum for every cruise

	Area			**Fishing**		**Seasonality**
Cruise	unfished	fished 1	fished 2	unfished	fished	
before (C1)	0.848	1.152		0.848	1.152	1.278
directly after (C2)	0.838	1.162		0.838	1.162	0.392
3 months (C3)	0.585	1.156	1.432	0.336	1.184	1.079
8 months (C4)	1.03	1.119	0.753	0.872	1.035	1.235
12 months (C5)	1.244	1.03	0.543	1.072	0.98	1.045
14 months (C6)	0.77	1.281	0.914	0.651	1.097	0.804

As a temporal development of the fauna can be expected after the construction of the platform, differences between fished and unfished areas should enlarge with time. This development of larger separation between unfished and fished areas over the timescale of the investigation is only partly supported by the ANOSIM R-values of pairwise test over time. The R-values varied through time of investigation (Figure.16.17 a,b; and Tab. 16.7).

Only at the last cruise, both R-values of unfished area vs. fished areas are higher than the R-value for the distinction of the fished areas. In addition to that, the fauna of F1 and F2 are no longer distinguishable, neither by abundance nor biomass data.

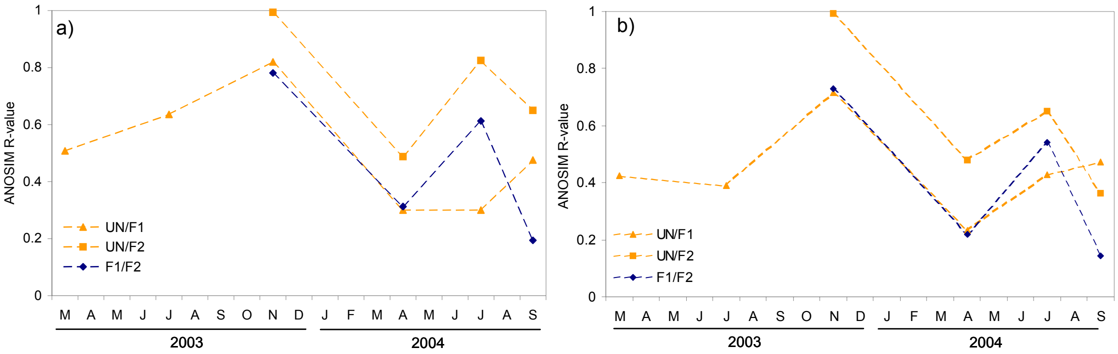

Figure.16.17. ANOSIM R-values of pairwise test for each cruise with a) abundance data and b) biomass data of infauna species (UN = Unfished; F1 = Fished 1; F2 = Fished 2)

Table 16.7. ANOSIM pairwise-test R-values and significance level p [%] for the distinction of unfished and fished areas with abundance and biomass data of infauna. Bold values are significant at 5 %.

	Abundance			Biomass		
	UN/F1 R ; p	**UN/F2 R ; p**	**F1/F2 R ; p**	**UN/F1 R ; p**	**UN/F2 R ; p**	**F1/F2 R ; p**
before	0.58 ; 0.8			0.42 ; 0.8		
directly after	0.64 ; 0.8			0.39 ; 0.8		
3 months	0.82 ; 0.8	0.99 ; 0.8	0.78 ; 0.8	0.72 ; 0.8	0.99 ; 0.8	0.73 ; 0.8
8 months	0.30 ; 4.8	0.49 ; 0.8	0.31 ; 4.8	0.23 ; 8.7	0.48 ; 1.6	0.22 ; 6.3
12 months	0.30 ; 4.0	0.83 ; 1.6	0.61 ; 0.8	0.43 ; 1.6	0.65 ; 1.6	0.54 ; 1.6
14 months	0.48 ; 1.6	0.65 ; 0.8	0.19 ; 7.9	0.47 ; 0.8	0.36 ; 4.8	0.14 ; 17.5

The BIOENV analyses identified the fishing effort as the main factor explaining faunal differences (Table 16. 8). The correlation between fauna and fishing effort was highest in summer of both years and autumn of 2003. Only low correlations were found in spring and autumn 2004. This is the case for abundance and biomass data. In addition to that, in summer and autumn of both years fishing effort is the single factor explaining the variations of the fauna.

Table 16. 8. Results of the BIOENV correlation I between abiotic data and the infauna community (abundance and biomass data). Selection of abiotic factors which are responsible for the best correlation: 1: effort; 3: total organic carbon (%); 4: median grain size (µm); 5: mud (%).

Cruise C1, before closure			
Abundance		**Biomass**	
R	Selections	R	Selections
0.535	1,5	0.432	1,5
0.480	1,3,5	0.365	1
0.451	1,4,5	0.361	1,3,5
0.437	1	0.314	1,4,5
0.426	1,3-5	0.272	1,3-5
Cruise C2, directly after closure			
Abundance		**Biomass**	
R	Selections	R	Selections
0.548	1	0.528	1,5
0.476	1,5	0.508	1,3,5
0.471	1,3,5	0.465	1,3-5
0.450	1,3	0.452	5
0.444	1,3-5	0.444	1,4,5
Cruise C3, 3 months after closure			
Abundance		**Biomass**	
R	Selections	R	Selections
0.739	1	0.653	1
0.501	1,5	0.451	1,3
0.442	1,3	0.443	1,5
0.403	1,4	0.349	1,3,5
0.342	1,4,5	0.348	1,4
Cruise C4, 8 months after closure			
Abundance		**Biomass**	
R	Selections	R	Selections
0.170	4	0.089	4
0.166	1,4	0.083	1,4,5
0.130	1,4,5	0.068	1,4
0.111	1,5	0.053	1,5
0.092	1,3,4	0.026	1,3-5
Cruise C5, 12 months after closure			
Abundance		**Biomass**	
R	Selections	R	Selections
0.555	1	0.442	1
0.536	1,4	0.364	1,3
0.466	1,5	0.357	1,4
0.453	1,4,5	0.349	1,3-5
0.441	1,3,4	0.347	1,5

Cruise C6, 14 months after closure

Abundance		**Biomass**	
R	Selections	R	Selections
0.303	1	0.104	1
0.254	1,5	0.008	1,5
0.213	1,3,5	-0.036	5
0.150	1,3	-0.067	1,3,5
0.071	3,5	-0.095	1,3

Community structure

The total abundance of organisms is higher in the unfished area during the whole investigation (Figure 16.18.a). This is due to the polychaete *Spiophanes bombyx* before the closure, the dominant *Phoronis* spp. during the following 3 cruises, and 12 and 14 months after closure *Phoronis* spp. with several polychaetes. The biomass is influenced by the occurrence of only one single species, the heart urchin *Echinocardium cordatum*. This species occurs in higher numbers in the fished area 2 (Figure 16.18.a). While the abundance was variable during the investigation time, the biomass seems to reach a more stable level in the unfished area with less seasonal variation compared to the fished areas (Figure 16.18.b).

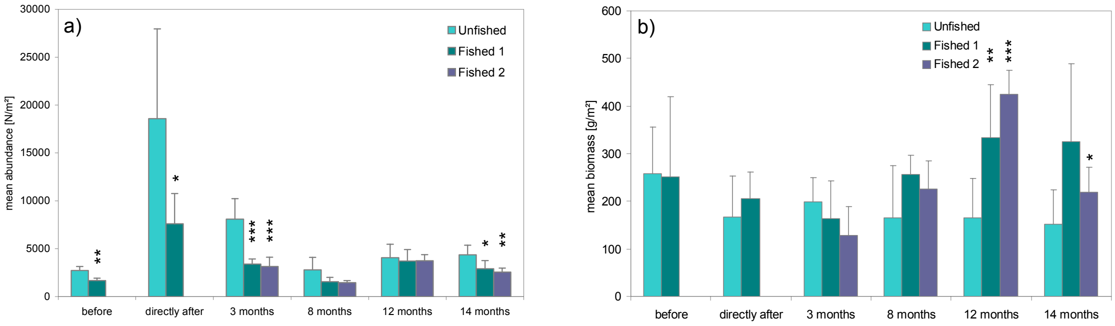

Figure 16.18. a) Mean abundance [N/m²] and b) mean biomass [g/m²] in the unfished, fished 1 and fished 2 area in relation to time (before or after) of the platform installation. (ANOVA significance level: * 0.05; ** 0.01; *** 0.001)

Species density varied seasonally with highest numbers in summer and lowest in spring (Figure 16.19.a). The initially lower species density in fished area 2 reached the same level as the other two areas by summer 2004. The species density at the end of the investigation was nearly the same in all areas (about 62 – 64 spp./0.3 m²). Diversity and evenness (Figure 16.19.b, c) were lower in the unfished area during the whole investigation. This was again due to the dominance of one species (*Phoronis* spp.).

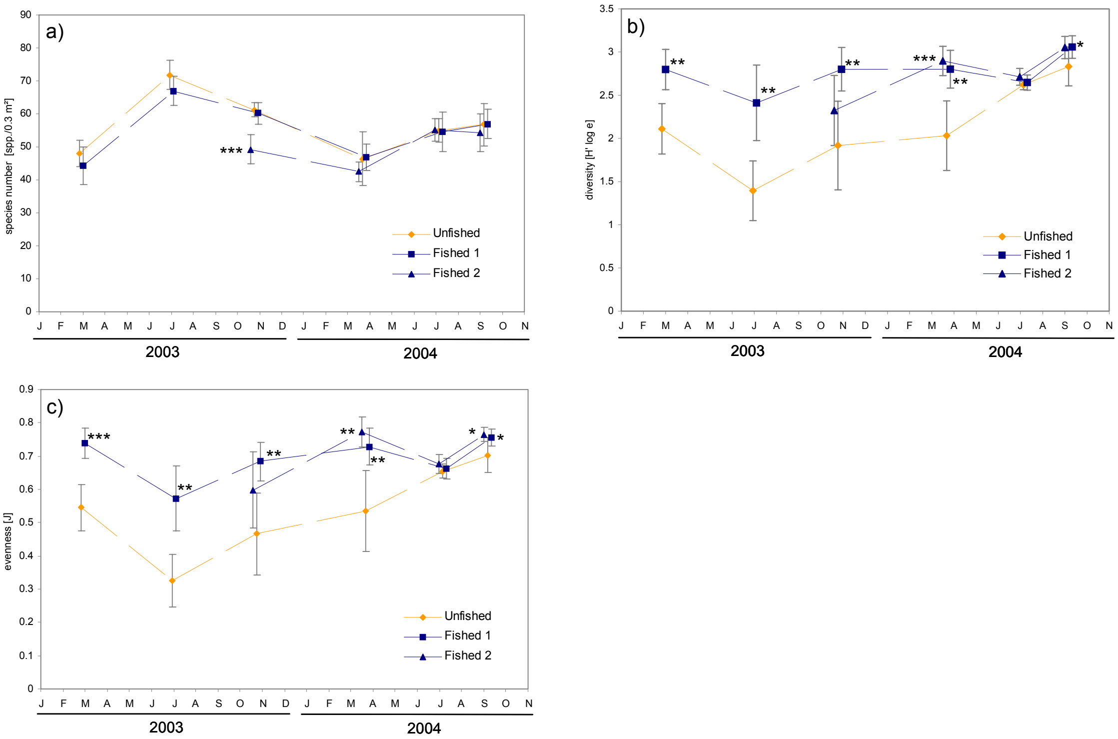

Figure 16.19. Mean species density [spp./0.3 m²] (a), mean diversity (H'loge) (b) and mean evenness (c) in the unfished, fished 1 and fished 2 area during time of investigation. ANOVA significance level: * 0.05; ** 0.01; *** 0.001

Excluding *Phoronis* spp. (Figure 16.20.), the diversity and evenness is still lower in the unfished area until the mid of the first year, but in the second year both indices were nearly the same in all areas independent of fishing activity.

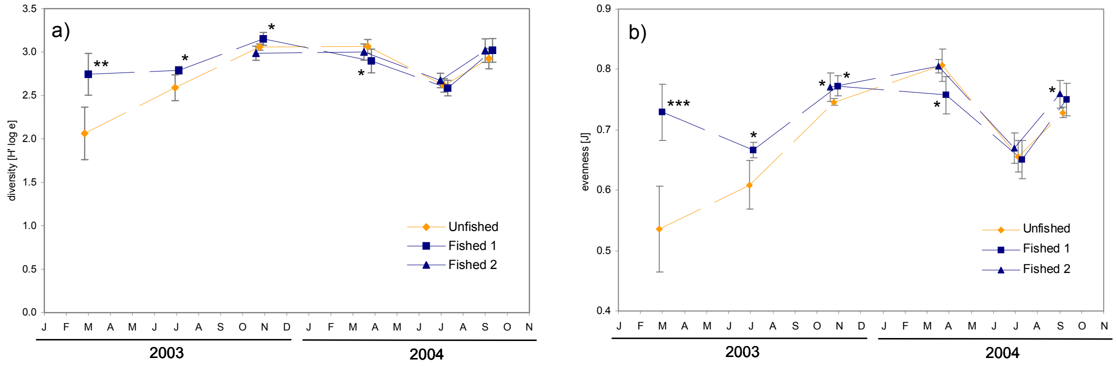

Figure 16.20. a) diversity (H'loge) and b) evenness (J) of the unfished and fished areas excluding Phoronis spp.. ANOVA significance level: * 0.05; ** 0.01; *** 0.001

Taxonomic groups

As generally the fauna shows slight differences between unfished and fished areas, taxonomic groups and functional groups were investigated in order to detect the fishing impact and to analyse which groups were responding to the trawling activity.

Higher abundances of Arthropods in the unfished area mainly depended on the occurrence of Amphipods (Figure 16.21.a). Only directly after the construction of the platform a higher number of juvenile swimming crabs in the unfished area was responsible for the differences between unfished and fished areas. At all other times several amphipods were responsible for differences between areas, mainly Urothoe poseidonis, which occurred in higher numbers in the unfished area. Biomass data of the arthropods show a clearer trend with similar wet weight until 8 months after platform construction and higher biomass in the fished areas 12 and 14 months after closure (Figure 16.21.b).

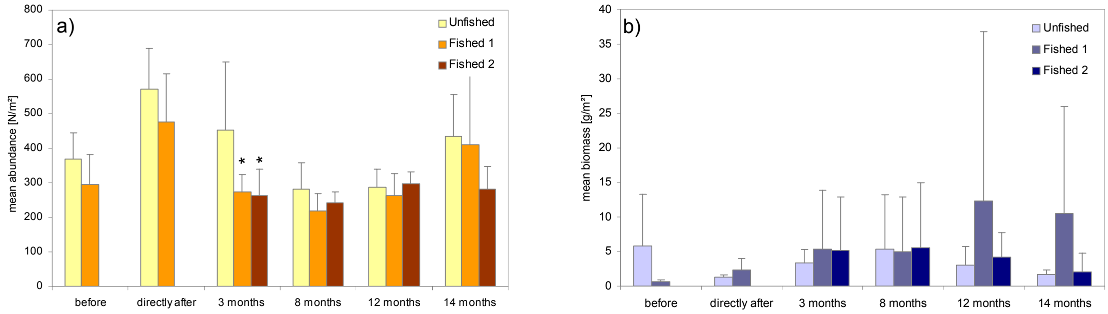

Figure 16.21. a) mean abundance [N/m²] and b) mean biomass [g/m²] of Arthropoda in the unfished and fished areas. ANOVA significance level: * 0.05

Despite the higher wet weight in both fished areas after 8 months of closure (Figure 16.22.b), which was due to heart urchins, no trends were reported for abundance data of Echinodermata. The abundance peak of this group directly after the platform construction is due to young brittle stars (unfished: 1247 ± 505 N/m²; fished 1: 1058 ± 546 N/m²)(Figure 16.22.a). Twelve months after construction, higher numbers of Echinodermata were recorded for the fished area: *Echinocardium cordatum* (fished 1: 253 ± 179 N/m²; fished 2: 201 ± 49 N/m²) and young ophiuroids.

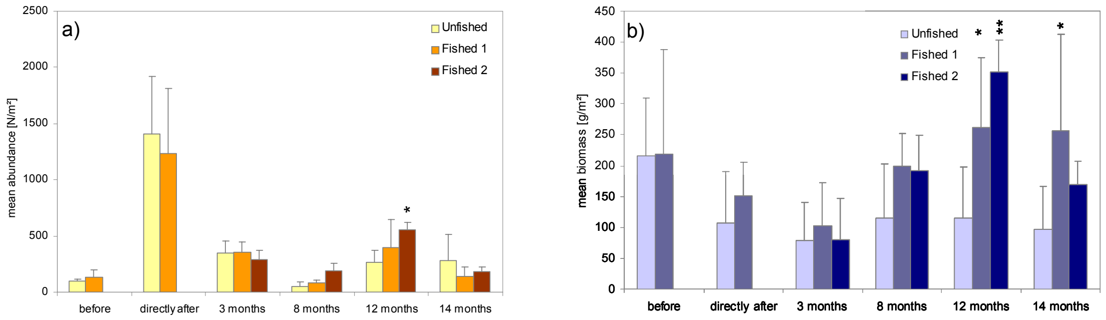

Figure 16.22. a) mean abundance [N/m²] and b) mean biomass [g/m²] of Echinodermata in the unfished and fished areas. ANOVA significance level: * 0.05; ** 0.01

After 14 months of investigation time high values of echinoderms occurred in the unfished area due to *Ophiura albida* (with a high variability within the area: 85 ± 153 N/m²) and young ophiuroids (139 ± 74 N/m²).

The group of molluscs showed higher abundances in the fished areas after longest times of closure (Figure 16.23.a). This was mainly caused by *Montacuta ferruginosa* (14 months fished 1: 159 ± 77 N/m²) and juvenile *Tellina fabula* (148 ± 76 N/m²). The biomass data showed the same trend as abundance data with higher values in the fished areas after 8 months of closure in both fished areas (Figure 16.23.b).

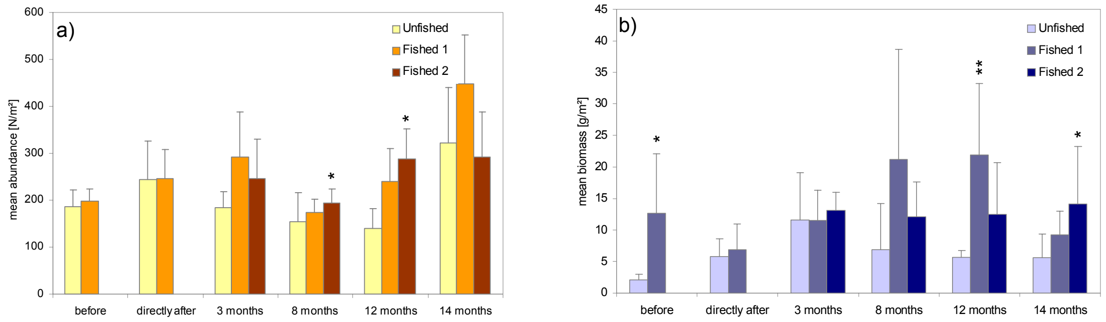

Figure 16.23. a) mean abundance [N/m²] and b) mean biomass [g/m²] of Mollusca in the unfished and fished areas. ANOVA significance level: * 0.05; ** 0.01.

The group of “others” showed the highest densities of all groups in the unfished area (Figure 16.24.a). This is due to the *Phoronis* spp. whose highest abundance was recorded in July 2003 directly after platform construction (12469 ± 8406 N/m²). Since this time the number decreased to 765 ± 691 N/m². The biomass data followed nearly the same trend (Figure 16.24.b). A higher wet weight for this group was recorded in the unfished area during the first three cruises (until 3 months after closure) and for the last two cruises (12 and 14 months after closure).

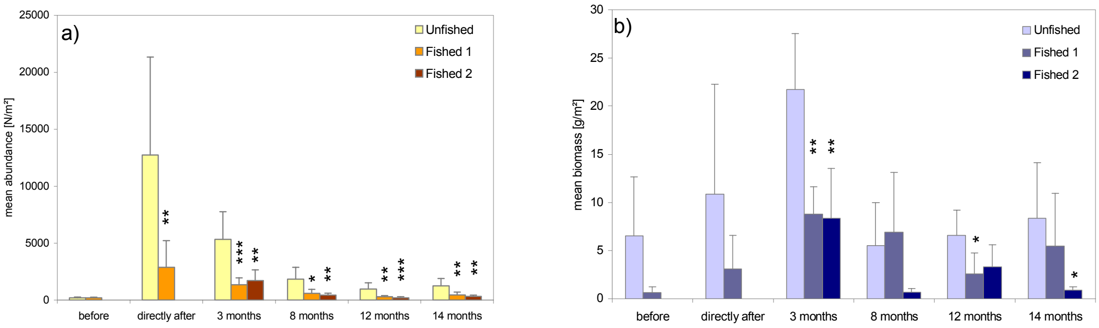

Figure 16.24. a) mean abundance [N/m²] and b) mean biomass [g/m²] of “others” in the unfished and fished areas. ANOVA significance level: * 0.05; ** 0.01; *** 0.001.

The biomass of Polychaeta did not follow any clear trend (Figure 16.25.b), but abundance data have been higher in the unfished area in the first year and 14 months after closure of the platform area (Figure 16.25.a). Before the construction of the platform, *Spiophanes bombyx* was dominant in the unfished area (1368 ± 443 N/m²), high values in this area directly after until 3 months after closure were due to *Spio decoratus* and *Lanice conchilega*.

At the end of the investigation time, in general tube building worms like *Spiophanes bombyx* (415 ± 79 N/m²), *Owenia fusiformis* (370 ± 200 N/m²), *Spio filicormis* (113 ± 65 N/m²) and *Spio decoratus* (83 ± 81 N/m²) were dominant in the unfished area.

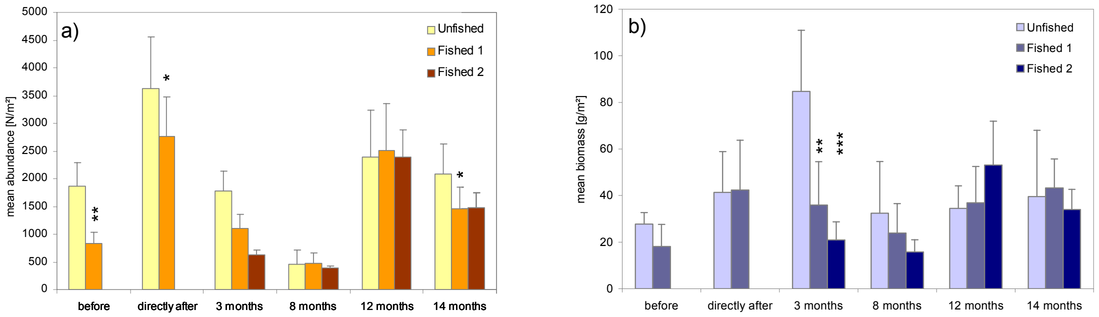

Figure 16.25. a) mean abundance [N/m²] and b) mean biomass [g/m²] of Polychaeta in the unfished and fished areas. ANOVA significance level: * 0.05; ** 0.01; *** 0.001.

Functional groups and main discriminating species

Tube building polychaetes and some amphipods caused a higher number of detritus feeder in the unfished area (Figure 16.26.), while *Phoronis* spp. and *Owenia fusiformis* explain the higher number of filter feeders in the unfished area. The same trend was found with the functional group “mobility” (sedentary, mobile, highly mobile) where sedentary species (mainly tube building worms) showed higher abundances in the unfished area (Table 16.9).

Table 16.9. Analyses of functional groups of the infauna. Significances tested with ANOVA (Significance level: * 0.05; ** 0.01; *** 0.001). U = higher abundance in the unfished area; F = higher abundance in the fished area. 1) and 2) = significant difference between fished areas with F1 = higher abundance in fished area 1

		Time of closure									
		before	**directly after**	**3 months**		**8 months**		**12 months**		**14 months**	
		UN/F1	UN/F1	UN/F1	UN/F2	UN/F1	UN/F2	UN/F1	UN/F2	UN/F1	UN/F2
Feeding	detritus feeder	U**		U***	U***$^{1)}$					U*	U*
	suspension feeder		U**	U***	U**	U*	U**	U*	U**	U**	U**
	predator/scavenger; omnivorous species			U*	U***$^{2)}$						
Position	surface			U*	U**						U*
	subsurface	U***	U**	U***	U***		U*			U*	U**
Mobility	highly mobile										F*
	mobile	U*		U*	U**						U**
	sedentary	U**	U**	U***	U***	U*	U*			U**	U**
Vulnerability	high		U**	U***	U**	U**	U**	U*	U*	U**	U**
	low										U*
	medium	U***		U**$^{1)}$	U***$^{1)}$					U*	U*

$^{1)}$F1/F2: F1** $^{2)}$F1/F2: F1*

The other functional groups “vulnerability” (low, medium, high) and position (surface, subsurface) showed also significant differences between the areas (Table 16.9) with higher abundances in the unfished area.

Omnivorous species followed no clear trend over time (Table 16.9, Figure 16.26.). The higher number of infaunal predators and scavengers in the unfished areas were due to Nemertini indet. And polychaetes (*Eumida sanguinea*, *Eteone longa* and juvenile *Nephtys* spp.) as well as at the longest time of closure the Echinodermata *Ophiura albida* and juvenile Ophiuridae.

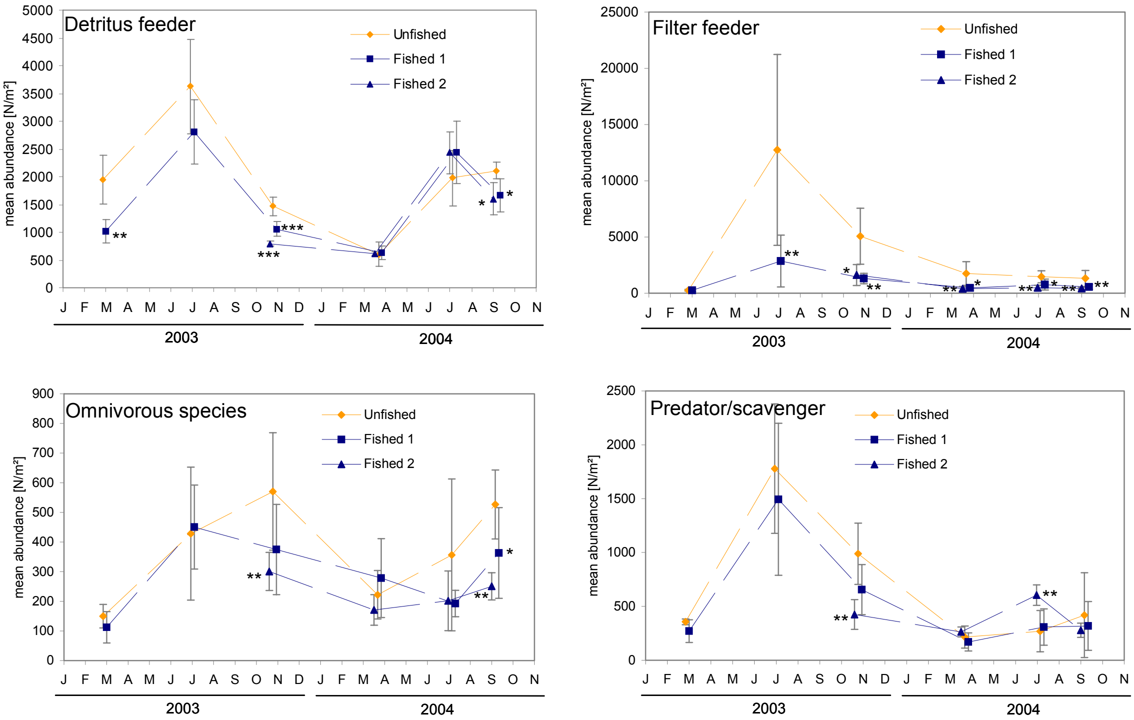

Figure 16.26. Mean densities [N/m²] of feeding groups of infauna. ANOVA significance level: * 0.05; ** 0.01; *** 0.001)

Sedentary species had higher abundances in the unfished area. This is the case for *Phoronis* spp., the polychaetes *Spiophanes bombyx*, *Owenia fusiformis*, *Chaetozone cf. setosa* and *Spio decoratus* as well as for sedentary Anthozoa (Figure 16.27.). Nemertini as infaunal scavenger showed also higher abundances in the unfished area, as well as some amphipods like *Bathyporeia* spp. was recorded in higher numbers in the unfished area at the end of the study period.

Infaunal species responded not clearly to the cessation of fishing. But some species which are filter and detritus feeder and sedentary such as tube building worms seems to be attracted to the unfished area, as there is a trend of higher abundances of these species in the unfished area.

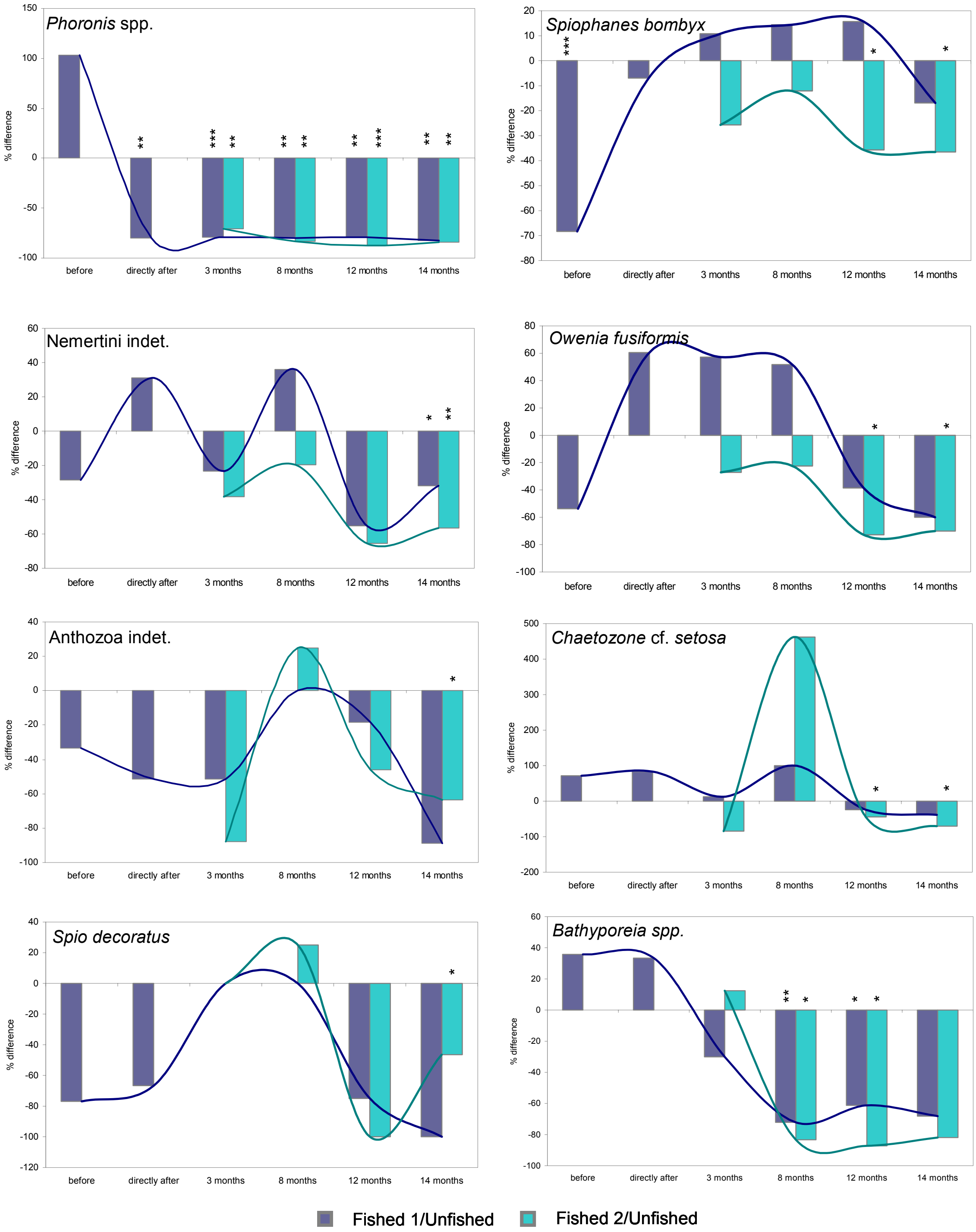

Figure 16.27. Percentage difference between fished and unfished areas of main discriminating species. Significance level: * 0.05; ** 0.01;*** 0.001). Positive values indicate higher values in fished area

The main discriminating groups and species which were responsible for the alteration of the fauna are summarized in Table 16.10. Fished area 1 and fished area 2 are pooled and percentage change between fished and unfished area are listed.

Table 16.10. Percentage differences between unfished and fished area (mean value of fished area 1 and fished area 2) of the main discriminating infaunal groups and species. Positive values indicate higher values in fished area. ANOVA Significance level: * 0.05; ** 0.01; *** 0.001.

	Time of closure					
	Before	**Directly after**	**3 months**	**8 months**	**12 months**	**14 months**
Taxonomic groups						
"Others"	-1.4	-77.3**	-71.7***	-71.5**	-73.8***	-68.0***
Polychaeta	-55.4***	-23.8	-49.5**	-6.0	2.6	-29.6*
Feeding type						
Detritus feeder	-47.9**	-22.6	-35.9***	3.4	23.3	-22.3**
Filter feeder	-2.3	-77.6**	-71.6***	-74.9**	-56.0**	-61.6**
Mobility						
Sedentary species	-46.3**	-66.7**	-65.8***	-60.7**	-11.2	-38.9**
Species						
Phoronis spp.	102.9	-79.6**	-75.5***	-81.3**	-82.6***	-83.2**
Spiophanes bombyx	-68.3***	-6.9	-5.4	2.6	-7.2	-25.6*
Nemertini indet.	-28.5	31.1	-30.0*	11.3	-59.8*	-42.8**
Owenia fusiformis	-53.8	60.5	19.7	18.8	-53.8*	-64.5**
Anthozoa indet.	-75.0	600.0	-37.5	94.4	-16.7	-86.1
Chaetozone cf. *Setosa*	71.4	83.3	-30.6	261.1	-33.0	-53.0**
Spio decoratus	-33.3	-51.3*	-67.7*	11.1	-30.6	-77.6*
Bathyporeia spp.	35.7	33.3	-11.1	-77.1**	-72.8**	-74.2

Epifauna

Description of the community

During the investigation 61 taxa were identified in beam trawls: 15 Arthropoda, 5 Echinodermata, 11 Mollusca, 27 fishes, 2 Polychaeta and 1 "other" phylum (Figure 16.28.).

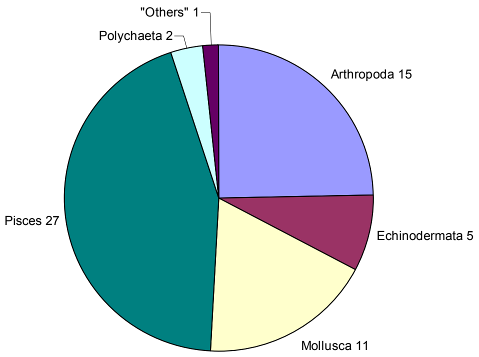

Figure 16.28. Total species number of the main taxonomic groups in the investigation area

Only four species were occurring regularly on all stations (Table 16.11) and only 12 species were recorded on ¾ of the stations over the whole study period. *Ophiura albida* was the most abundant species in the study area (78 %). Although *Asterias rubens*, *Crangon crangon* and *Liocarcinus holsatus* appeared in relatively high numbers, they played a minor role in the dominance spectrum due to the extreme dominance of *O. albida*.

Table 16.11. Dominance, mean abundance (±SD) (N/1000 m²) and presence of the most dominant epifaunal species in the investigation area

Species	**dominance** [%]	**mean abundance (± SD)** [N/1000 m²]	**presence** [%]
Ophiura albida	78.44	2762 ± 3258	100
Asterias rubens	8.93	314 ± 231	100
Crangon crangon	3.06	108 ± 139	76
Liocarcinus holsatus	3.03	107 ± 165	95
Buglossidium luteum	1.98	70 ± 74	100
Pomatoschistus minutus	1.35	48 ± 49	95
Ophiura ophiura	0.74	26 ± 58	95
Astropecten irregularis	0.38	13 ± 14	87
Arnoglossus laterna	0.38	13 ± 16	97
Limanda limanda	0.34	12 ± 9	100
Crangon allmani	0.26	9 ± 15	55
Pagurus bernhardus	0.18	6 ± 8	75
Pleuronectes platessa	0.17	6 ± 6	88
Callionymus lyra	0.17	6 ± 5	90
Makropodia spp.	0.12	4 ± 6	68
Syngnathus rostellatus	0.11	4 ± 7	61

Temporal variability

Abundances and biomass of the epifaunal community were both higher in the year 2004 (Figs. 16.29 and 16.30). Lowest values were recorded during the autumn cruise (C3) in the first year for abundance (462 ± 361 N/1000 m², Fig.16.29) and biomass (1607 ± 1130 g/1000 m², Fig. 16.30). Highest values were recorded at the summer cruise C5 (abundance: 6635 ± 5355 N/1000 m²; biomass: 7754 ± 3735 g/1000 m²).

Nearly all cruises were dominated by Echinodermata except for the cruise C3 in autumn where Arthropoda were the dominant group (Fig. 16.29). Responsible for the high dominance of Echinodermata was mainly the species *Ophiura albida* and secondly *Asterias rubens*. In autumn 2003 (cruise C3) the abundance of *Crangon crangon* caused the dominance of Arthropoda. This species were recorded with nearly the same abundances during the cruises C1 and C4 but high numbers of brittle stars put the dominance of Arthropoda into perspective. In general, the development of biomass and abundance data of the main groups was similar. Cruise C1, C2, C4 and C5 were dominated by the high biomass of Echinodermata (*Asterias rubens* and *Ophiura albida*).

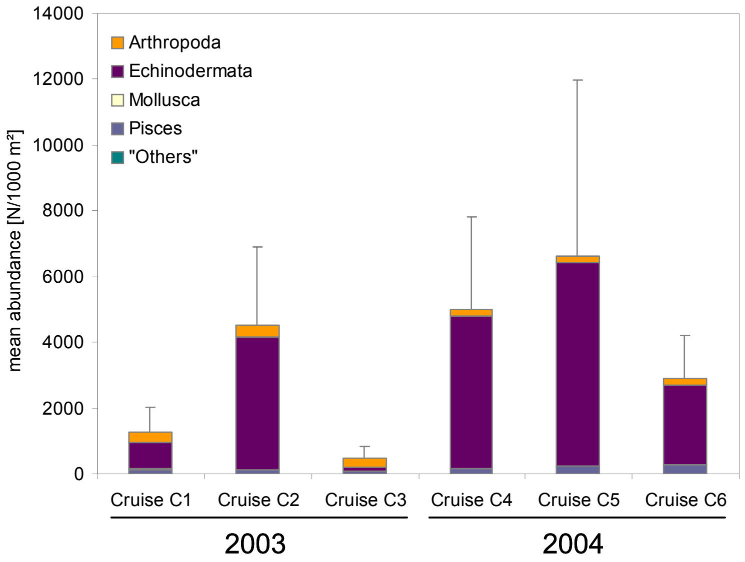

Figure 16.29. Mean abundance (± SD) [N/1000 m²] split by main groups of epifauna

The biomass at cruise C3 was also dominated by Arthropoda (*Liocarcinus holsatus* and *Crangon crangon*). The only difference was the biomass composition of the last cruise C6. The highest biomass was recorded for fishes (Fig. 16.30). Main species responsible for the dominance in biomass were *Limanda limanda*, *Buglossidium luteum* and *Pleuronectes platessa*. The fishes were followed again by the group of Echinodermata and Arthropoda.

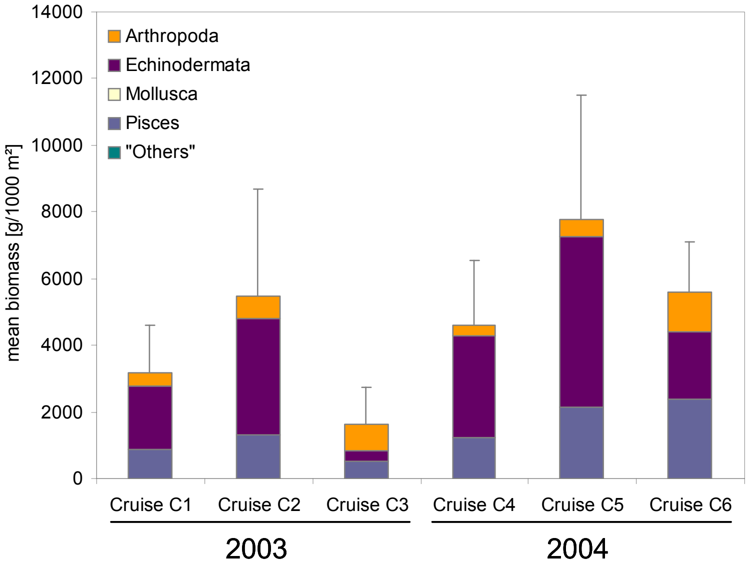

Figure 16.30. Mean biomass (± SD) as wet weight [g/1000 m²] split by main groups of epifauna

The species number decreased continuously during the first year of investigation (Figure 16.11a) with the lowest value of only 14 in autumn 2003, while in autumn 2004highest number of species (23) was recorded. Diversity and evenness were higher in the first year with a peak in autumn 2003 (Figure 16.11b, c). Minimal values were recorded in spring of the second year and both indices increased continuously through the second year.

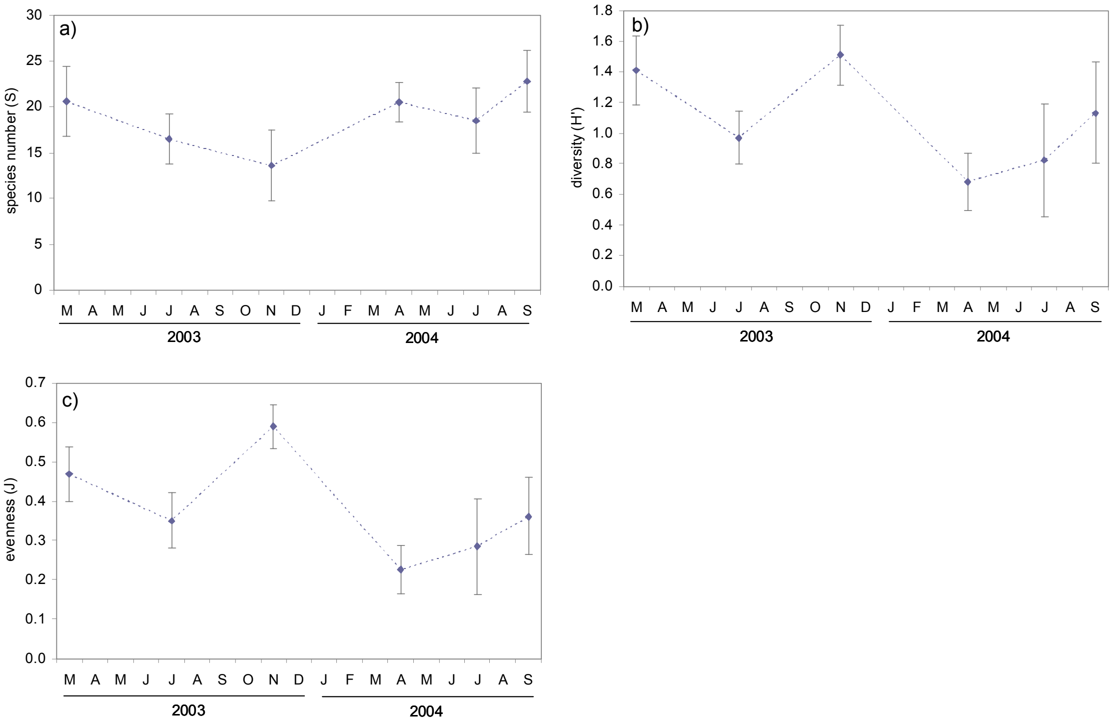

Figure 16.11. a) mean species number (S) (± SD), b) mean diversity (H'loge) (± SD) and c) mean evenness (± SD) of the epifauna over time

Like the infauna, also the epifauna in the study area is strongly influenced by seasonality. The MDS-plot shows 2-3 groups (Figure 16.32.). The cruises were well separated by the factor seasonality (ANOSIM Global R-value = 0.81; p = 0.1 %).The fauna of the spring and late autumn cruise C3 (right side of the MDS-plot) can be distinguished from that of the summer and early autumn cruise (left side of the plot). In additional, the three seasons (spring, summer and autumn) can be separated (different colours). While the fauna of the spring and summer cruises were relatively homogenous, the fauna of the autumn cruise 2003 had a higher variability. The multivariate dispersion indices for the summer and spring cruises were low (see also Table 16.13, seasonality) while that of the autumn cruise 2003 was the highest.

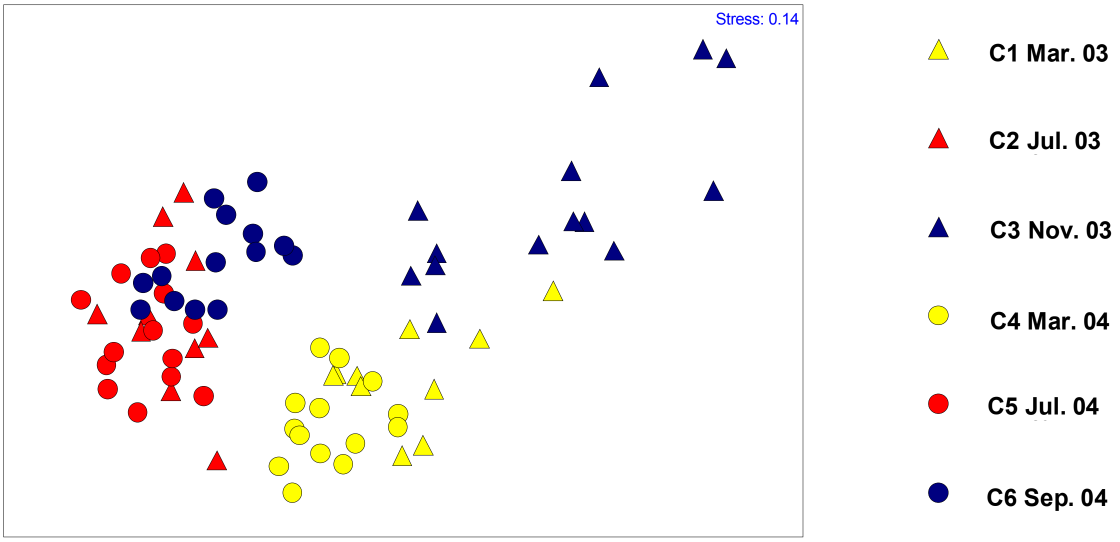

Figure 16.32. MDS-plot of all epifauna-samples (Bray-Curtis-Index; transformation: 4th root)

The combination of epifaunal biotic and abiotic data over the time of investigation (BIOENV) showed that the main explaining factor is the bottom temperature, like the infauna results (Table 16.12). This factor correlates highest with abundance as well as biomass data. Adding other factors decrease the correlation.

Table 16.12. Results of the BIOENV correlation I between abiotic data and the epifauna community (abundance and biomass data). Selection of abiotic factors which are responsible for the best correlation: 1: effort; 2: time; 3: total organic carbon (%); 4: median grain size (µm); 5: mud (%); 6: turbidity; 7: temperature bottom.

Abundance		**biomass**	
R	Selections	R	Selections
0.531	7	0.498	7
0.391	5,7	0.353	5,7
0.380	3,7	0.350	3,7
0.359	3,5,7	0.320	3,5,7
0.348	1,7	0.314	1,7
0.327	1,5,7	0.301	4,7

Effects on community composition

On the MDS-plot, the influence of fishing is not directly obvious (Figure 16.33.). Only on the left side, the stations of the unfished area are closer together. These are mainly those stations where time of closure of the platform has been longest in summer and autumn ’04. The fauna of the unfished area seems to become more similar, while the benthic community of the fished areas is more variable.

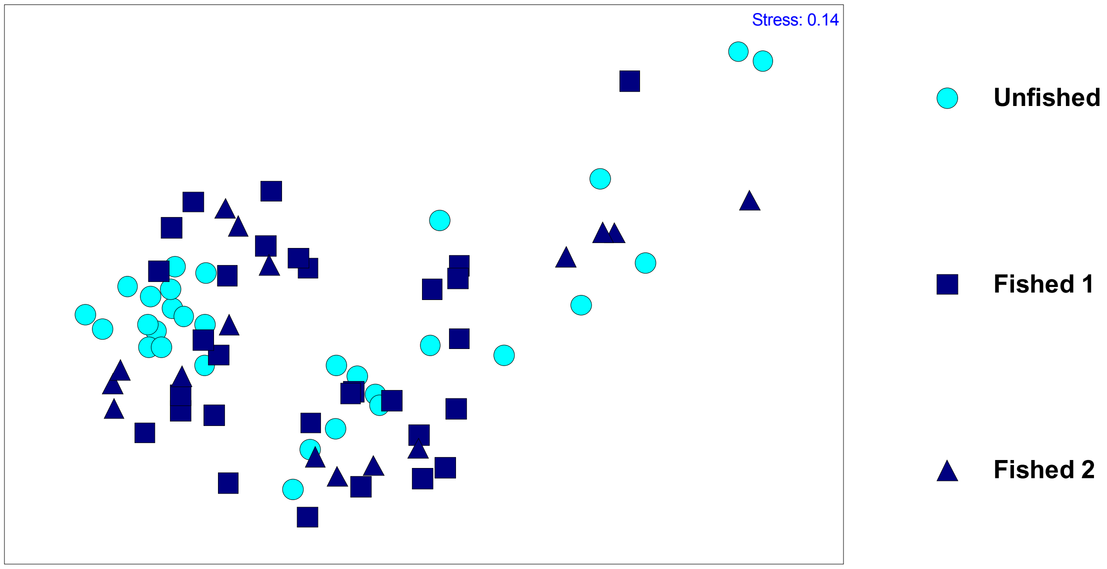

Figure 16.33. MDS-plot of all cruises of epifauna abundance (Bray-Curtis-Index; transformation: 4th root)

These results are supported by the MDI (Table 16.13). Whereas the variability for the fished areas remains high (8 to 12 months after closure), the MDI for the unfished area decreases.

Table 16.13. Multivariate dispersion indices for the epifaunal community of the three areas, related to the factor fishing (both fished areas pooled) and the sum for every cruise

	Area			**Fishing**		**Seasonality**
Cruise	unfished	fished 1	fished 2	unfished	fished	
before (C1)	0.962	1.038		0.962	1.038	0.997
directly after (C2)	0.743	1.257		0.743	1.257	0.928
3 months (C3)	1.2	1.052	0.58	1.081	0.978	1.389
8 months (C4)	0.8	1.007	1.321	0.557	1.123	0.792
12 months (C5)	0.859	1.437	0.506	0.596	1.112	0.962
14 months (C6)	0.652	1.081	1.444	0.502	1.138	0.894

Two way crossed ANOSIM (factors: cruise/seasonality and fishing impact) showed a significant distinction between the unfished and fished areas in both: abundance and biomass data. This becomes even clearer looking at the pairwise test (Table 16.14).

Table 16.14. Results of two way crossed ANOSIM. R-values and significance level p [%] for the distinction of unfished and fished areas with abundance and biomass data of the epifauna

	Abundance		**Biomass**	
	R	**p [%]**	**R**	**p [%]**
Global	**0.51**	**0.1**	**0.47**	**0.1**
Unfished/Fished 1	0.50	0.1	0.46	0.1
Unfished/Fished 2	0.71	0.1	0.65	0.1
Fished 1/Fished 2	0.41	0.1	0.39	0.1

The difference between unfished and both fished areas was larger than between the fished areas. This is the case for abundance as well as biomass data. The fished area 2 showed a larger separation from the unfished area than from the fished area 1. To exclude seasonal effects, the data were analysed for each cruise separately to highlight the fishing effects.

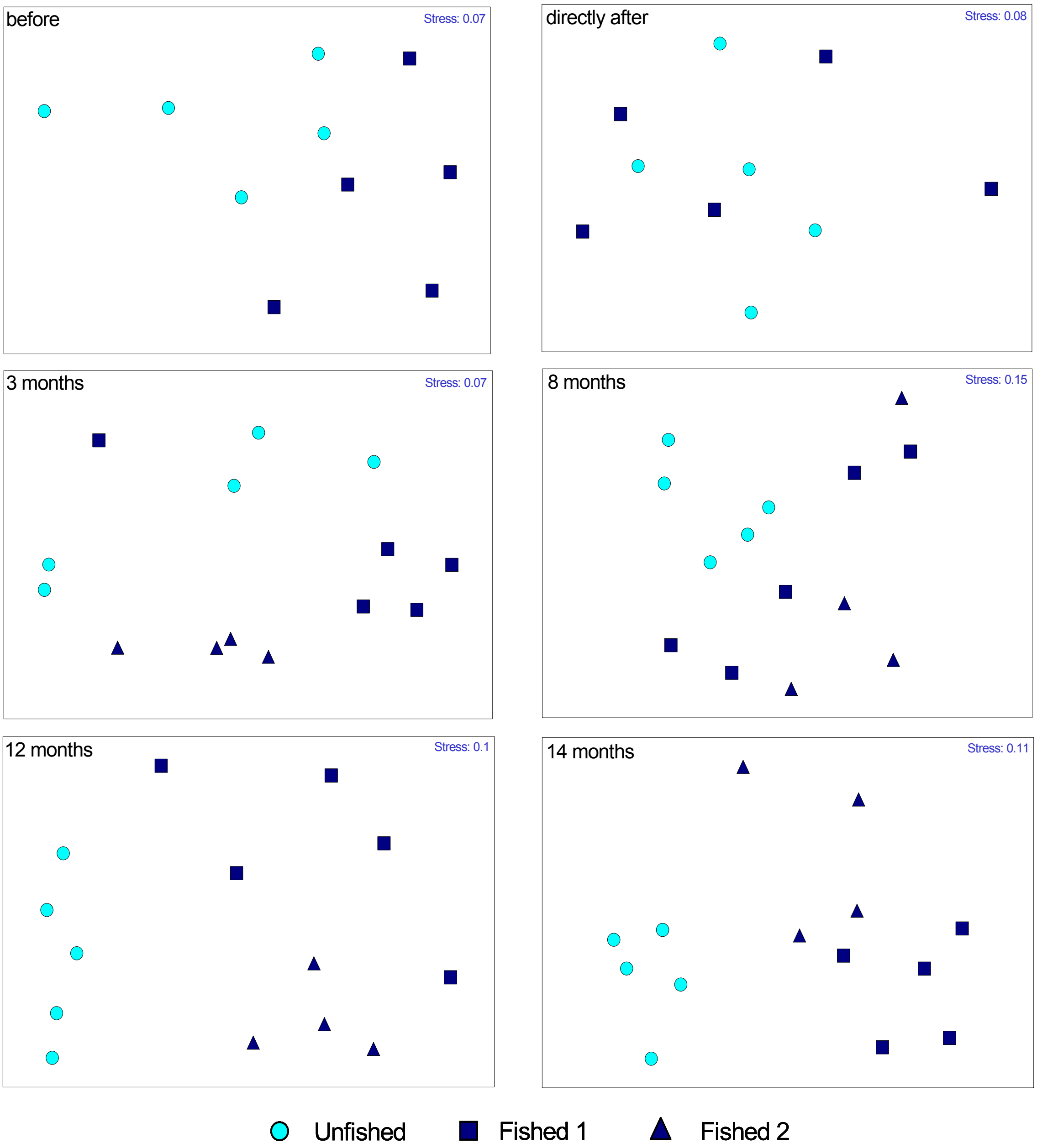

Figure 16.34. MDS-plot of epifauna abundance (Bray-Curtis-Index; transformation 4th root) during the study period (before until 14 months after closure)

The fauna of the unfished and fished areas was very similar during the first three cruises (Figure 16.34). Eight months after the closure, the fauna of the unfished area became significantly different. Especially 12 and 14 months after the closure of the platform area the benthic community of the unfished area is fully separated from both fished areas (Figure 16.34 and 16.35).

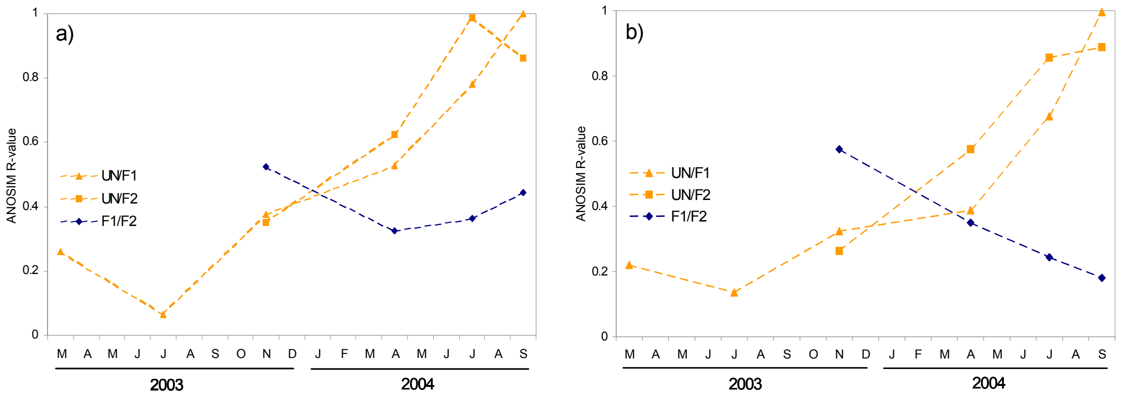

Figure 16.35. ANOSIM R-values of pairwise test for each cruise with a) abundance data and b) biomass data of epifauna species (UN = Unfished; F1 = Fished 1; F2 = Fished 2)

Figure 16.35 shows the distinction over the time of closure. The unfished area is increasingly separated from the fished areas, as well in abundance data (Figure 16.35.a) as in biomass (Figure 16.35.b). After 14 months of closure the value between unfished and fished area 1 reached even the highest distinction possible and communities are thus fully separated (Table 16.15).

Table 16.15. ANOSIM pairwise-test R-values and significance level p [%] for the distinction of unfished and fished areas with abundance and biomass data of the epifauna. Bold values significant at 1 %.

	Abundance			**Biomass**		
	UN/F1	**UN/F2**	**F1/F2**	**UN/F1**	**UN/F2**	**F1/F2**
	R ; p	**R ; p**	**R ; p**	**R ; p**	**R ; p**	**R ; p**
before	0.26 ; 5.6			0.22 ; 7.1		
directly after	0.06 ; 30.2			0.14 ; 19.8		
3 months	0.38 ; 4.0	0.35 ; 6.3	0.53 ; 3.2	0.32 ; 4.0	0.26 ; 10.3	0.58 ; 1.6
8 months	**0.53 ; 0.8**	**0.63 ; 0.8**	0.33 ; 8.7	0.39 ; 2.4	**0.58 ; 0.8**	0.35 ; 6.3
12 months	**0.78 ; 0.8**	**0.99 ; 0.8**	0.36 ; 4.8	**0.68 ; 0.8**	**0.86 ; 0.8**	0.24 ; 5.6
14 months	**1.00 ; 0.8**	**0.86 ; 0.8**	0.44 ; 1.6	**1.00 ; 0.8**	**0.89 ; 0.8**	0.18 ; 9.5

The same analyses carried out excluding the rather mobile fishes showed similar results: a clear distinction of unfished and fished areas, but the response was a little bit weaker (Tab. 16.16).

Table 16.15. ANOSIM pairwise-test R-values and significance level p [%] for the distinction of unfished and fished areas with abundance and biomass data of the epifauna. Bold values significant at 1 %.

	Abundance			**Biomass**		
	UN/F1	**UN/F2**	**F1/F2**	**UN/F1**	**UN/F2**	**F1/F2**
	R ; p	**R ; p**	**R ; p**	**R ; p**	**R ; p**	**R ; p**
before	0.36 ; 2.4			0.33 ; 3.2		
directly after	-0.1 ; 77.8			0.04 ; 37.3		
3 months	0.56 ; 1.6	0.38 ; 4.0	0.52 ; 2.4	0.47 ; 1.6	0.28 ; 5.6	0.54 ; 2.4
8 months	0.53 ; 0.8	0.61 ; 0.8	0.36 ; 5.6	0.59 ; 0.8	0.71 ; 0.8	0.61 ; 0.8
12 months	0.62 ; 0.8	0.90 ; 0.8	0.33 ; 3.2	0.39 ; 1.6	0.70 ; 0.8	0.13 ; 18.3
14 months	0.97 ; 0.8	0.84 ; 0.8	0.54 ; 0.8	1.00 ; 0.8	0.79 ; 0.8	0.38 ; 1.6

Correlations between the abiotic and epifaunal biotic data (BIOENV) showed, like for the infauna, that the main factor explaining faunal variability was the fishing effort (Table 16.17).

The correlation between the fishing effort and the fauna increased during the investigation and was highest 12 months after closure. While at the beginning of the study, several factors combined reached the highest correlations, at the end mainly fishing explained the distinction of fauna. In autumn 2003 and 2004 fishing effort was the main describing factor and correlations in autumn 2003 were higher whereas in 2004 it was lower than in summer.

Table 16.17. Results of the correlation I between abiotic data and the epifauna community (abundance and biomass data). Selection of abiotic factors which are responsible for the best correlation: 1: effort; 3: total organic carbon (%); 4: medium grain size (µm); 5: mud (%).

Cruise C1, before closure			
Abundance		**Biomass**	
R	Selections	R	Selections
0.315	1,3,5	0.241	1,5
0.301	3,5	0.229	1,3,5
0.275	1,3-5	0.227	1,3-5
0.275	1,5	0.218	1,4
0.250	1,3	0.212	1,3,4
Cruise C2, directly after closure			
Abundance		Biomass	
R	Selections	R	Selections
0.076	5	0.117	1
0.055	1	0.103	1,3-5
0.024	1,5	0.097	5
-0.069	1,3-5	0.064	1,4,5
-0.072	1,4,5	0.060	1,5

Cruise C3, 3 months after closure			
Abundance		Biomass	
R	Selections	R	Selections
0.155	1	0.156	1
0.093	1,5	0.117	1,5
0.064	1,4,5	0.095	1,4,5
0.046	1,4	0.079	5
0.042	5	0.076	4,5
Cruise C4, 8 months after closure			
Abundance		Biomass	
R	Selections	R	Selections
0.322	1	0.385	1
0.318	1,4	0.340	1,3
0.306	1,5	0.339	1,4
0.293	1,3	0.300	1,5
0.289	1,4,5	0.281	1,3,4
Cruise C5, 12 months after closure			
Abundance		Biomass	
R	Selections	R	Selections
0.698	1,3	0.523	1,3
0.624	1	0.485	1
0.558	1,3,4	0.460	1,3,4
0.536	3	0.368	1,3,5
0.536	1,3,5	0.363	3
Cruise C6, 14 months after closure			
Abundance		Biomass	
R	Selections	R Selections	
0.372	1	0.340	1
0.266	1,3	0.239	1,3
0.214	1,3,5	0.153	1,3,5
0.175	3	0.148	3
0.133	3,5	0.057	3,5

Community structure

The mean abundance of the epifauna varied in dependence on spatial and temporal variability and thus no clear differences between unfished and fished areas were found (Figure 16.36.a). Highest numbers of individuals were found in the fished area 2 twelve months after closure (11714 ± 3972 N/1000 m²). These high numbers were mainly due to the dominant species Ophiura albida.

The mean biomass increased in the fished areas. 12 and 14 months after the construction of the platform higher biomass in both fished areas was recorded (Figure 16.36.b). The higher biomass in the fished areas was caused by Echinodermata, Pisces and Arthropoda.

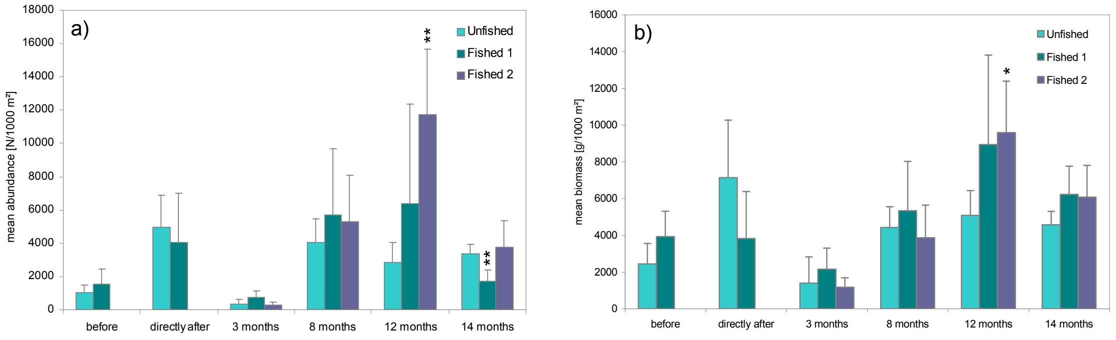

Figure 16.36. Mean abundance [1000 N/m²] (a) and mean biomass [g/1000 m²] (b) in the unfished, fished 1 and fished 2 areas in relation to time (before or after) of the platform installation. Significances tested with ANOVA (Significance level: * 0.05; ** 0.01)

While in the first year the biomass of the unfished area was varying with season, in the second year (8 months after closure) the biomass of this area stayed on a similar level (4429 to 5097 N/1000 m²).

The species number was generally lower in the unfished area over the time of investigation compared to the fished area 1 (Figure 16.37.a). Species density increased in the fished area 2 (November ’03: 12 ± 2 until September ’04: 25 ± 4 spp./per haul). The diversity and evenness varied throughout the first year in all areas due to species which showed seasonal patterns. But after the longest time of closure diversity and evenness in the fished area 1 increased, while values for unfished and fished area 2 nearly ended on the same level (Figure 16.37.b). Overall, both values in the unfished area varied less than those of the fished areas in the second year of investigation (Figure 16.37.b, c).

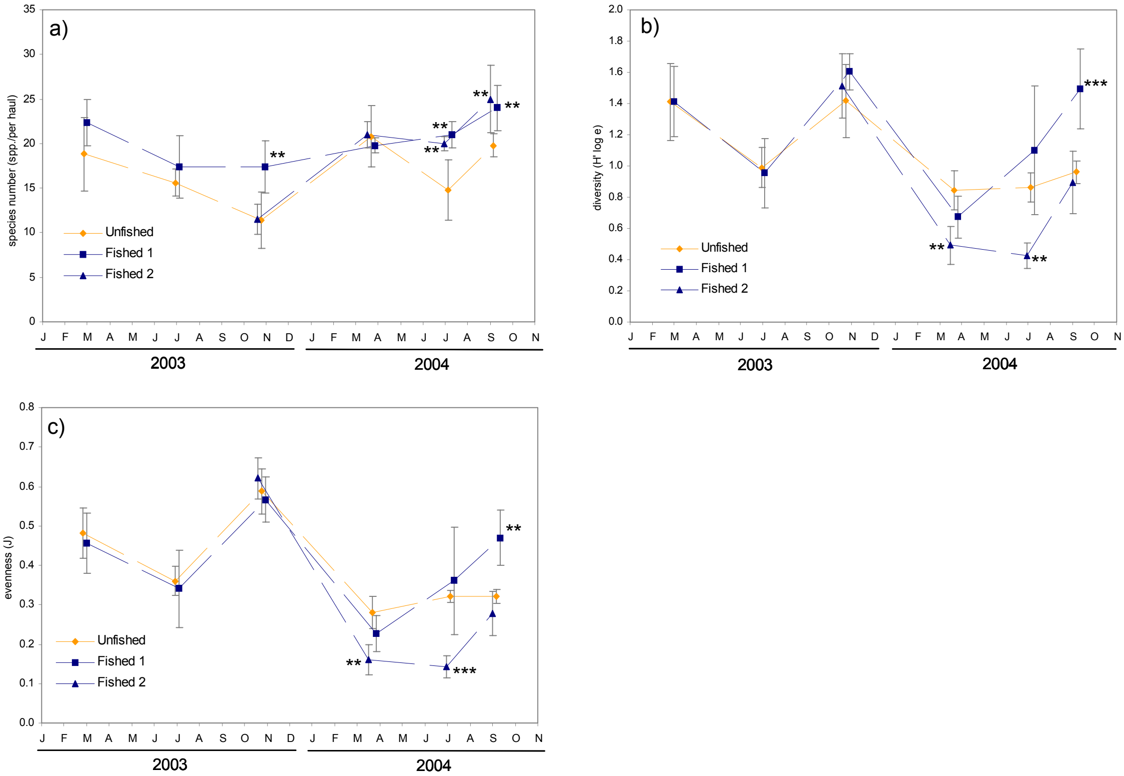

Figure 16.37. Mean species number (S) (a), mean diversity (H'loge) (b) and mean evenness (c) in the unfished, fished 1 and fished 2 areas during time of investigation. Significances tested with ANOVA (Significance level: ** 0.01; *** 0.001)

Taxonomic groups

The epifaunal community showed a clear separation of the unfished and fished areas after the longest time of closure. In order to detect the reasons for this development, taxonomic groups and functional groups were investigated to get out which groups were responding to the trawling activity.

The relation of the unfished and fished areas of mean Arthropoda abundance switched over time of closure (Figure 16.38.a): while during the first two cruises higher values in the unfished area were recorded, during all following cruises higher values in the fished areas, especially in the fished area 1 (maximum was 12 months after closure 428 ± 320 N/1000 m^2) were found.

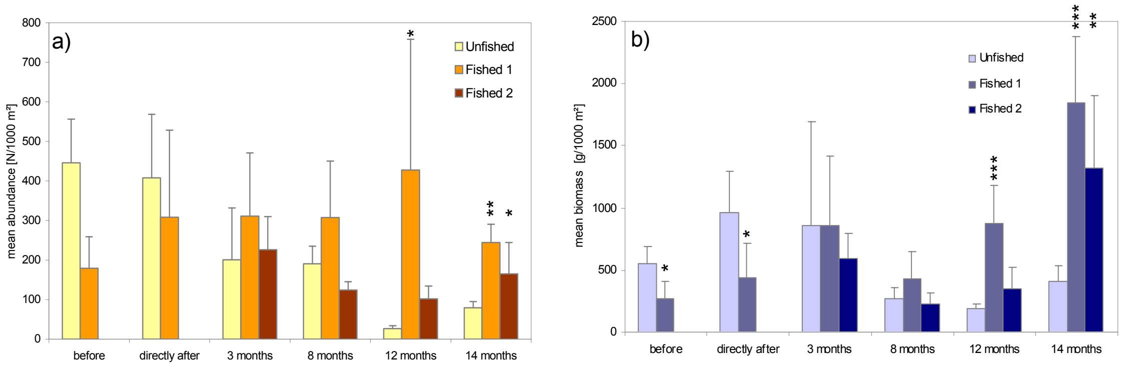

Figure 16.38. a) mean abundance [N/1000 m²] and b) mean biomass [g/ 1000 m²] of Arthropoda in the unfished and fished areas. ANOVA significance level: * 0.05; ** 0.01; *** 0.001

The biomass data showed the same trend (Figure 16.38.b). While during the first two cruises a higher biomass in the unfished area was recorded and stayed nearly on the same level since 3 months of closure, after 8 months (fished 1) resp. 12 months (fished 2) after the construction of the platform, the biomass was higher in those areas which were trawled.

Echinodermata showed generally high abundances (Figure 16.39.a). Highest values were recorded after 12 months of closure in the fished areas (fished 1: 5643 ± 5829 N/1000 m²; fished 2: 11351 ± 3899 N/1000 m²). These peaks are due to *Ophiura albida* which occurred in masses during this cruise. Biomass of Echinodermata was higher in fished area 1 before platform construction and from 8 months on after closure (Figure 16.39.b).

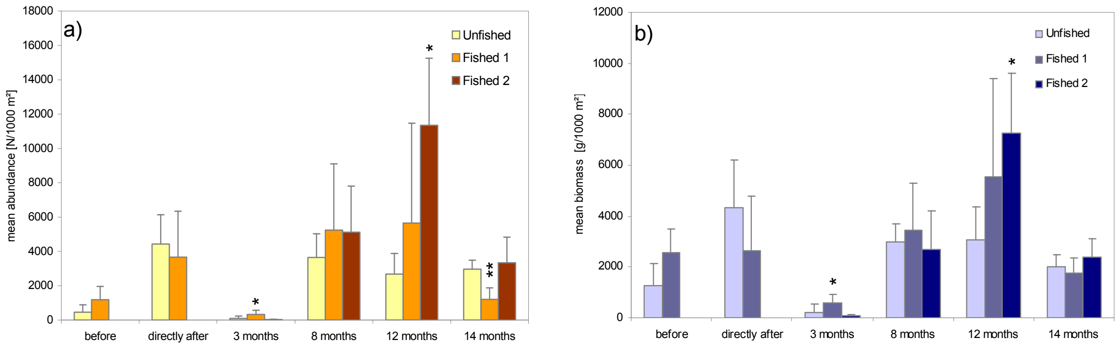

Figure 16.39. a) mean abundance [N/1000 m²] and b) mean biomass [g/ 1000 m²] of Echinodermata in the unfished and fished areas. ANOVA significance level: * 0.05; ** 0.01.

The fished area 2 showed higher values than the unfished area from 12 months on. Only directly after closure, the biomass as well as the abundance of Echinodermata was higher in the surrounding of the platform.

Molluscs (Figure 16.40.a, b) and the group of “others” (Figure 16.41.a, b) were rarely or not qualitative caught due to the gear type (beam trawl). Thus trends can not be reported of these groups as abundances show high variability at low values.

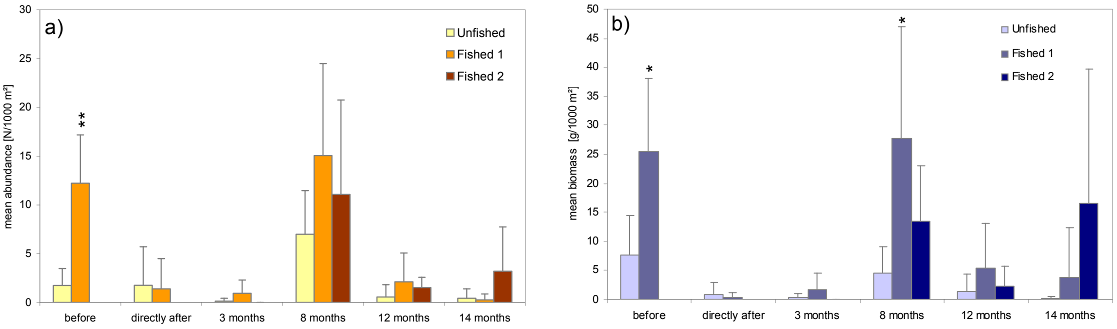

Figure 16.40. a) mean abundance [N/1000 m²] and b) mean biomass [g/ 1000 m²] of Mollusca in the unfished and fished areas. ANOVA significance level: * 0.05; ** 0.01.

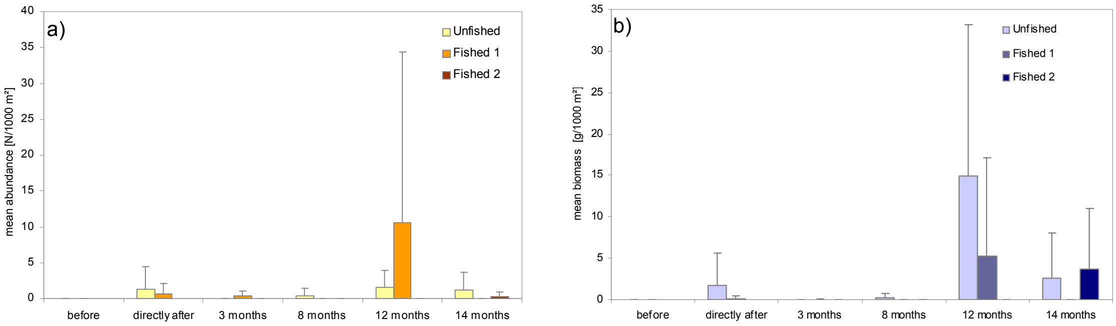

Figure 16.41. a) mean abundance [N/1000 m²] and b) mean biomass [g/ 1000 m²] of “others” in the unfished and fished areas. (no significant differences)

Fishes generally showed higher numbers at the longest time of closure but independent to fished and unfished area (12 and 14 months, Figure 16.42.a). Only biomass data indicated higher wet weight in the fished area 1 after 8 months of closure and 12 months for fished area 2 (Figure 16.42.b).

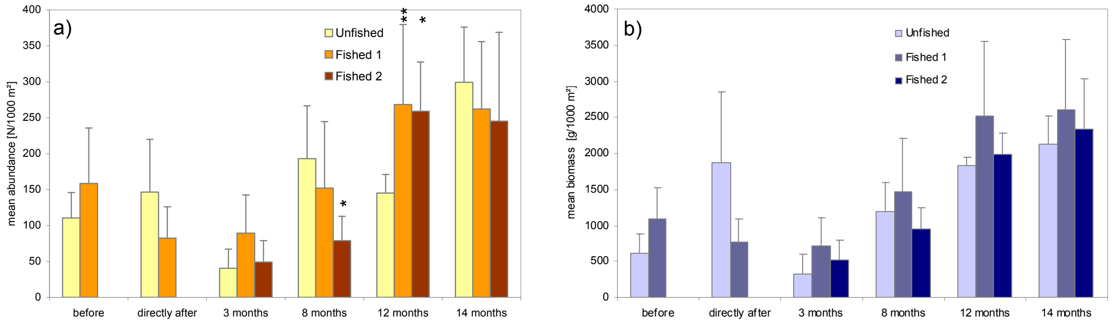

Figure 16.42. a) mean abundance [N/1000 m²] and b) mean biomass [g/ 1000 m²] of Pisces in the unfished and fished areas. Significances tested with ANOVA (Significance level: * 0.05; ** 0.01)

Functional groups and main discriminating species

Analyses of functional groups showed a clear response to fishing disturbance (Table 17). Species which are highly mobile and have a low or medium vulnerability are more abundant in the fished area 8 and 12 months after closure. Only 14 months after closure the abundance of this group is significantly higher in the unfished area. The same development shows the predator/scavenger and omnivorous species.

Table 16.18 Analyses of functional groups of the epifauna. Significances tested with ANOVA (Significance level: * 0.05; ** 0.01; *** 0.001). U = higher abundance in the unfished area; F = higher abundance in the fished area. 1),2),3) and 4) = significant difference between fished areas with F1 = higher abundance in fished area 1 and F2 = higher abundance in fished area 2

		Time of closure									
		before	**directly after**	**3 months**		**8 months**		**12 months**		**14 months**	
		UN/F1	UN/F1	UN/F1	UN/F2	UN/F1	UN/F2	UN/F1	UN/F2	UN/F1	UN/F2
Feeding	detritus feeder										
	suspension feeder	F**									
	predator/scavenger; omnivorous species								F**	U**1)	
Position	surface								F**	U**1)	
	subsurface	F*								F*4)	
Mobility	highly mobile						U*1)	F***3)	F*3)		
	mobile			F*3)					F**3)	U**1)	
	sedentary	F**									
Vulnerability	high										
	low			F3)					F**3)	U**1)	
	medium						F*2)	F***3)	F*3)		

1) F1/F2: F2** 2) F1/F2: F1** 3) F1/F2: F1* 4) F1/F2: F2*

While there were in general more omnivorous species and predator/scavenger in the fished areas in the second year of investigation (Figure 16.43.), there was no clear tendency for detritus and filter feeder in the different areas, neither for abundance nor for biomass data. While in the fished area 1 there were more omnivorous species (12 months: 421 ± 322 N/1000 m²; 14 months: 232 ± 46 N/1000 m²), in the fished area 2 there were more predators and scavengers (8 months: 5306 ± 2730 N/1000 m²; 12 months: 11617 ± 3949 N/1000 m²; 14 months: 3597 ± 1593 N/1000 m²). But both feeding types were more abundant in the fished areas at least 8 – 12 months after closure. Most of the predators/scavengers and omnivorous species are arthropods or echinoderms.

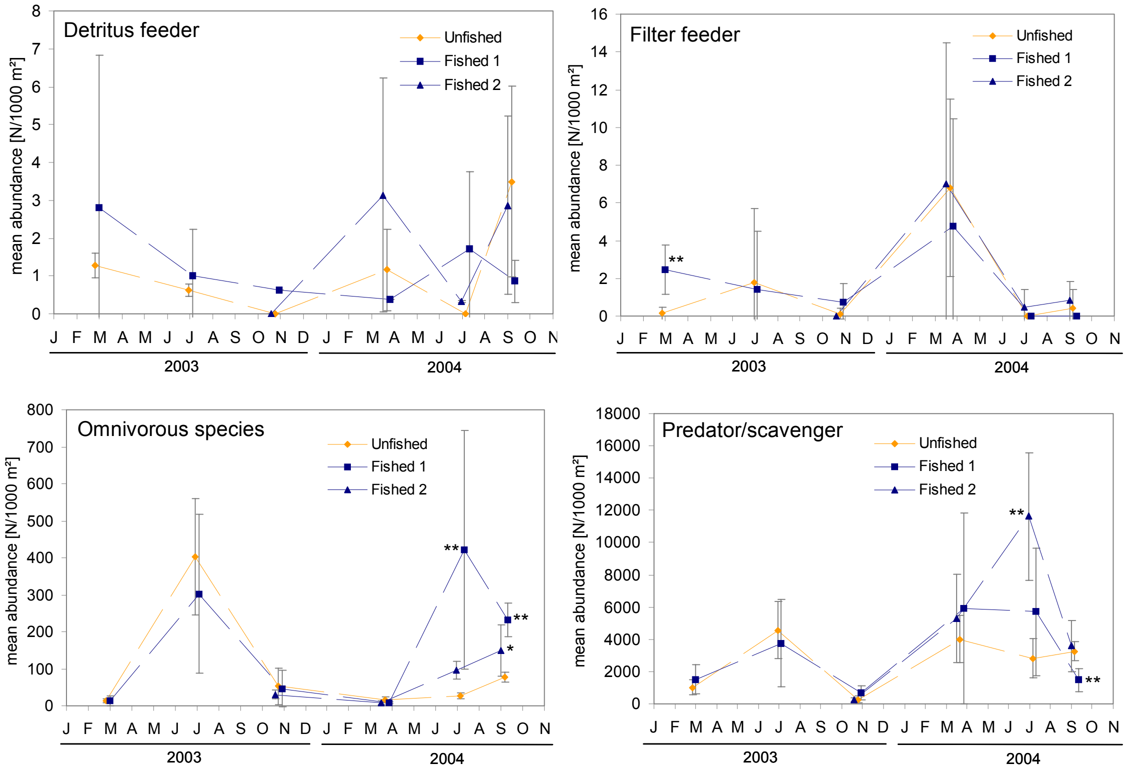

Figure 16.43. Mean densities [N/1000 m²] of feeding groups of epifauna. Significances tested with ANOVA (Significance level: * 0.05; ** 0.01)

This is linked to some single species which are shown in Figure 16.44. *Liocarcinus holsatus* and *Pagurus bernhardus* show a positive response to fishing activity with higher abundances in the fished area after 12 months of closure. *Crangon Crangon* (predator/scavenger) showed also a clear positive response to trawling (higher numbers of individuals in the fished area). The response of *Ophiura albida* seems to be more dependant on the seasonality but shows in general also a positive response to the fished area.

Table 16.19. summarises the differences between the fished and unfished area. The two fished areas are pooled to see the main change due to fishing disturbance.

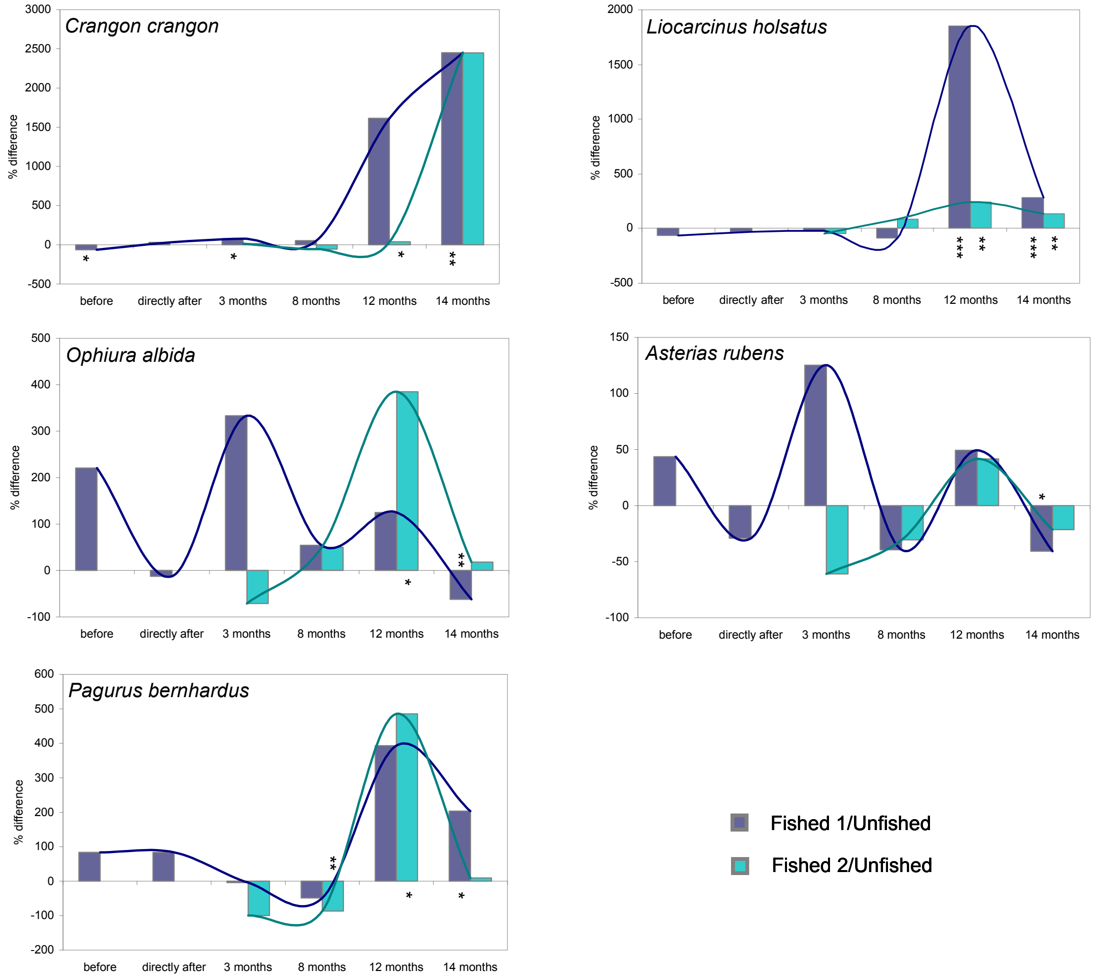

Figure 16.44. Percentage difference between fished and unfished areas of main discriminating species. ANOVA significance level: * 0.05; ** 0.01; *** 0.001. Positive values indicate higher values in fished area

Table 16.19. Percentage differences between unfished and fished area (mean value of fished area 1 and fished area 2) of the main discriminating epifaunal groups and species. Positive values indicate higher values in fished area. ANOVA significance level: * 0.05; ** 0.01; *** 0.001.

	Time of closure					
	Before	**Directly after**	**3 months**	**8 months**	**12 months**	**14 months**
Taxonomic groups						
Echinodermata	156.4	-17.2	114.4	42.2	205.1	-27.4
Arthropoda	-59.7**	-24.4	36.0	18.3	952.1***	163.2**
Feeding type						
Predator/scavenger; omnivorous species	50.1	-18.6	62.2	37.4	205.9*	-21.7
Species						
Liocarcinus holsatus	-58.8	-25.7	-31.3	-9.3	1137.7***	216.8**
Crangon crangon	-63.8**	31.4	49.2	5.3	912.3	2449.7
Ophiura albida	220.4*	-12.5	153.4	52.2	240.7	-26.5
Asterias rubens	43.6	-29.2	42.5	-35.5	45.9*	-32.2
Pagurus bernhardus	83.8	-34.7	-46.8	-65.8*	434.1*	117.0

Photo and Video

Like the epifauna caught with beam trawls, the photo and video data showed a high seasonality. The species of the dominant taxa (Table 16.20.) showed a high variability in abundance due to seasonality.

Table 16.20. Top 5 dominant taxa from photo and video data [N/20 m²], x = no photos taken during this cruise

	C1	C2	C3	C4	C5	C6	C7
Photo							
Ophiuroidea	95	827	735	266	324	x	100
Pomatoschistus spp./*Callionymus* spp.	15	19	49	4	6	x	22
Asterias rubens	6	54	14	7	12	x	14
Liocarcinus spp.	2	21	5	0	6	x	1
Crangon spp.	2	0	21	0	0	x	1
Video							
Ophiuroidea	22	120	83	52	371	80	79
Asterias rubens	6	18	11	9	25	5	12
Pomatoschistus spp./*Callionymus* spp.	4	1	19	5	11	4	5
Liocarcinus spp.	1	8	3	1	5	4	0
Crangon spp.	1	0	6	0	0	0	0

Two-way crossed ANOSIM tests of photo and video data confirmed that seasonal factors (photo: Global R=0.72; p=0.1%; video: Global R=0.80, p=0.1%) have a higher influence on the epibenthic community structure than fishing impact (Table 16.21.).

Table 16.21. Results of two way crossed ANOSIM. R-values and significance level p [%] for the distinction of unfished and fished areas with photo and video data

	Photo		**Video**	
	R	**p [%]**	**R**	**p [%]**
Global	**0.64**	**0.1**	**0.42**	**0.2**
Unfished/Fished 1	0.25	9.1	0.57	1.1
Unfished/Fished 2	1.00	3.7	0.35	7.4
Fished 1/Fished 2	0.92	3.7	0.40	7.4

Photo and video data showed no clear distinction between unfished and fished areas. Only with photo data the fished area 2 was separable but from the unfished area as well as from the fished area 1 (Table 16.21.; Figure 16.45. and 16.46).

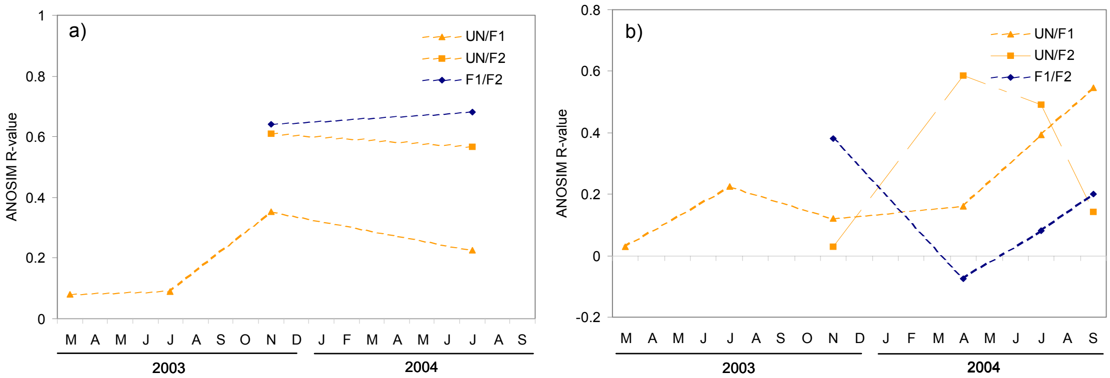

Figure 16.45. ANOSIM R-values of pairwise test for each cruise with a) photo data and b) video data of epifauna species (UN = Unfished; F1 = Fished 1; F2 = Fished 2)

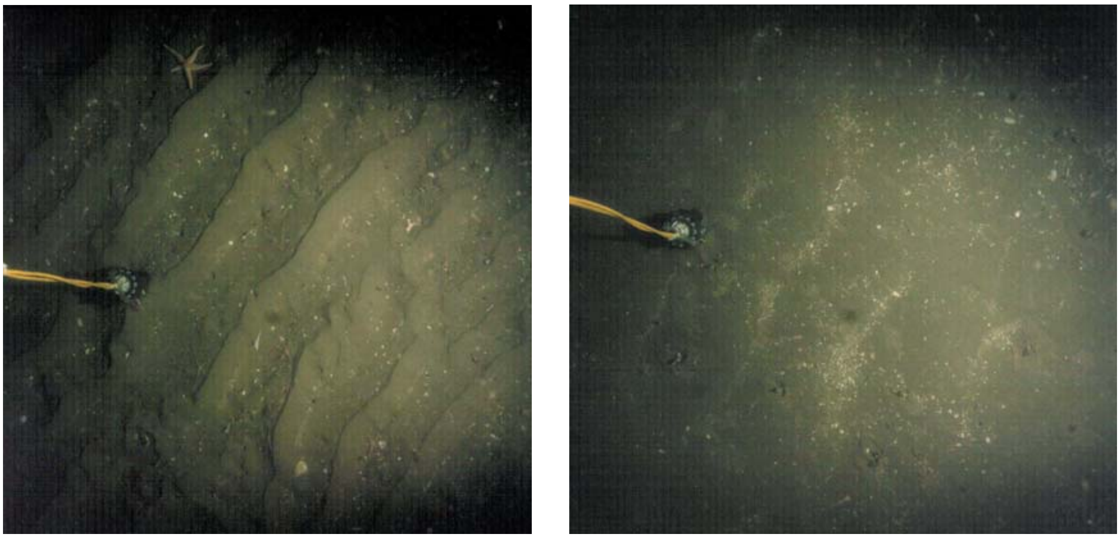

Figure 16.46. Two following photos in the fished area 2 (distance ~14 m). Left side: normal state with ripple structure and epifauna, right side: probable fresh trawl track with featureless sand bottom and absence of epifauna.

Amongst the most abundant species (Figure 16.47.), Liocarcinus spp. and Ophiuroidea were primarily responsible for differences between areas. But the percentage difference between unfished and fished areas showed inconsistent results depending on the method (photo and video data, Figure 16.47.7).

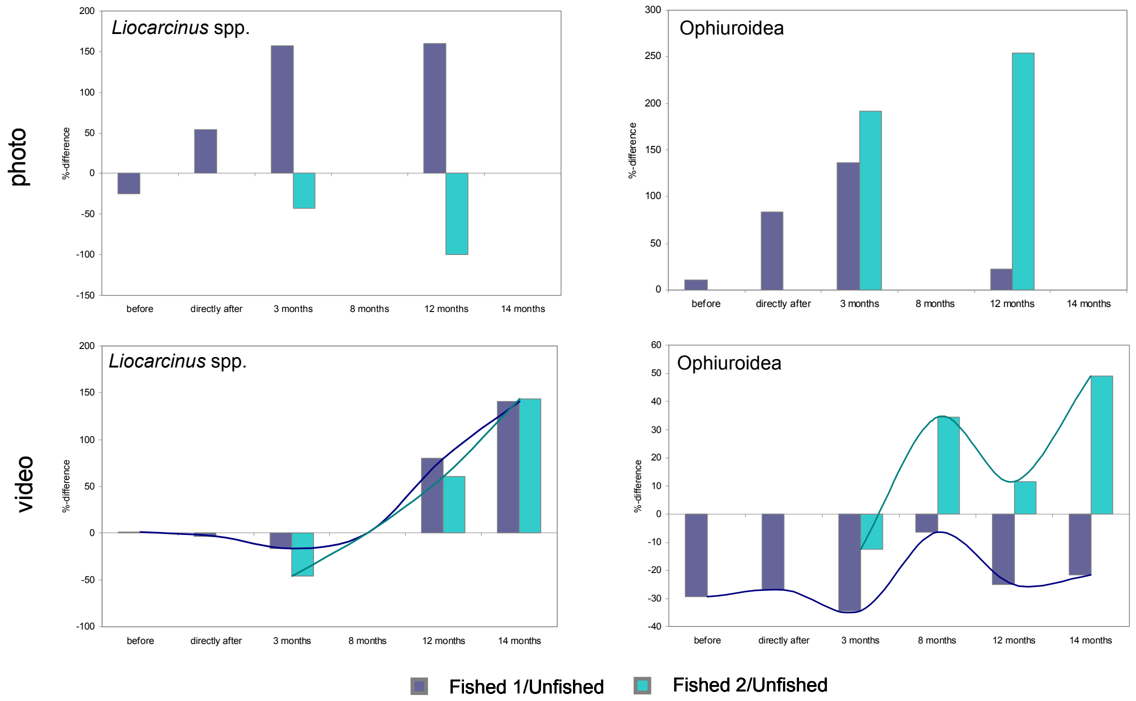

Figure 16.47. Percentage difference between unfished and fished areas of main discriminating species of video and photo data. Positive values indicate higher values in fished area

While Ophiuroidea analyzed by photo showed a positive response to fishing impact in both fished areas, video data showed a positive response only for the fished area 2. The same results were recorded for *Liocarcinus* spp. which showed a positive response to fishing with video for both fished areas, while analyses with photo showed a negative response to fishing for the fished area 2 with lower abundances in this area.

Discussion

Benthic community in the ASA

The community found within the North Sea ASA is a typical *Tellina-fabula*-community (sensu Salzwedel et al. 1985). In its present form, the benthic fauna of the German Bight is not only well adapted to natural disturbances and seasonal influences but also shaped by numerous anthropogenic effects. Long-term investigations indicated that benthic communities in large parts of the North Sea generally showed an increase in biomass and a change in community structure with a dominance of opportunistic short-lived species and a decrease of long-living sessile organisms over the 20th century (Duineveld et al. 1987, Rachor 1990, Kröncke 1992, 1995, Witbaard & Klein 1993, Rumohr et al. 1998, Schröder 2003). Also in the present study the community is dominated by organisms with short life cycles, most of which can be considered opportunistic species (e.g. *Phoronis* spp., *Spiophanes bombyx*, *Lanice conchilega*, Nemertini, *Ophiura albida*, *Asterias rubens*, *Crangon crangon* and *Liocarcinus holsatus*). How far exactly these changes were caused by natural or anthropogenic factors can not be precisely determined. But demersal fishery has become a key factor causing or at least affecting the detected changes of the benthic fauna of the North Sea (Groot & Lindeboom 1994).

Temporal variability

Seasonal variability is the most prominent feature of the benthic fauna in the investigation area. The community in summer and early autumn was clearly distinct from that in spring and late autumn. Additionally, the spatial variability was higher in spring and autumn than in summer. The larval spat fall of a few species in high densities over wider areas renders the community more homogenous. The link between the benthic community structure and the natural annual cycle is confirmed by the BIOENV analyses, showing the highest correlation between fauna and bottom temperature – a proxy for seasonality.

In addition to the seasonal differences, a strong interannual variability was observed. Infauna abundance appeared lower in the second year of investigation, while epifaunal abundance and biomass was higher than in the first year. While the infaunal community of the second year formed only one cluster of summer and early autumn cruise, in the first year the fauna of the summer is distinct. This is due to the recruitment of *Phoronis* spp. in summer 2003, which is known to have a two year spawning cycle (Niermann 1996). In summer 2004 the total abundance of organisms was the highest of the study period which can be linked to the recruitment of ophiuroids and several polychaetes.

These intra- and interannual changes caused even shifts in the numerical dominance of the major taxonomic groups. While the infauna was dominated by polychaetes during spring 2003, *Phoronis* spp. took over for the next three cruises and at the end of the investigation polychaetes regained the dominant position. However, within both years, all community indices of in- and epifauna showed this seasonal variability.

Response to cessation of fishing activity

Besides the natural spatio-temporal variability of the fauna, the community of the unfished and fished areas developed differently. The separation was in general increasing with time, more clearly in the epifauna than in the infauna. Beyond seasonality, the fishing effort represented the main explaining factor for faunal changes.

The influence of fishing comprises three different aspects, each contributing its share to the development of the separation of the areas. From the analyses of the fishing activity and effort, it seems that there are three main aspects influencing the development of the fauna:

The closure of the platform area

Due to the closure of the platform area, the fauna within this area got the chance to recover from fishing disturbance. This aspect remains over the whole time of the investigation and is considered the mayor one.

The seasonal variability of the fishing activity

The fishing effort within the ASA is not continuously the same, neither within one year (high activity in summer – low activity in winter) nor between the years (higher fishing activity in 2004).

The spatial variability of the fishing activity

The trawling activity within the ASA is not spatially homogenously distributed. In both years fished area 2 (F2) received a higher trawling intensity than fished area 1 (F1). The quantification of differences between unfished and fished benthic communities is not only complicated by the natural spatio-temporal variability of benthic communities, but further by the spatially not homogenously distributed fishing activity. In addition to that, not only the total amount of trawling during one year is decisive for the impact on the benthic community, but also the timing of the disturbance and temporal spread. It is more than likely that the same kind of disturbance will produce different effects when exerted during different seasons.

However, the effects are also dependant on the type of benthic community, which is reflected in the differential response of infauna and epifauna to the cessation of fishing in the present study.

Infauna

Because of its more or less sessile lifestyle, the infauna is not able to respond actively to the fishing disturbance. The response of the infaunal community is therefore rather indirect, e.g. by a stronger settlement or survival in the unfished area.

The cessation of fishing resulted particularly in higher abundances of filter (mainly Phoronis spp.) and detritus feeders (several polychaetes and some amphipods), mainly tube building worms, which live subsurface and sedentarily. Furthermore, all these species which benefit from the closed area are classified as highly or medium vulnerable to fishing disturbance.

The distinction of the areas (as reflected by the ANOSIM R-values) followed the seasonal pattern induced by settlement. In both years an increasing distinction between the areas followed the recruitment of some species. In summer 2003 Phoronis spp. was the main dominant taxon in the unfished areas and the distinction remains high in autumn due to this massive dominance. This resulted also in lower values of evenness and consequently diversity (H’) in the unfished area. In the summer of 2004 several polychaetes settled again predominantly in the unfished area and increased the difference to the community in the fished areas. The abundance of many polychaetes remained higher in the unfished area until the end of the investigation.

Excluding the seasonal variability by analysing each cruise separately, the fishing effort becomes one of the most explanatory factors for the multivariate similarity of the fauna (BIOENV). During the first two cruises, two factors explain most of the variability of the fauna (fishing and mud content or median grain size), thenceforward the fishing activity is the single factor explaining the highest proportion of the faunal variability. Any addition of further factors only decreases the fit. The sole exception was spring 2004 when the median grain size was the strongest single effect.

The separation of the unfished and fished areas may be seen as a result of a reduced chance to settle under high fishing intensity leading to a higher recruitment success in the unfished area. It is not surprising that this first gives a chance to opportunistic species. All species with considerable differences in abundance between unfished and fished areas are opportunistic and have a short lifecycle. However, this is contrary to the theoretically expected development to large and long-living species in undisturbed areas (Pearson & Rosenberg 1978). Within an environment like the German Bight with its fauna generally dominated by a short living opportunistic species (Frid et al. 2000, Wieking & Kröncke 2003), these also have the largest chance to reach a dominant position when a suitable habitat becomes available. On the other hand, the benthic fauna of the North Sea is probably also altered by chronic but patchy trawling (Jennings et al. 1999) and does not only reflect a community adapted to a variable environment. The succession towards a mature community with longer lived species will take much longer, not only because these species need more time to grow, but also because their production of offspring is smaller.

Several species show significantly higher densities in the unfished area towards the end of the study (e.g. *S. bombyx*, *Owenia fusiformis*, *Nemertini*, *Chaetozone cf. setosa* and *Spio decoratus*). Due to the higher spatial variability of the fauna in the fished areas in autumn, some of these differences were no longer statistically significant. The observed small-scale variability of trawling intensity might have contributed to the spatial variability of the fauna especially in F1, while sampling locations in F2 are closer together and probably received about the same fishing intensity. However it may also be seen as a result of the considerably higher fishing intensity in F2 compared to the unfished area but also to F1.

However, not only the spatial variability of the community is lower in the unfished area, also the temporal variability decreased. The similarity of the fauna between the stations of the unfished area was higher and the abundance and especially the biomass of the infaunal community remained more stable over the course of 2004 in the unfished area. The larger faunal variability within the fished areas may thus be seen as results from the spatial and temporal variability of fishing activity in the trawled areas.

Overall, the infauna showed a weaker distinction of the unfished and fished area over time than the epifauna. Effects were mostly observed in the density of organisms, as total biomass followed mainly the occurrence of the heart urchin *Echinocardium cordatum*, a species which is known to have a high spatial variability (Buchanan 1966). However, even if the separation of the community between unfished and fished areas is low, it is still larger than the spatial variability in the fished areas, which themselves are no more distinguishable at the end of the investigation.

Epifauna

For the epifauna mobility and feeding type seem to be the main aspect determining the response to the fishing disturbance respectively the closure of the platform area. The main change of the epifauna is a shift in the community structure. A larger number of predators and scavengers as well as omnivorous species were found in the fished areas in the second year, especially in summer (*Liocarcinus holsatus*, *Crangon crangon*, *Pagurus bernhardus*, *Asterias rubens* and *Ophiura albida*).

Mobile epifaunal species are able to react behaviourally to spatial differences and actively move to preferable areas. During high fishing season, the supply of damaged and discarded organisms from bottom trawling presents an ample food supply to predators and scavengers. These actively move to recently trawled areas to search for food (Ramsay et al. 1998, Groenewold & Fonds 2000, Rumohr & Kujawski 2000, Ramsay et al. 2001) and consequently leave the unfished area. This decreases the time until a clear distinction of the unfished and fished community can be found, in abundance as well as in biomass data.

Besides, this interpretation explains why some species are found to have significantly different densities in the unfished and fished area only during summertime. Predators and scavengers, as well as all arthropods in general, showed on average a higher abundance in the fished areas but significant differences were found only 12 months after closure, thus within the high fishing season.

This effect of the closure is supported by the results of the BIOENV-routine. While during the first two cruises 2 – 3 factors explain the distinction (mud content in combination with fishing intensity or TOC), thenceforward the fishing intensity is the main explaining factor with the exception of summer 2003, when the highest correlations at all were found caused by fishing intensity and TOC. However, the difference in TOC between the sampling areas may also be influenced by the trawling activities itself. While a dense filter and deposit feeding benthic fauna can continuously utilise the incoming organic material in the unfished area, in the heavily fished areas, this fauna is sparse and a higher proportion of the organic material is retained in the sediment.

The observation that predators and scavengers profit from the by-catch and discards of fishing and feeding on damaged or dead benthic species hit by the gear is nothing new

(Arntz & Weber 1970, Rauck 1989, Kaiser & Spencer 1994, Kaiser & Ramsay 1997, Kaiser 1998, Ramsay et al. 1998, Philippart 1998, Groenewold & Fonds 2000). Groenewold & Fonds (2000) found that dead fish was rapidly consumed by epibenthic scavengers such as swimming crabs, hermit crabs and starfish, while damaged invertebrates like bivalves, sea urchins and crabs are more consumed by the demersal fish fauna. Fish bait within traps had been consumed during hours by shrimps. Omnivorous species are also attracted by the supplementary food source, as e.g. brittle stars show a strong attraction to fish bait (Nagabhushanam & Colman 1959), although they are usually known as micro-carnivores or detritus feeders. This means that in general these feeding groups are well adapted to variability of community structure as they can switch their feeding habit and use additionally food sources. The intensive fishing may thus have contributed to the general characterisation of the epifauna of the German Bight and the southern North Sea as a scavenging one (Groenewold & Fonds 2000).

On the other hand, in periods with low fishing activities the behaviour may change. During winter, fishing activity is very low and the additional food source produced by bottom trawling does not play an important role. The lower abundance of predators and scavengers in the unfished area may thus only be a seasonal effect, especially in such a small area.

However, fishing activity was not only found to be variable within one year, differences between the years can be also stated with higher fishing effort in 2004. Mobile predators, scavengers and omnivorous species (e.g. brittle stars) showed as well a stronger increase in the fished areas during the second year. Whether the higher abundance of predators and scavengers can be linked to the higher fishing effort in 2004 or the other way around remains dubious.

The response to the cessation of trawling disturbance is also strongly tied to the spatial fishing variability between both fished areas. As mentioned before, F2 is more heavily trawled than F1 in both years. The corresponding answer of the fauna is a lower evenness and diversity in F2. But the variability between both fished areas made it difficult to find significant differences to the unfished area. For example, the biomass is generally higher in the fished areas, but no significances could be stated due to the high variability of the fished areas.

The response of the epifauna is a clear response to the cessation of fishing activity. The development of the community structure is coupled with the seasonal fishing variability, the ability to react directly on different intensities of fishing, the feeding habit and the capability to use a large variety of food sources. One aspect of the closure is a reduction of the seasonal variability of the fauna. In the first year several community indices followed a strong seasonal pattern (total density, biomass, diversity and evenness) in all areas. In 2004 the fauna of the unfished area was less variable compared to the fished areas, which might also be linked to the seasonal variability of fishing.

Photo and Video

Quantitative analysis of the epibenthic communities based on optical methods showed no consistent differences between unfished and fished areas. Only the fauna of F2 showed a clearly separable community. Omnivorous or scavenging species such as Liocarcinus spp. and Ophiuroidea were generally observed in higher abundances in the fished areas.

Like the epifauna investigated by beam trawls, a response to the high trawling disturbance in F2 was also observable on photos and videos. However, while significant differences have been obtained with beam trawl samples, the limiting factor in this study with optical methods must be attributed to the small scale of sampling accomplished with imaging methods (Cranmer et al. 1984, Piepenburg & Von Juterzenka 1994) and the high degree of spatial variability. This effect is even stronger for the photo sampling with its smaller scale, whereas results from video were more similar to those from beam trawl sampling. Further fishing impact studies using imaging methods should therefore provide a larger spatial scale despite the additional analysis efforts this entails. Nevertheless, imaging methods provide an overview of the natural bottom habitat and may even reveal interesting features such as possible trawl tracks (see Figure 16.46.).

Conclusions

During the time of this study, the community structure of the protected area developed distinct differences to that in the fished areas. Predators and scavengers showed significantly higher abundances in the fished area especially towards the end of the investigation time. In consequence, biomass was also higher in the fished areas as many mobile species like swimming crabs, brown shrimps, sea stars, brittle stars and hermit crabs may have been attracted by discards and organisms physically damaged by fishing gears. For other mobile species with a higher vulnerability the size of the protected area may have been to small to produce observable effects.

However, these responses are coupled with seasonal effects and spatial variability which have profound influences on the infaunal community structure of the North Sea. A high spatial variability within the areas and between the two fished areas makes the distinction of fishing effects from natural spatial variability more difficult. This spatial variability may in part also be an effect of the fishing, which is itself not homogeneously distributed in the investigation area.

On the other side, several sedentary species, especially tube building worms, which are filter or detritus feeders, showed significantly higher abundances in the unfished area following the cessation of fishing. These species are permanently disturbed by the scratching and ploughing of the seabed, probably most importantly during the settlement phase. Generally known as opportunistic species, they may have very rapidly benefited from the closure. Contrary to the expected recovery of long-living species, this led to an increased dominance of opportunists and consequently lower values of evenness and diversity indices in the unfished area. This can be seen as a first step from a heavily disturbed community towards some intermediate successional state still dominated by opportunistic species.

The further development towards a more mature community of long-living larger species will require a much longer time span and a larger scale. However, we do not even know how this undisturbed community would look like. The present benthic fauna of the German Bight is not only well adapted to seasonal influences but also shaped by numerous anthropogenic effects for a long time. Real changes in the community composition towards an undisturbed state can not be expected in short term and on small spatial scales.

Most differences observed so far represent rather trends than final conclusions. Especially for the infauna the development in response to the cessation of fishing seems just at the beginning after one year of closure. Long-living species which are predicted to suffer most from frequent disturbances, will need a longer time span to establish vital populations. This suggests that a longer time of closure is necessary to record a steady recovery from the impact of fishing.

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Annex I. 16

List of infaunal and epifaunal taxa in the investigation area; x marks occurrence in the grab or beamtrawl

Group	Class	Order	Family	Species	Infauna	Epifauna
Arthropoda	Crustacea	Amphipoda	Caprellidae	*Pariambus typicus*	x	
				Phtisica marina	x	
			Ampeliscidae	*Ampelisca brevicornis*	x	
				Ampelisca tenuicornis	x	
			Amphilochidae	*Amphilochus neapolitanus*	x	
			Aoridae	*Aora gracilis*	x	
			Argissidae	*Argissa hamatipes*	x	
			Atylidae	*Atylus falcatus*	x	
				Atylus swammerdami	x	
			Calliopiidae	*Apherusa ovalipes*	x	
			Corophiidae	*Siphonoecetes krøyeranus*	x	
			Haustoriidae	*Bathyporeia elegans*	x	
				Bathyporeia guilliamsoniana	x	
				Bathyporeia tenuipes	x	
				Urothoe poseidonis	x	
			Isaeidae	*Microprotopus maculatus*	x	
				Photis longicaudata	x	
			Ischyroceridae	*Jassa falcata*	x	
			Leucothoidae	*Leucothoe incisa*	x	
			Lysianassidae	*Acidostoma obesum*	x	
				Orchomene nana	x	
			Megaluropidae	*Megaluropus agilis*	x	
			Melitidae	*Abludomelita obtusata*	x	
			Oedicerotidae	*Perioculodes longimanus*	x	
				Pontocrates altamarinus	x	
				Pontocrates arenarius	x	
				Synchelidium maculatum	x	
			Stenothoidae	*Stenothoe marina*	x	
		Cumacea	Bodotriidae	*Bodotria scorpioides*	x	
				Iphinoe trispinosa	x	
			Diastylidae	*Diastylis bradyi*	x	
				Diastylis laevis	x	
				Diastylis rathkei	x	
			Leuconidae	*Eudorella truncatula*	x	
			Pseudocumatidae	*Pseudocuma longicornis*	x	
				Pseudocuma similis	x	
		Decapoda	Callianassidae	*Callianassa subterranea*	x	
				Callianassa tyrrhena	x	
			Cancridae	*Cancer pagurus*		x
			Corystidae	*Corystes cassivelaunus*	x	x
			Crangonidae	*Crangon allmani*	x	x
				Crangon crangon	x	x
				Philocheras bispinosus	x	
				Philocheras trispinosus	x	
			Galatheidae	*Galatea* spp.	X	
			Leucosiidae	*Ebalia cranchii*	x	x
				Ebalia tumefacta		x

Annex I: Species list – continued

Group	**Class**	**Order**	**Family**	**Species**	**Infauna**	**Epifauna**
			Majidae	*Hyas* spp.		**x**
				Macropodia spp.		**X**
				Macropodia rostrata	**x**	
			Paguridae	*Pagurus bernhardus*	**x**	**x**
			Pandalidae	*Pandalus montagui*		**x**
			Porcellanidae	*Pisidia longicornis*	**x**	**x**
			Portunidae	*Liocarcinus arcuatus*		**x**
				Liocarcinus depurator	**x**	**x**
				Liocarcinus holsatus	**x**	**x**
			Processidae	*Processa* spp.		**X**
				Processa modica	**x**	
				Processa nouveli holthuisi	**x**	
			Thiidae	*Thia scutellata*	**x**	
			Upogebiidae	*Upogebia deltaura*	**x**	
		Mysidacea	Mysidae	*Gastrosaccus spinifer*	**x**	
		Pantopoda	Ammotheidae	*Achelia chinata*	**x**	
			Nymphonidae	*Nymphon brevirostre*	**x**	
				Nymphon gracile	**x**	
			Phoxichilidiidae	*Anoplodactylus petiolatus*	**x**	
		Tanaidacea	Nototanaidae	*Tanaissus lilljeborgi*	**x**	
Echinodermata	Asteroidea	Forcipulatida	Asteriidae	*Asterias rubens*	**x**	**x**
		Paxillosida	Astropectinidae	*Astropecten irregularis*	**x**	**x**
	Echinoidea	Clypeasteroida	Fibulariidae	*Echinocyamus pusillus*	**x**	
		Echinoida	Echinidae	*Psammechinus miliaris*		**x**
		Spatangoida	Loveniidae	*Echinocardium cordatum*	**x**	**x**
	Ophiuroidea	Ophiurida	Amphiuridae	*Acrocnida brachiata*	**x**	
				Amphiura filiformis	**x**	
			Ophiothrichidae	*Ophiothrix fragilis*		**x**
			Ophiuridae	*Ophiura albida*	**x**	**x**
				Ophiura ophiura	**x**	**x**
Mollusca	Gastropoda	Cephalaspidea	Acteonidae	*Acteon tornatilis*	**x**	
			Cylichnidae	*Cylichna cylindracea*	**x**	
		Heterostropha	Pyramidellidae	*Turbonilla acuta*	**x**	
		Mesogastropoda	Eulimidae	*Vitreolina philippi*	**x**	
			Naticidae	*Euspira catena*	**x**	**x**
				Euspira pulchella	**x**	**x**
			Turritellidae	*Turritella communis*		**x**
		Neogastropoda	Conidae	*Mangelia brachystomum*	**x**	
				Raphitoma linearis	**x**	
	Cephalopoda	Sepioidea	Sepiolidae	*Sepiola atlantica*		**x**
		Teuthoida	Loliginidae	*Alloteuthis spp.*		**x**
				Loligo vulgaris		**x**
	Bivalvia	Myoida	Corbulidae	*Corbula gibba*	**x**	
		Nuculoida	Nuculidae	*Nucula nitidosa*	**x**	
		Pholadomyoida	Thraciidae	*Thracia papyracea*	**x**	
		Veneroida	Donactidae	*Donax vittatus*	**x**	
			Mactridae	*Mactra stultorum*	**x**	**x**
				Spisula elliptica	**x**	
				Spisula subtruncata	**x**	**x**
			Montacutidae	*Montacuta ferruginosa*	**x**	
				Mysella bidentata	**x**	

Annex I: Species list – continued

Group	**Class**	**Order**	**Family**	**Species**	**Infauna**	**Epifauna**
			Pharidae	*Ensis directus*	**x**	
				Ensis ensis	**x**	
				Phaxas pellucidus	**x**	**x**
			Psammobiidae	*Gari fervensis*	**x**	
			Semelidae	*Abra alba*	**x**	
			Tellinidae	*Tellina fabula*	**x**	**x**
			Veneridae	*Chamelea gallina*	**x**	**x**
Annelida	Polychaeta	Capitellida	Capitellidae	*Capitella capitata*	**x**	
				Notomastus latericeus	**x**	
			Magelonidae	*Magelona alleni*	**x**	
				Magelona filiformis	**x**	
				Magelona johnstoni	**x**	
		Cirratulida	Cirratulidae	*Chaetozone* cf. *Setosa*	**x**	
		Opheliida	Opheliidae	*Ophelia limacina*	**x**	
			Scalibregmatidae	*Scalibregma inflatum*	**x**	
		Orbiniida	Orbiniidae	*Scoloplos armiger*	**x**	
		Oweniida	Oweniidae	*Owenia fusiformis*	**x**	
		Phyllodocida	Aphroditidae	Aphrodita aculeata		**x**
		Phyllodocida	Glyceridae	Glyceridae	**x**	
			Goniadidae	*Glycinde nordmanni*	**x**	
				Goniada maculata	**x**	
				Goniadella bobretzkii	**x**	
			Hesionidae	*Podarkeopsis helgolandica*	**x**	
			Nephtyidae	*Nephtys assimilis*	**x**	
				Nephtys caeca	**x**	
				Nephtys cirrosa	**x**	
				Nephtys hombergii	**x**	
				Nephtys longosetosa	**x**	
			Nereididae	*Eunereis longissima*	**x**	
			Pholoidae	*Pholoe baltica*	**x**	
			Phyllodocidae	*Eteone foliosa*	**x**	
				Eteone longa	**x**	
				Eumida sanguinea	**x**	
				Phyllodoce groenlandica	**x**	
				Phyllodoce lineata	**x**	
				Phyllodoce mucosa	**x**	
				Phyllodoce rosea	**x**	
			Polynoidae	*Eunoe nodosa*	**x**	
				Gattyana cirrosa	**x**	
				Harmothoe glabra	**x**	
				Malmgrenia marphysae	**x**	
			Sigalionidae	*Sigalion mathildae*	**x**	
				Sthenelais limicola	**x**	
			Syllidae	*Autolytus prolifer*	**x**	
				Streptosyllis websteri	**x**	
		Spionida	Poecilochaetidae	*Poecilochaetus serpens*	**x**	
			Spionidae	*Aonides paucibranchiata*	**x**	
				Polydora pulchra	**x**	
				Scolelepis bonnieri	**x**	
				Scolelepis tridentata	**x**	
				Spio decoratus	**x**	

Annex I: Species list – continued

Group	**Class**	**Order**	**Family**	**Species**	**Infauna**	**Epifauna**
				Spio filicornis	x	
				Spio goniocephala	x	
				Spiophanes bombyx	x	
		Terebellida	Pectinariidae	*Pectinaria koreni*	x	
				Pectinaria spp.		X
			Terebellidae	*Lanice conchilega*	x	
Chordata	Osteichthyes	Gadiformes	Gadidae	*Gadus morhua*		x
				Merlangius merlangus		x
				Trisopterus luscus		x
				Trisopterus minutus		x
			Lotidae	*Ciliata mustela*		x
		Perciformes	Ammodytidae	*Ammodytes tobianus*		x
				Hyperoplus lanceolatus		x
			Callionymidae	*Callionymus lyra*		x
				Callionymus reticulatus		x
			Gobiidae	*Pomatoschistus minutus*		x
			Mullidae	*Mullus surmuletus*		x
			Pholidae	*Pholis gunnellus*		x
			Trachinidae	*Echiichthys vipera*		x
		Pleuronectiformes	Bothidae	*Arnoglossus laterna*		x
			Pleuronectidae	*Limanda limanda*		x
				Microstomus kitt		x
				Platichthys flesus		x
				Pleuronectes platessa		x
			Soleidae	*Buglossidium luteum*		x
				Solea solea		x
		Scorpaeniformes	Agonidae	*Agonus cataphractus*		x
			Cottidae	*Myoxocephalus scorpius*		x
			Cyclopteridae	*Liparis liparis*		x
			Triglidae	*Chelidonichthys gurnardus*		x
				Chelidonichthys lucerna		x
		Syngnathiformes	Syngnathidae	*Entelurus aequoreus*		x
				Syngnathus rostellatus		x
Others	Anthozoa	Actiniaria	Edwardsiidae	*Edwardsia* spp.	x	
		Ceriantharia	Cerianthidae	*Cerianthus lloydi*	x	
				Anthozoa indet.	X	x
	Nemertini			Nemertini indet.	X	
	Phoronida		Phoronidae	*Phoronis* spp.	X	
	Cephalochordata	Amphioxiformes	Branchiostomidae	*Branchiostoma lanceolatum*	x	

Trophic look at soft-bottom communities – the long way of recovery from trawling

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ABSTRACT

We evaluate whether the trophic structure of the German Bight soft-bottom benthic community changes after cessation of bottom trawling. Trophic elevation (indicated by nitrogen stable isotope ratios, $\delta^{15}N$) and trophic significance (indicated by species metabolism approximated by body mass scaled abundance) of dominant species were compared in trawled areas and an area protected from fisheries for 14 months.

Differences between protected and trawled area were detected in five trophically relevant aspects: In the protected area (1) community trophic significance was lower; (2) trophic significance of predating and scavenging species was lower; (3) trophic significance of interface feeders was higher; (4) trophic elevations of small predators and scavengers were lower and (5) trophic elevations of deposit feeders were higher. Two major reasons for these changes from the fished to the unfished stage are discussed: the absence of artificial and additional food sources (discards, bycatch, gear-induced mortality) that causes emigration of predators and scavengers, and the absence of physical sediment disturbance, that facilitates settlement and survival of less mobile species as well as a gradual shift in food availability and quality.

The observed changes are small compared to changes induced by trawling in hitherto pristine benthic systems. We presume that decades of intense bottom trawling led to a highly artificial but trophically robust system with many weak interactions and high functional redundancy. Hence, this artificially created resistance enables the benthic community to withstand the permanent trawling stress but the return to a kind of 'pre-trawling' state will require a very long time.

Keywords: trawling impact, trophic functioning, resistance, trophic elevations, energy flow, stable isotopes, macrozoobenthos, North Sea

INTRODUCTION

Fishing, in particular bottom trawling, is one of the most severe anthropogenic impacts on marine environments (e.g. Jennings & Kaiser 1998, Thrush et al. 2001). Besides the removal of fish and bycatch, bottom trawling has two mayor impacts on benthic communities: On the one hand, a direct physical effect that causes sediment disturbance and resuspension (e.g. Jennings et al. 2001b, Watling et al. 2001) as well as dislocation, damage and mortality of benthic organisms (e.g. Bergman & van Santbrink 2000, Ramsay et al. 2000). On the other hand, an indirect trophic impact through fishery bycatch and discards which become a significant additional food source for scavengers and predators (e.g. Arntz & Weber 1970, Groenewold & Fonds 2000, Rumohr & Kujawski 2000).

Long-term bottom trawling pushes the community towards smaller, short-lived and fast growing species. After at least five decades of intense trawling (Lindeboom & de Groot 1998, Rijnsdorp et al. 1998) changes add up to a shift from high to low diversity and from a high biomass-low turnover to a low biomass-high turnover system (e.g. McConnaughey et al. 2000, Kaiser et al. 2002, Hiddink et al. 2006a).

Most likely, complex feedback processes are involved here that will affect overall ecosystem services (*sensu* Worm et al. 2006), particularly fishery itself, too. Scientists, having realised this already, call for a comprehensive management at the ecosystem level to make fisheries sustainable (e.g. Browman & Stergiou 2004, 2005). Therefore, the actual question is how and to what extent bottom trawling affects the ecosystem as a whole (Jennings & Kaiser 1998, Malakoff 2002).

If we assume that the organism is the principal lever of trawling effects on the community, then the life-history traits of the constituting species are of particular significance (e.g. Collie et al. 2005, Tillin et al. 2006). Hence, taking a close look at species properties (e.g. trophic elevations, see below) and at species dependent properties (e.g. energy flow patterns) seems to be a promising approach.

Several recent studies followed this lead, albeit more indirectly or with low resolution: they looked at changes in habitat complexity (e.g. Thrush et al. 2001, Thrush & Dayton 2002), at community size spectra and derived energy flow patterns (e.g. Jennings et al. 2001b, Jennings et al. 2002a, Hiddink et al. 2006a), and at benthic community functioning as indicated by biological trait composition (e.g. Blanchard et al. 2004, Tillin et al. 2006). Previous studies of trawling effects on trophic structure suffered their own difficulties, they either compared partial systems only, such as fish communities, and/or did lack appropriate untrawled reference sites (e.g. Jennings et al. 2001a, Jennings et al. 2002b, Badalamenti et al. 2002), as fishery impact studies were hampered by “shifting baseline” problems (e.g. Jackson et al. 2001, Lotze et al. 2005).

Particularly in coastal zones with a long fishing history it seems difficult to identify distinct and consistent effects of bottom trawling (e.g. Gray et al. 2006, Thrush & Dayton 2002).

Shallow coastal marine systems are hydrographically extremely dynamic. Abundance, biomass and species inventory are shaped by seasonal and year-to-year variability, governed by and adapted to abiotic and biotic forcing factors (e.g. Kröncke et al. 2001, Clark & Frid 2001). Last not least, bottom trawling itself creates variability by an uneven distribution of trawling impact in space and time (e.g. Rijnsdorp et al. 1998). Hence, statistical "noise" is the principal problem of studies on trawling effects in shallow water systems, particularly in sandy habitats. Therefore working with purely numerical parameters (e.g. abundance, biomass) and at coarser systematic resolution (e.g. feeding guilds) might not be sufficient to capture subtle changes (see Queirós et al. 2006, Tillin et al. 2006).

We hypothesize that species' trophic characteristics are less affected by natural environmental variability than numerical measures and are thus more suitable to detect trawling effects in highly dynamic systems. On the one hand trophic interactions between organisms are the biological base of ecological functioning (e.g. May 1974, Cohen 1978, Pimm 1982), and these interaction patterns entail communities' ability to cope with perturbations (e.g. McCann 2000, Dunne et al. 2002). On the other hand, this argument leads back to the nature of trawling, which does not only cause direct mortality, but also alters the physical and biogeochemical composition of the sediment and causes trophic distortion by food input (bycatch, discards and gear-induced mortality).

The hypothesis was tested by analysing changes in the trophic structure of a shallow sand-bottom community after cessation of trawling. The construction of the research platform FINO 1 in the German Bight (North Sea) and the concurrent closure of the site for fishery in the year 2003 provided the opportunity to compare the development of the benthic community at a protected and further trawled sites. We evaluate whether there are changes in species trophic position and species contribution to energy flow over the course of 14 months after closure of the fishery.

MATERIALS AND METHODS

Study site. In July 2003 the research platform FINO 1 was build as a pilot project for future offshore wind farms. The platform is located at 28 m water depth in the German Bight, 45 km off the island Borkum (Fig. 1). The surrounding of the platform (500 m radius) is closed to all shipping activities and is thus protected from fisheries (see Schröder & Dannheim 2006).

Sampling areas were defined as follows: The "protected area" (hereafter referred to as PA) comprised the zone between an inner circle of 150 m radius and an outer circle of 400 m radius around the platform, i.e. an area of about 5 km^2. These distances from the platform itself and from the border of the protected area were kept to minimize edge effects caused by the construction and by the surrounding trawling area. Two zones beyond the 500 m radius 9 km apart from the protected area in north-western and eastern direction (25 and 5 km^2) were chosen as reference sites, the "trawled area" (hereafter referred to as TA). Data of the two TA zones were pooled as the zones did not differ statistically in species composition, abundance and biomass (according to Schröder & Dannheim unpubl. data).

Hydrographic conditions are identical in PA and TA, as the prevailing strong tidal currents ($\leq$ 1 m s^{-1}) displace the water masses over far larger scales than the study area.

Sampling and sample treatment. Sampling in both areas, PA and TA, was carried out with *RV Heincke* during 2 periods. The first sampling period, defined as “pre-closure”, includes samples taken 3 months before and 2 weeks after fishery closure of PA (March/April and July/August 2003). “Post-closure” sampling was carried out in July/August and September/October 2004, i.e. 12 – 14 months after fishery closure of PA. During each cruise epifauna, infauna and sediment samples were taken at 5 stations in PA, and at 5 stations (pre-closure period) and 9 stations (post-closure period), respectively, in TA.

Infauna was sampled with a 0.1 m^2 van Veen grab (95 kg). Samples were taken exclusively in the area north of the platform (see Fig. 1, 3 replicates per station). Grab content was sieved on 1 mm mesh size and fixed in 4 % buffered formalin. At each station 2 surface sediment samples were collected from the first grab with 5 and 2 cm^3 PVC corers. Samples were stored at -20°C until further analysis.

Epifauna was sampled with a beam trawl (3 m opening width, haul duration <=10 min at 3 knots). Trawled distance at the bottom was determined by Differential Global Positioning System (DGPS). Hauls in PA were restricted to the part south of the platform in order to avoid self-made trawling disturbance at the grab stations (see Fig.1). Epifaunal subsamples from each catch were stored frozen until further treatment.

Sampled specimens were determined to the lowest possible taxonomic level. Species wet biomass (mg m^{-2}) and average body mass (M, mg) were converted to joule (kJ) by conversion factors taken from Brey (2001).

From additional grab and trawl samples, 464 specimens of the 23 most abundant species (PA: 181 / 22; TA: 283 / 22) were collected for stable isotope analysis during a cruise in November 2003 (samples only from TA) and the post-closure cruise in September/October 2004 (samples from TA and PA). Animals were sorted directly on board and stored at –20°C until further treatment. Upon return to the laboratory, frozen tissue samples were lyophilised for 24 h (Finn-Aqua Lyovac GT2E), homogenized in a ball mill and treated with 1 mol l^{-1} hydrochloric acid (HCl) to eliminate calcareous shells (see Jacob et al. 2005). Subsequently, samples were dried again at 55°C and ground to powder in a mortar prior to analysis. Mass-spectrometric measurement of stable nitrogen isotope composition was carried out in the GeoBioCenter^{LMU}, University of Munich (Thermo/Finnigan Delta Plus). Current gaseous standards for calibration were used. Experimental precision was better than ±0.2 ‰.

Environmental parameters. *Trawling intensity.* Fishing intensity in TA was calculated by means of the satellite-based “Vessel Monitoring System” (VMS; unpublished data provided by S. Ehrich, Federal Research Centre for Fisheries and by G. Piet and F. Quirins, Netherlands Institute for Fisheries Research). Trawling intensity was calculated as times trawled month^{-1} (i.e. x spot^{-1}) following Rijnsdorp et al. (1998). For further details see Schröder & Dannheim (2006).

Sediment analyses. Sediment fractions were determined by wet and dry sieving of the larger sample (5 cm^3) with a sonic sifter (ATM) over a Wenthworth scaled standard sieve set (Wenthworth 1922), and median grain size (MdGS, µm) was calculated. The smaller sample (2 cm^3) was freeze dried and homogenised in a mortar. Nitrogen and carbon content (%N, %C, C/N by mass) were determined with an elemental analyser (LECO CNS-2000). Inorganic carbon was removed by adding 12 mol l^{-1} hydrochloric acid to an additional subsample to determine C_{org} content (LECO CS-125). Mahalanobis jackknife distances (Barnett & Lewis 1994) identified one multivariate outlier in the sample space [MdGS, %N, %C, %C_{org}, C/N]. The remaining data (N = 47) were checked for normality and homogeneity of variances (Barlett test). Percentages (%C, %N, %C_{org}) were arcsine-transformed. Differences in sediment parameters between areas (PA, TA) were tested by two-way analysis of variance (ANOVA) and one-way ANOVA for data available only from one sampling period.

Trophic parameters. Two trophic parameters were applied to compare the trophic structure in PA and TA: trophic elevation and trophic significance.

Trophic elevation. The tissue stable nitrogen isotope ratio ($^{15}N/^{14}N = \delta^{15}N$) is a proxy of an organism's position within the trophic hierarchy of an ecosystem. With each assimilation step along the food chain, the heavier isotope ^{15}N becomes enriched in consumer tissues owing to an enzymatic selection. Fractionation of ^{15}N results in a $\delta^{15}N$ increase ranging from 1.4 to 3.4 ‰ per trophic level (e.g. Post 2002, McCutchan et al. 2003). According to Yodzis (1984) and Cohen et al. (2003), we define trophic elevation TE_i of species *I* by

$$TE_i = \delta^{15}N_i \qquad [‰] \qquad (1)$$

We measured trophic elevation for 23 species. For the remaining 183 species encountered in the sampling areas (PA and TA) trophic elevations were estimated indirectly: We collected $\delta^{15}N$ data of species which were taxonomically and geographically as close as possible from published and unpublished sources (for $\delta^{15}N$ data sources see ANNEX). To account for between-systems differences in $\delta^{15}N$, we adjusted all data by the difference in $\delta^{15}N$ of the primary food source (POM, particulate organic matter) between the German Bight (our data, POM = 6.07 ‰) and the corresponding ecosystem, i.e.

$$TE_i = \delta^{15}N_i + (\delta^{15}N_{POM,GB} - \delta^{15}N_{POM,OS}) \quad [‰] \qquad (2)$$

where *GB* is German Bight and *OS* is other systems. When $\delta^{15}N$ of primary consumers (*PC*) and not of POM was given as a baseline, we used

$$TE_i = \delta^{15}N_i + (\delta^{15}N_{PC,GB} - \delta^{15}N_{PC,OS}) \qquad [‰] \qquad (3)$$

accordingly (see ANNEX for *PC* $\delta^{15}N$ values, species marked with an asterisk).

For species we were not able to find $\delta^{15}N$ data from sufficiently close relatives, we assigned the average $\delta^{15}N$ value of the appropriate feeding guild (for feeding guilds and corresponding literature see ANNEX). Parasites (*Vitreolina philippi*, *Turbonilla acuta*) were excluded from analyses (7 individuals).

Trophic significance. Energy flow through a particular population is related to abundance and to average body size, because metabolic rate scales with body size by an exponent of about 0.75 (rate = a * $M^{0.75}$, see West & Brown 2005 for the general validity of the scaling factor 0.75). We define the trophic significance of a species as its contribution to overall community energy flow. Therefore trophic significance TS_i of species *I* is approximated by

$$TS_i = N_i * M_i^{0.75} \qquad [\mathrm{kJ\ m^{-2}}] \tag{4}$$

where N_i and M_i are abundance and mean body mass of species *i*. Overall community trophic significance (i.e. community energy flow) TS_{com} is estimated accordingly by

$$TS_{com} = \sum_{i=1}^{n} (N_i * M_i^{0.75}) \qquad [\mathrm{kJ\ m^{-2}}] \tag{5}$$

where *n* is number of species. These parameters were computed for each sample (each grab and beam-trawl station) separately.

We applied two different indices, absolute trophic significance TS_i (comparable to a scaled abundance) as described above, and relative trophic significance RTS_i that describes the contribution of species *i* to community trophic significance TS_{com} (i.e. comparable to the species' dominance within a community)

$$RTS_i = 100 * TS_i / TS_{com} \qquad [\%] \tag{6}$$

where '*com'* refers to the community of TA and PA, respectively.

Trophic analyses. Community trophic characteristics. Trophic elevation frequency distributions (TEFD) were used to compare community trophic structure between areas, before and after cessation of trawling. A TEFD identifies the distribution of species trophic significance (TS_i) over the trophic elevation range ($\delta^{15}N$) of the community.

Community trophic significance (TS_{com}) was calculated for TA and PA prior to closure of the fishery (March and July/August 2003, N = 10 samples in TA and PA, each) and one year after closure (July/August and September/October 2004, N = 18 and 10 samples in TA and PA, respectively). Data were checked for normality and homogeneity of variances (Barlett test). Significant differences of TS_{com} versus area (PA, TA) and closure (pre – post) were tested by full interaction 2-way analysis of variance (ANOVA), followed by a post-hoc test (Student's t-test) on least significant differences between means (LS means).

Species trophic characteristics. To evaluate shifts in species trophic characteristics, we tested on differences of (a) trophic elevation (*TE*) and (b) trophic significance (*TS*) after the cessation of trawling and compared both parameters in (c) a composite view.

(a) *Shifts in trophic elevation*. For 20 species (see Fig. 4) $\delta^{15}N$ values were determined in specimens from both TA and PA 14 months after closure. Outliers in $\delta^{15}N$ were identified by Mahalanobis Jackknife distances (Barnett & Lewis 1994) and excluded from further analysis. $\delta^{15}N$ values were checked for normality and homogeneity of variances (Barlett test) and subsequently subjected to a full interaction 2-way ANOVA of $\delta^{15}N$ versus area (PA, TA) and species, followed by a post-hoc test (Student's t-test on LS means). Variances were different at the 5% level albeit did not increase with the mean, hence we increased our threshold level of significance from $p = 0.05$ to $p = 0.01$ (see results). Trophic elevation difference ΔTE_i between PA and TA of species *I* was calculated by

$$\Delta TE_i = TE_{i,PA} - TE_{i,TA} \qquad [‰] \qquad (7)$$

(b) *Shifts in trophic significance*. Species trophic significances were calculated for TA and PA prior to closure of the fishery and one year after closure (for no. of samples see trophic analyses of TS_{com}). Both indices, TS_i and RTS_i of the most dominant species (comprising 99 % of TS_{com}), were tested on differences between TA and PA by Mann Whitney U-test (RTS_i [%] values were arcsine-transformed). Species that showed significant differences of the same sign between TA and PA before and after closure, i.e. shifts apparently not caused by closure of the fishery, were excluded from further analysis.

I *The composite view*. In order to relate shifts in species trophic significance to shifts in species trophic elevation (ΔTE_i), we plotted two different measures of difference in trophic significance versus ΔTE_i:

(1) The magnitude of the shift in trophic significance of species *I* (ΔTS_i) was described by the difference in trophic significance between PA and TA, expressed as fraction (%) of the average trophic significance in PA and TA

$$\Delta TS_i = 100 * (TS_{i,PA} - TS_{i,TA}) / (TS_{i,PA} + TS_{i,TA}) \qquad [\%] \qquad (8)$$

(2) The change in relative trophic significance of species *I* (ΔRTS_i), i.e. of its share in community trophic significance, was computed by the difference in RTS_i between PA and TA

$$\Delta RTS_i = 100 * (TS_{i,PA} / TS_{Com,PA}) - (TS_{i,TA} / TS_{Com,TA}) \qquad [\%] \qquad (9)$$

RESULTS

Sediment. Median grain size (µm) and organic carbon content (C_{org}, %) differed significantly between sampling dates (pre- and post-closure: $p < 0.01$, Table 1). The nitrogen content (N, %) was significantly affected after one year of closure to fishery with a lowered content in the protected area ($p = 0.02$, Table 1).

Community trophic characteristics. Trophic elevation frequency distributions (TEFD) did not differ in median and varied slightly only in skewness and kurtosis, both between TA and

PA and between sampling periods (pre- and post-closure, Fig. 3). Thus, there was no apparent effect of the high trawling intensity during summers 2003 and 2004 (Fig. 2) or of trawling cessation (compare Fig. 3b with 3d and Fig. 3c with 3d).

Neither pre-/post-closure ($p = 0.30$) nor area (PA – TA, $p = 0.57$) significantly affected community trophic significance (TS_{com}, see Fig. 3). Only the interaction pre-/post-closure x area (PA – TA) was significant ($p < 0.05$), indicating an effect of trawling cessation on community trophic significance. The post-hoc test identified TA one year after closure to be significantly different from the others ($TA_{pre} = PA_{pre} = PA_{post} < TA_{post}$; $p < 0.05$).

Species trophic elevation. 14 months after trawling closure, trophic elevations (*TE*) were significantly affected by species ($p < 0.001$) and by species x area (PA – TA) interaction ($p < 0.001$). Significant effects were detected in 4 species (Fig. 4). Within PA, *TE* was significantly ($p < 0.01$) higher in the suspension feeder *Tellimya ferruginosa* (ΔTE_i = 1.18 ‰), and significantly lower in the interface feeder *Scolelepis bonnieri* (-2.14 ‰) as well as in the predators/scavengers *Euspira pulchella* (-1.28 ‰) and *Ophiura albida* (-1.03 ‰). A similar analysis on the level of major feeding guilds (with DF, SF, SL, IF and PS, see Fig. 4) detected no significant area effects (2-way ANOVA, area $p = 0.49$, feeding guilds x area $p = 0.46$).

Species trophic significance. Before closure, trophic significance TS_i differed significantly ($p < 0.05$) between PA and TA in 5 of those 70 species that represented 99 % of community trophic significance (TS_{com}) (Fig. 5a). TS_i was lower in PA in *Tellina fabula* and *Magelona filiformis*, and higher in *Poecilochaetus serpens*, *Nephtys assimilis* and *Spiophanes bombyx*. Corresponding significant differences in RTS_i were present in *T. fabula* and *N. assimilis* only ($p < 0.05$, Fig. 5b).

One year after closure, TS_i differed in 17 out of the 70 species ($p < 0.05$, Fig. 6a). In 7 species TS_i was lower in PA with ΔTS_i ranging from -17.82 kJ m^{-2} (*Echinocardium cordatum*) to -0.24 kJ m^{-2} (*T. ferruginosa*). 10 species showed a higher TS_i in PA, with differences in ΔTS_i ranging between +0.06 kJ m^{-2} (*Spio decoratus*) and +3.44 kJ m^{-2} (*Owenia fusiformis*). Note that *T. fabula* (lower in PA) and *S. bombyx* (higher in PA) showed the same pattern before closure (Fig. 5). Relative trophic significance RTS_i differed in 12 out of the 70 species (Fig. 6b). Only *E. cordatum* and *T. ferruginosa* had lower trophic significance in PA with ΔRTS_i = -13.66 % and -0.23 %, respectively. RTS_i was significantly higher in PA in the same 10 species as above (see TS_i), with ΔRTS_i ranging between 0.12 % (*S. decoratus*) and 5.91 % (*O. fusiformis*).

The composite view. ΔTS_i was negative in 17 but positive in 8 species only (Fig. 7a). Anthozoa (+53 %) and O. fusiformis (+41 %) showed the most pronounced increase, while the predators *Corystes cassivelaunus* and *Asterias rubens* showed the most pronounced decrease, -100 % and -47 %, respectively. ΔRTS_i values were more evenly distributed, but comparatively small, ranging from +6 % (*O. fusiformis* and *S. bombyx*) to -14 % (*E. cordatum*, Fig. 7b). Those species with a significant difference in trophic elevation ΔTE_i (*S.*

bonnieri, *E. pulchella*, *O. albida* and *T. ferruginosa*) contributed comparatively little to community trophic significance (ΔRTS_i < 1 %; Fig. 7b). Moreover, only one of these, *T. ferruginosa*, showed a significant difference in both TE_i and TS_i (or RTS_i, respectively) between TA and PA.

DISCUSSION

Cause and effect studies that single out one certain impact factor in benthic communities are hampered by complex multi-factorial interactions and a general lack of non-affected control areas. Particularly in areas such as the North Sea, that combine strong environmental dynamics with numerous and continuous anthropogenic impacts, such studies are extremely difficult (e.g. Collie et al. 2000, Gray et al. 2006). Accordingly, present estimates of recovery time for North Sea benthos are based on experimental trawling or on the comparison of "lightly" and "heavily" trawled areas. Models, derived from these estimates, predict recovery rates from beam trawling for sandy bottom communities of 100 days in terms of numerical abundance (Collie et al. 2000) and 1 – 3 years in terms of biomass and production (Hiddink et al. 2006b). Soft-bottom monitoring studies indicate longer recovery times after perturbations, in terms of biomass more than 3 years (see e.g. Pearson & Rosenberg 1978, Arntz & Rumohr 1982). Accordingly, Smith et al. (2006) found lowered epifaunal biomass even 3 years after closure of the fishery in a southern North Sea area. Collie et al. (2005) report an increase in benthic abundance, biomass and production after 2.5 years on gravel bottoms (Georges Bank) that continued until 5 years after closure (end of observational period). Only two studies so far dealt with infaunal recovery. De Juan et al. (2007) found fewer scavengers but increased surface infauna and more epifauna, in particular suspension feeders and predatory fish 1 year after closure of a muddy habitat situated in the north-western Mediterranean Sea. Duineveld et al. (2007) report an increase in species richness, evenness, and abundance of mud shrimps and fragile large bivalves for epifaunal beam-trawl samples, but inconsistent results in infaunal box-core samples of a sandy habitat (southern North Sea) even after 20 years of closure.

Other comparable data for shallow sandy bottoms are missing or difficult to estimate owing to systems natural dynamics (e.g. Collie et al. 2000, Kaiser et al. 2006); Tillin et al. (2006) were unable to demonstrate consistent changes in functional diversity at the Dogger Bank (North Sea), although they provided evidence that continuous bottom trawling affects community functional composition. Here, we turn the argument of Tillin et al. (2006) upside down: we found that cessation of trawling leads to subtle changes in the trophic functioning of sandy bottom benthic communities that can be measured with species' trophic characteristics (see results). In the following, the causal relations between trawling cessation and the observed changes are discussed.

The absence of physical sediment disturbance by fishing gear appears to be the principal cause. Frequent trawling affects sediment physics (e.g. resuspension) and biogeochemistry, i.e. it enhances the availability of otherwise buried organic compounds (e.g. Watling et al. 2001, Trimmer et al. 2005). At the surface, concentrations of organic compounds are reduced by biological processing (see below). Lower sediment nitrogen and organic carbon contents in the protected area (PA) support this view (Table 1). Accordingly, community trophic significance was lower in PA, too, particularly owing to lower trophic significance of the infaunal deposit feeder *Echinocardium cordatum*. It prefers sediments rich in organic content (Wieking & Kröncke 2003, Kröncke et al. 2004) and its populations appear to be rather less affected by beam trawling (Kaiser et al. 2006, Tillin et al. 2006), particularly larger specimens which burrow deep in the sediment (e.g. Bergman & Hup 1992).

In contrast, small interface feeders with a more or less sessile life-style (*Owenia fusiformis, Spiophanes bombyx*, *Chaetozone cf. setosa*, *Edwardsia* spp. and *Spio decoratus*) had a higher trophic significance in PA. They feed selectively on high quality (indicated by low C/N ratio, Brown et al. 2005) food particles (e.g. Kröncke et al. 2004, Wieking & Kröncke 2005). Sediment C/N ratios, however, did not differ between trawled area (TA) and PA. Therefore, not enhanced food quality but the absence of physical disturbance is responsible for their increased settlement in PA. Their stronger presence might have led to an increased processing of sedimentary organic compounds (as evident in lower nitrogen and carbon content), i.e. a biological feedback process as also observed by Brown et al. (2005).

Increased trophic elevations in deposit feeders such as *Pectinaria koreni* and *E. cordatum*, as well as its commensal *Tellimya ferruginosa* which feeds on refractory material of the heart urchin (Gage 1966), may be related to an altered sediment biogeochemistry in PA, too: Microbial degradation alters the composition of sediment particulate organic matter (POM, e.g. Lee et al. 2004), but also increases $\delta^{15}N$ of bulk POM by preferentially assimilating the lighter isotope (e.g. Wada 1980, Macko & Estep 1984). Trawling causes a decrease in benthic microbial activity (Pusceddu et al. 2005) and thus a microbially induced shift in POM $\delta^{15}N$. Hence, if POM in PA has a higher $\delta^{15}N$, this signal will be passed on to the benthic primary consumers, in particular to those feeding on refractory material such as deposit feeders.

The second cause for a cessation induced trophic signal in the benthic community is the absence of fishery generated additional and artificial food sources, i.e. gear-induced mortality and discards. Primarily, trawling causes mortality of benthic organisms, but many survivors, especially mobile predators and scavengers profit from this source of comparatively high trophic level food (Arntz & Weber 1970, Groenewold & Fonds 2000, Rumohr & Kujawski 2000). Accordingly, trophic elevations of predators and scavengers are expected to be lower in PA. Such shifts in trophic elevation were observed in the apparently facultative predating/scavenging *Ophiura albida*, *Euspira pulchella* and *Scolelepis bonnieri* (see Nagabhushanam & Colman 1959, Kenchington et al. 1998) but, surprisingly, not in those large, mobile predators and scavengers that are known to benefit from such additional food sources, such as *Liocarcinus* spp., *Asterias rubens* and *Astropecten irregularis* (Fig. 4 and 7). Obviously, these large, opportunistic feeders cover such a trophically wide prey range (e.g. Pimm & Lawton 1978, Cohen et al. 1993, Davenport & Bax 2002) that a fishery related shift in diet is not detectable in species trophic elevation. There is, however, a clear signal in trophic significance, which is distinctly lower in PA in predators and scavengers such as *Corystes cassivelaunus* and *Asterias rubens* (Fig. 7). Scarcity of those food items commonly generated by trawling may have forced them to emigrate from PA (see Groenewold & Fonds 2000, Smith et al. 2006, De Juan et al. 2007).

At the community level, however, we were not able to detect changes in the distribution of trophic elevation among species as were Jennings et al. (2001a), although we expected on average lower trophic elevations in PA due to lower trophic significance of predators and scavengers. At the species level, shifts in trophic elevation are rather small, compared to trawling effects in hitherto pristine systems. Those species with a significant difference in trophic elevation contributed comparatively little to community trophic significance and vice versa (Fig. 7). This indicates that no single species pushes the system towards one direction and explains why community trophic structure is still similar in TA and PA after 14 months of trawling cessation. Bottom trawling created an alternate, artificially robust trophic system which is likely to gain resistance in terms of rather weak interactions between the benthic species (e.g. McCann et al. 1998, Berlow 1999, McCann 2000) and functional redundancy of the survivors (Menge & Sutherland 1987, Naeem & Shibin 1997, Yachi & Loreau 1999). Hence, postulating an adaptation of the benthic fauna to intense trawling for at least 5 decades (e.g. Lindeboom & de Groot 1998, Rumohr & Kujawski 2000), we should rather call the non-fishing site “non-trawled area for only 14 months” instead of “protected area”.

Is there any chance that without fisheries the German Bight soft-bottom benthos will return to a condition that resembles the pre-trawling “pristine” state? We think, rather not for the foreseeable future. Many decades of bottom trawling caused quite irreversible changes, such as the loss of habitat diversity e.g. through the disappearance of once common biogenic reefs (e.g. Riesen & Reise 1982, Auster & Langton 1999). Additionally, a significant impact of external factors persists, such as pollution (e.g. Duineveld et al. 1991, Basford et al. 1993) and climate change (Kröncke et al. 2001, Lotze et al. 2005, Frid 2006). Hence, large scale cessation of trawling, such as the planned offshore wind parks will entail in the German Bight, is likely to cause a benthic regime shift (*sensu* Amaro 2005, Allen & Clarke 2007, Van Nes et al. 2007) towards a high biomass-low turnover system, presumably with higher biodiversity (see Worm et al. 2006). However, we can not predict what this community will look like in terms of species inventory and food web structure and how long this process will take. Nevertheless, our two-dimensional approach towards community trophic functioning may lead to a robust albeit sensitive standardised tool for qualitative measurement of community trophic status and its development over time.

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TABLE

Table 1. Sediment parameters (mean ± standard deviation) for trawled (TA) and protected (PA) area prior and after the closure to fishery: median grain size (MdGS, µm), carbon content (C, %), organic carbon content (C_{org}, %), nitrogen content (N, %) and C/N ratio (mass based). One-way and two-way analyses of variance (ANOVA) show significant differences ($p<0.05$, bold) between TA and PA, respectively pre- and post- closure. N.d.: no data.

Parameters	MdGS (µm)	C (%)	C_{org} (%)	N (%)	C/N
pre-closure					
TA	179 ± 6	0.24 ± 0.09	0.08 ± 0.03	n.d.	n.d.
PA	180 ± 4	0.30 ± 0.18	0.08 ± 0.02	n.d.	n.d.
post-closure					
TA	175 ± 4	0.32 ± 0.07	0.15 ± 0.02	0.022 ± 0.004	7.04 ± 1.11
PA	177 ± 3	0.27 ± 0.05	0.13 ± 0.02	0.018 ± 0.002	6.97 ± 0.74
one-way ANOVA					
treatment (TA – PA)				**0.02**	0.15
two-way ANOVA					
treatment (TA – PA)	0.33	0.74	0.07		
closure (pre – post)	**<0.01**	0.23	**<0.01**		

FIGURES

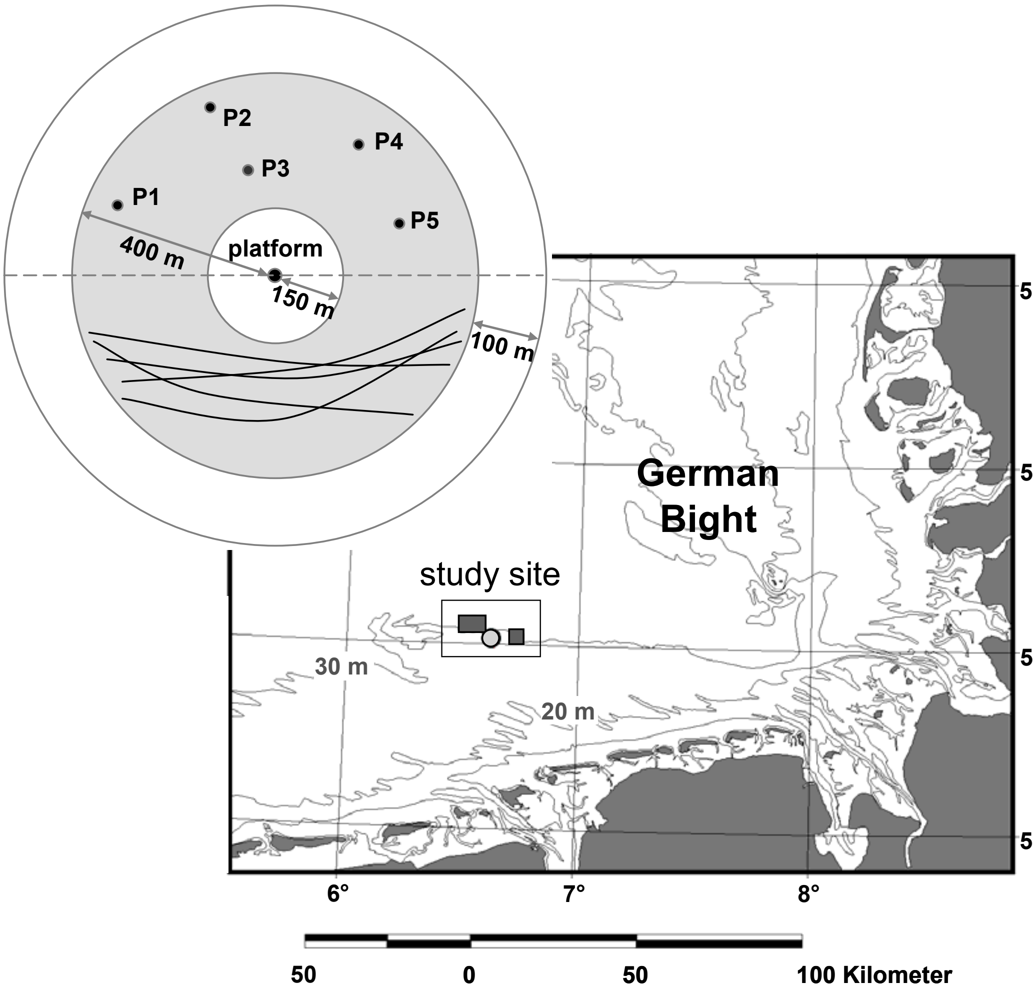


Fig. 1. Map of the study site in the German Bight with the two trawled areas (dark grey squares) and the protected area (light grey circle). The upper left circle shows the sampling scheme in the protected area, the zone between an inner circle of 150 m radius and an outer circle of 400 m radius around the platform. P: grab sampling stations north of the platform, grey lines: exemplary beam-trawl tracks south of the platform.

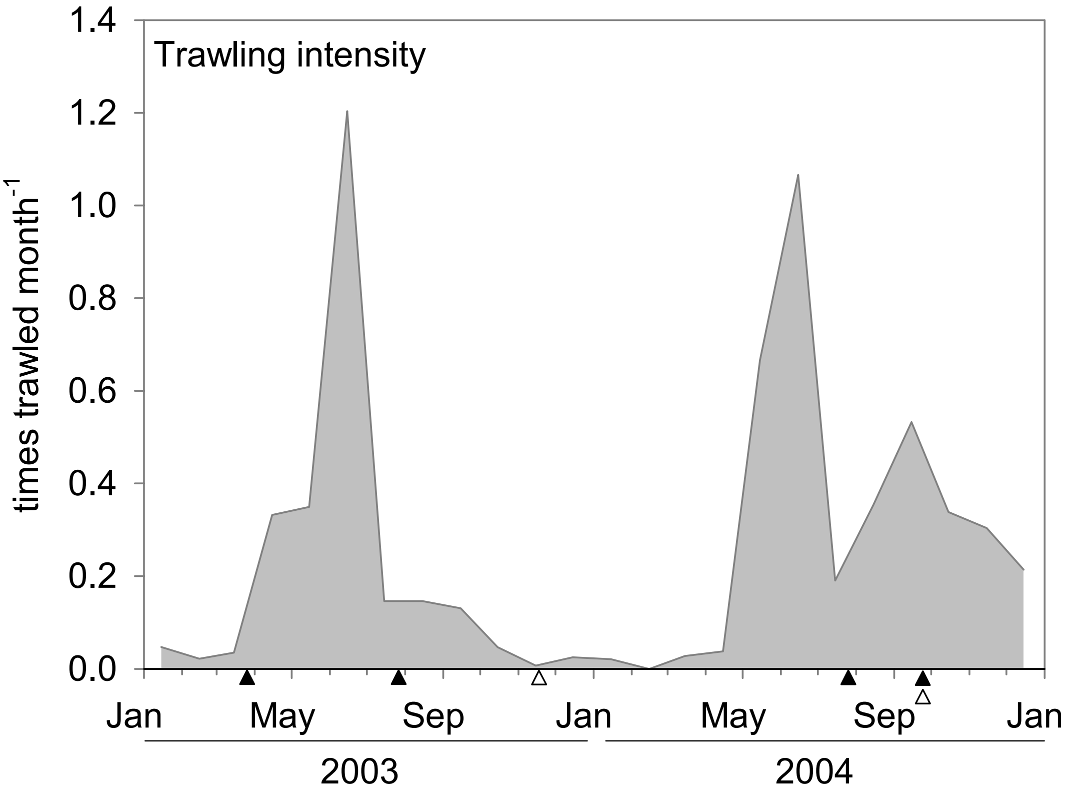


Fig. 2. Trawling intensity (times trawled month^{-1}) for the trawled area during the study period. Black triangles mark dates of pre-closure sampling in March and July/August 2003 (3 months before and 2 weeks after closure) and post-closure sampling in July/August and September/October 2004 (12 – 14 months after closure). White triangles mark dates of sampling for stable isotope analyses.

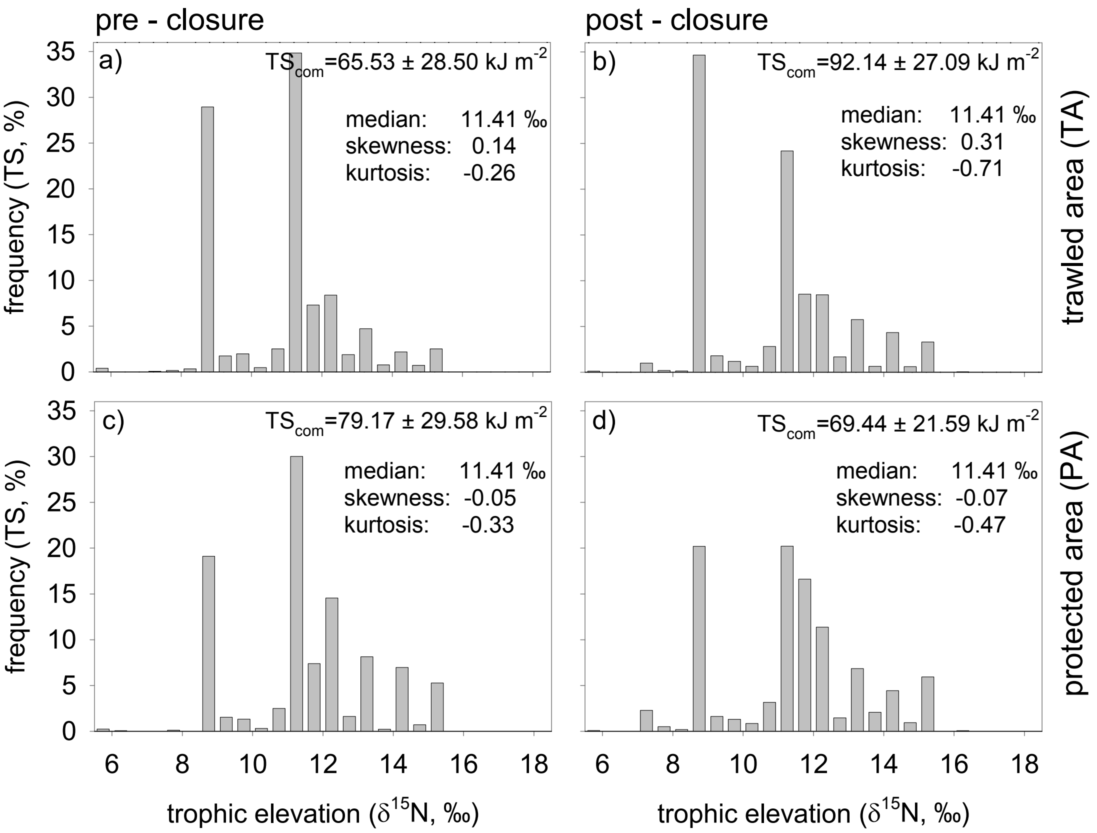


Fig. 3. Distribution of species trophic significance (TS = $N^*M^{0.75}$, %) across species trophic elevation (δ^{15}N, ‰) in (a) the trawled area (TA) before trawling closure, (b) TA 12 to 14 months after closure, (c) the protected area (PA) before closure and (d) PA 12 to 14 months after closure. Corresponding community trophic significance (TS_{com}, kJ m^{-2}) for area (TA – PA) at pre- and post-closure are given in the graphs.

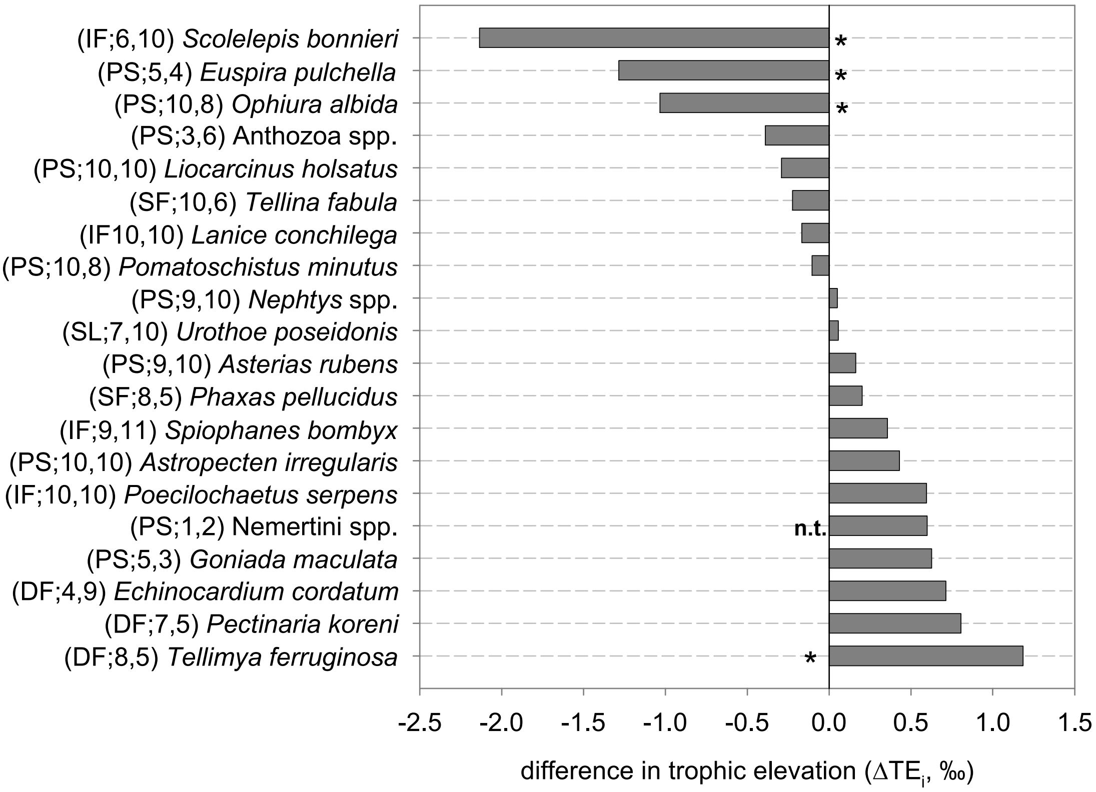


Fig. 4. Mean difference in species trophic elevation (ΔTE_i, ‰) between protected (PA) and trawled area (TA) 14 months after closure (DF = deposit feeder, IF = interface feeder, PS = predator/scavenger, SF = suspension feeder, SL = sandlicker. Species are ordered by ascending difference in trophic elevation. Number of samples per species of each treatment are given in parentheses (trawled, protected). * significant difference ($p < 0.01$), n.t. means not tested.

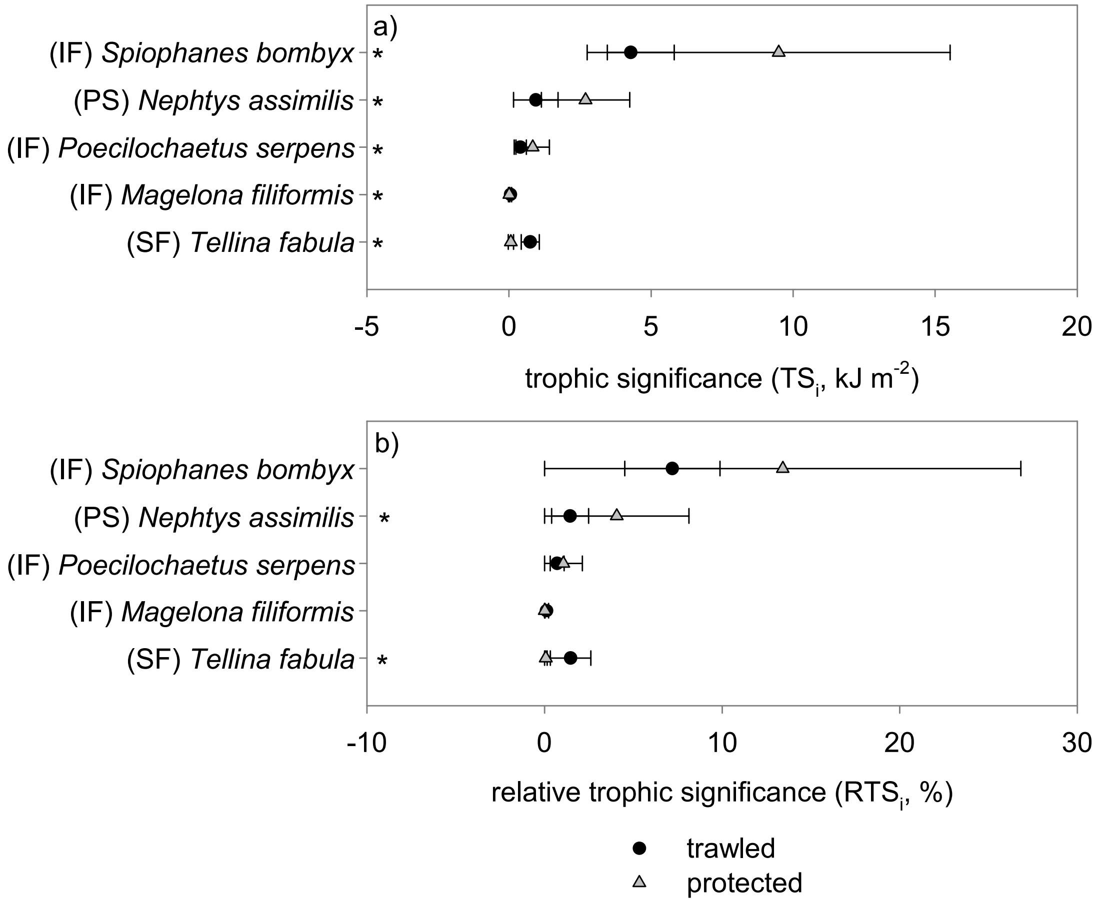


Fig. 5. Pre-closure differences between trawled and protected area of (a) trophic significance TS_i (N_i*$M_i^{0.75}$, kJ m^{-2}) and (b) relative trophic significance RTS_i, (N_i*$M_i^{0.75}$ in % of total trophic significance TS_{com}). The plot includes all species that (i) reveal significant differences in TS_i and (ii) belong to those 70 species that account for 99% of TS_{com}. Horizontal bars indicate standard deviation. IF = interface feeder, PS = predator/scavenger, SF = suspension feeder. Species were ordered by increasing difference in trophic significance (PA minus TA). * significant difference ($p < 0.05$).

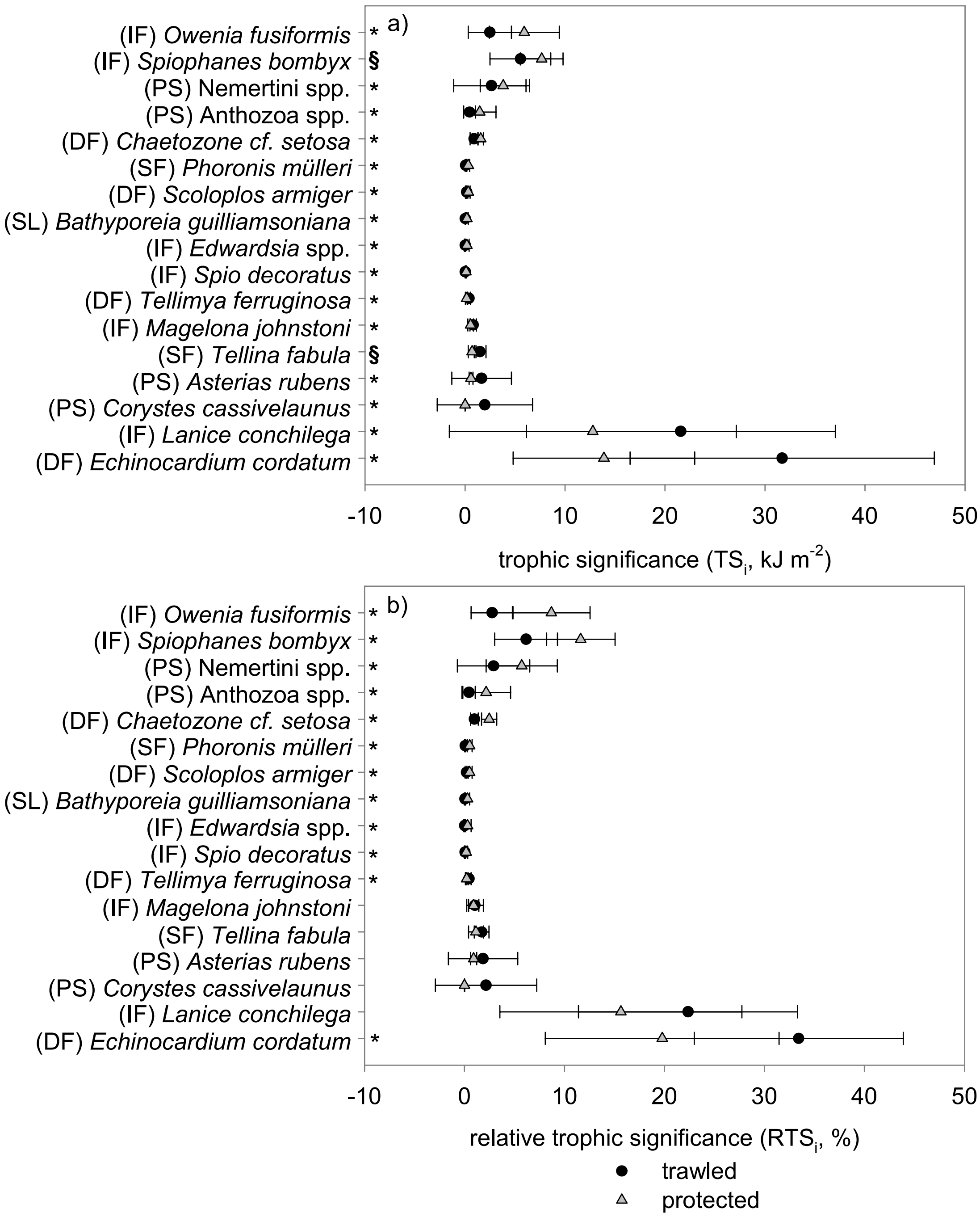


Fig. 6. Post-closure differences between trawled and protected area of (a) trophic significance TS_i (N_i*$M_i^{0.75}$, kJ m^{-2}) and (b) relative trophic significance RTS_i (N_i*$M_i^{0.75}$ in % of total trophic significance TS_{com}). The plot includes all species that (i) reveal significant differences in TS_i and (ii) belong to those 70 species that account for 99% of TS_{com}. Horizontal bars indicate standard deviation. DF = deposit feeder, IF = interface feeder, PS = predator/scavenger, SF = suspension feeder, SL = sandlicker. Species were ordered by increasing difference in trophic significance (PA minus TA). * significant difference ($p < 0.05$), § significant difference of the same sign before and after closure ($p < 0.05$).

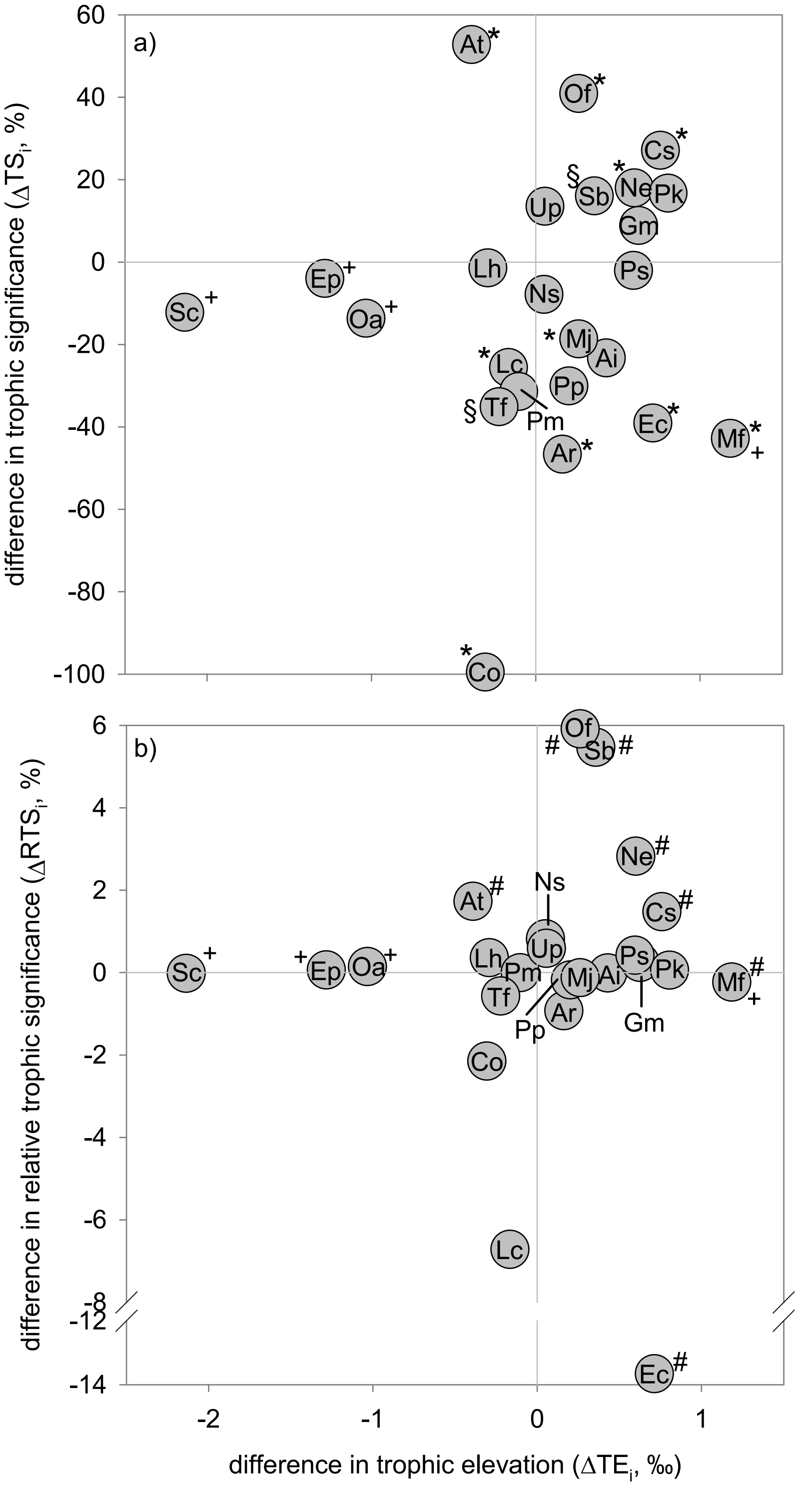


Fig. 7. Differences in species trophic elevation (ΔTE_i, ‰) versus (a) difference in species trophic significance (ΔTS_i) as % of species value in the whole study area and (b) difference in relative trophic significance (ΔRTS_i) as change in the % share of the species in total trophic significance. Species are At: Anthozoa spp., Ar: *Asterias rubens*, Ai: *Astropecten irregularis*, Cs: *Chaetozone cf. setosa*, Co: *Corystes cassivelaunus*, Ec: *Echinocardium cordatum*, Ep: *Euspira pulchella*, Gm: *Goniada maculata*, Lc: *Lanice conchilega*, Lh: *Liocarcinus holsatus*, Mj: *Magelona johnstoni*, Nm: Nemertini spp., Ns: *Nephtys* spp., Oa: *Ophiura albida*, Of: *Owenia fusiformis*, Pk: *Pektinaria koreni*, Pp: *Phaxas pellucidus*, Ps:

Poecilochaetus serpens, Pm: *Pomatoschistus minutus*, Sc: *Scolelepis bonnieri*, Sb: *Spiophanes bombyx*, Mf: *Tellimya ferruginosa*, Tf: *Tellina fabula*, Up: *Urothoe poseidonis*.
For species Cs, Co, Mj and Of mean ΔTE_i, of the corresponding feeding guild were used. * significant difference in TE_i ($p<0.01$), $^{+}$ significant difference in TS_i ($p<0.05$), $^{\#}$ significant difference in RTS_i ($p<0.05$), § significant difference of the same sign before and after closure ($p<0.05$).

5 Synthesis

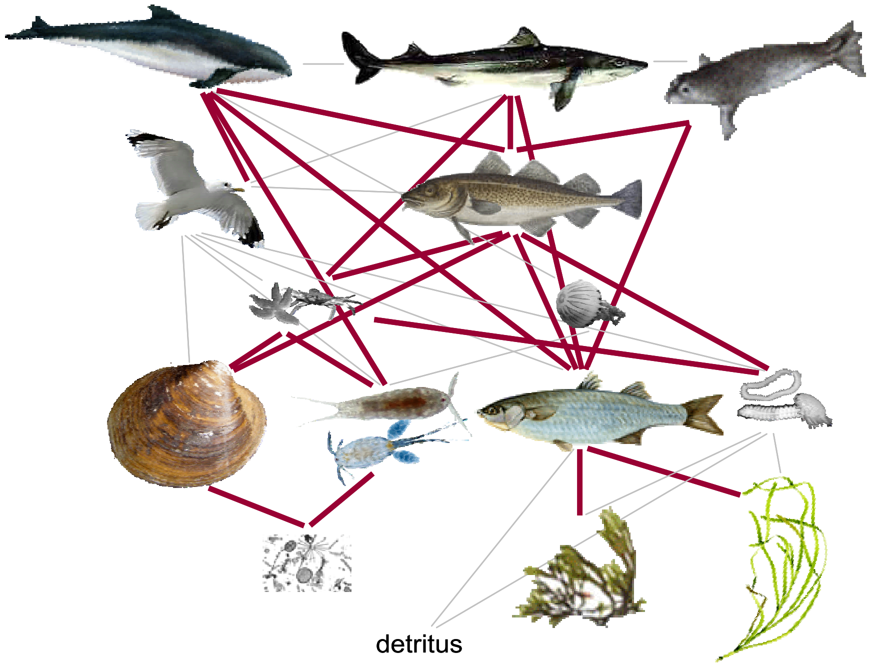
In view of the steadily increasing demand for services and goods provided by marine ecosystems, scientists call for a sustainable resource management based upon an ecosystem approach (e.g. Pauly et al. 2002, Browman & Stergiou 2004, 2005). Correspondingly, the relationship between biodiversity and trophic functioning has become a central issue of ecology during recent years (e.g. Loreau et al. 2001, Ives et al. 2005). Trophic complexity, i.e. taxonomic and trophic diversity, and trophic redundancy are major determinants of ecological functioning in terms of stability properties (e.g. Paine 1992, Polis & Strong 1996, Thébault & Loreau 2003, De Ruiter et al. 2005, Duffy et al. 2007). Recent studies followed this lead, examining the consequences of human impacts, such as the loss or extinction of species (e.g. Dunne et al. 2002, Christianou & Ebenman 2005), on ecosystems or the response of communities to perturbations (e.g. McCann 2000, Dunne et al. 2004).

Human interference in marine ecosystems affects trophic complexity and thus overall ecological functioning (Vitousek et al. 1997). Decimation or even elimination of top predators by fisheries (e.g. Pauly et al. 1998, Dobson et al. 2006) skews ecosystems trophically (Duffy 2003) and may cause a cascade of unintended ecological changes (e.g. Post 2002a, Bascompte et al. 2005). One classical example for such cascading effects is the kelp – sea urchin – sea otter food chain in the northeast Pacific Ocean (Estes & Palmisano 1974): The removal of otters caused a population explosion of their sea urchin prey. Overgrazing of kelp forests by the urchin led to habitat destruction and a severe loss of biodiversity.

Beyond the human impact on top predators, fishery constitutes a permanent disturbance that causes a gradual degradation in overall food web complexity: by and by all but the most resistant species are eliminated which are mainly those near the base of the food web (Menge & Sutherland 1987), and this obviously affects prey species diversity for consumers at higher trophic levels (Briand & Cohen 1987, Duffy 2003).

Fishery causes not only a loss in biodiversity but, through reduction of food web complexity, a degradation of ecological functioning, possibly leading to a loss in community stability properties (Figure 9, Menge & Sutherland 1987, Pauly et al. 1998, Jackson et al. 2001, Worm et al. 2006). Apparently, these changes are more obvious in hitherto pristine communities such as cold coral reefs off the Norwegean coast (e.g. Fosså et al. 2002, Hall-Spencer et al. 2002), but continue more subtle in already affected areas. Ecologists predict that a decrease in food web complexity will – finally – lead to a reduction in services and goods, e.g. through a reduced trophic flow to those high trophic level species that are preferred fishery targets (see e.g. Naeem & Shibin 1997, Chapin III et al. 2000, Loreau et al. 2001).

(a) before industrial exploitation



(b) after/ongoing exploitation

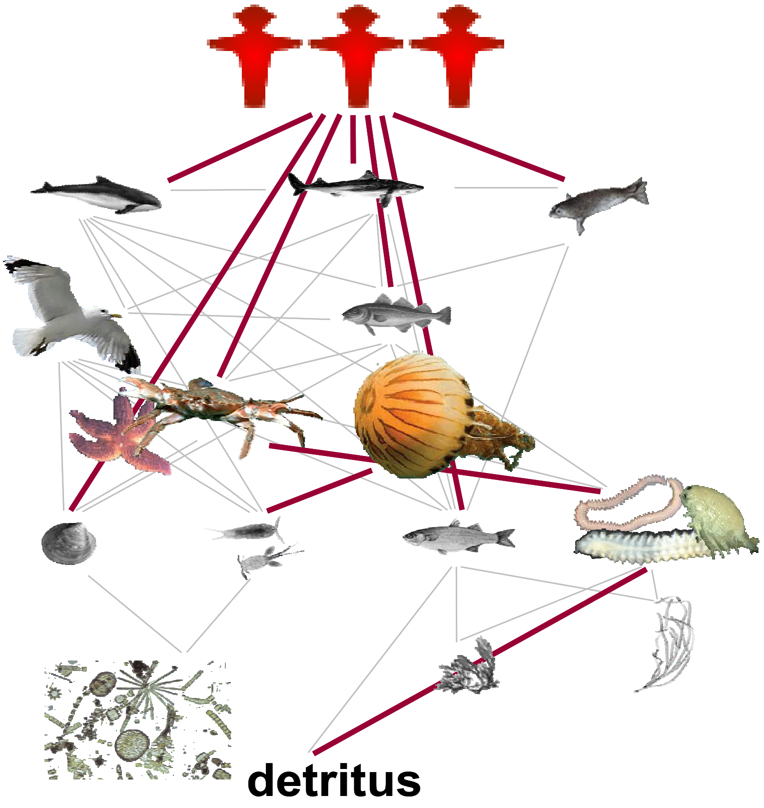


Figure 9: Simplified coastal food web with and without effects of overfishing (a) before industrial fishing exploitation and (b) after/ongoing exploitation. Large-sized coloured symbols indicate abundance or dominance of species; small-sized grey symbols indicate reduction or rarity of species. Thick red lines indicate important interactions within the web (modified from Jackson et al. 2001).

The severity of change depends on structure and dynamics of the system, i.e. the number and kinds of species, their trophic traits and interactions which are lost or potentially added to the system (e.g. Duffy 2003, De Ruiter et al. 2005). Most marine food webs are comparatively flexible, and able to adapt quickly in terms of species inventory and trophic traits (Link 2002, Link et al. 2005). Concurrently, the maintenance of key trophic features and thus the main trophic pathways in the food web is essential for community resilience and resistance despite perturbations (De Ruiter et al. 2005).

Furthermore, the severity of change depends on the strength and frequency of perturbations (Connell 1978). 'Persistent' systems are expected to remain essentially unchanged through time; 'resilient' systems might get changed with respect to their traits only temporarily, and return to a reference state (or dynamics) after the perturbation; 'resistant' systems are changed continuously by frequent perturbations which requires a profound internal system reorganisation to withstand the permanent stress (e.g. Arntz 1981, Boesch & Rosenberg 1981, Grimm et al. 1992, Pimm 1984).

Human impact on marine systems is strongest in coastal regions (Vitousek et al. 1997), and the German Bight is one of most intensely used and impacted marine areas of the world. The system is confronted with and shaped by numerous anthropogenic interferences, but especially by bottom trawling. Statistically, each spot of sea bottom is trawled at least once every year (see PUBLICATION V). Regarding the benthic community structure, it seems to be quite contradictory to adapt to frequent disturbance through a continuously changing species inventory on the one hand, and to keep the main trophic pathways and thus maximum capacity for resistance on the other hand.

5.1 Macrozoobenthic response to fishery

In highly dynamic ecosystems, it is problematic to single out a certain effector such as bottom trawling owing to the overall high variability caused by a variety of natural and anthropogenic perturbations (see Chapter 2.1). More often than not, cause-and-effect studies based on multivariate community analysis fail to detect significant effects of their target parameter, e.g. bottom trawling, because of the predominance of seasonal and year-to-year patterns, see e.g. PUBLICATION IV (compare Fig. 16.14 with Fig. 16.15 and Fig. 16.32 with Fig. 16.33). Moreover, some of the structural changes observed in the North Sea benthos over the last decades might rather be related to climatic changes or eutrophication (e.g. Kröncke 1992, Kröncke et al. 1998, Frid 2006). Nevertheless, historical data and scientific evidence clearly indicate that decades of bottom trawling have changed the German Bight ecosystem distinctly in its structure (see e.g. Jennings et al. 2001a, Callaway et al. 2007) and this chapter will focus on this particular question. The relative role of multi-factorial effects on the benthic community structure will be discussed below (Chapter 5.2 and 5.3).

Ecologcial theory predicts that trophic complexity defines the variety of trophic traits within a community, and thus its potential trophic flexibility (MacArthur 1955, McCann 2000, Duffy 2003, Duffy et al. 2007). Natural dynamics and intense bottom trawling over at least five decades (Lindeboom & de Groot 1998, Rijnsdorp et al. 1998, Rumohr & Kujawski 2000) have structured the benthic community of the German Bight in terms of species inventory and trophic traits (see Chapter 2.3, PUBLICATION II). So far, trawling impact studies have failed to address the full taxonomic diversity of a food web, although there is a general agreement that the species is the evolutionarily derived basic entity of ecological functioning. Thus it is likely that those studies failed to resolve the full impact of trawling on the trophic system.

In this context, there are two obvious questions: (1) If the ecological functioning is defined by the species based trophic complexity, and the community structure has been continuously affected by trawling, what kind of trophic structure can we expect in such a system? and (2) What happens to the trophic structure of the benthic ecosystem if trawling stops?

5.1.1 Response to frequent bottom trawling

Food-web structure is not merely a reflection of species trophic elevation, i.e. the relative distance of a species to the primary food source within the food web hierarchy, but eventually the sum of all trophic interactions in the system. Species with seemingly ‘similar’ trophic elevations may play quite different roles for ecological functioning, owing to differences in the strength of specific trophic links (e.g. Pimm & Lawton 1978, Polis & Holt 1992, Polis & Strong 1996, Duffy et al. 2007). Hence, trophic interactions constitute a crucial part of ecological functioning and thus are a significant determinant of community stability properties (e.g. MacArthur 1955, May 1974, McCann 2000). Particularly ‘weak’ interactions are predicted to enhance community resistance (e.g. McCann et al. 1998, Berlow 1999, McCann 2000).

The German Bight benthic system comprises no typical specialised species, i.e. species with few prey items and thus, few comparatively strong trophic links (PUBLICATION II). Most species are trophic generalists and hence the food web is characterised by a high proportion of ‘weak’ links (PUBLICATION II). The dominance of generalists results from the continuous trawling impact: species that profit from bottom trawling are (i) predators/scavengers that utilise the additional food subsidies (bycatch, discards and gear-induced mortality) such as *Corystes cassivelaunus*, *Asterias rubens*, *Liocarcinus holsatus* and *Pagurus bernhardus* (PUBLICATION IV, PUBLICATION V, e.g. Arntz & Weber 1970, Ramsay et al. 1998, Fonds & Groenewold 2000, Groenewold & Fonds 2000, Bergmann et al. 2002), and (ii) species which feed more or less unselectively on the ‘storage pool’ detritus such as *Echinocardium cordatum* and *Lanice conchilega* (PUBLICATION V, e.g. Pearson & Rosenberg 1978, Wieking & Kröncke 2003, Kröncke et al. 2004). Owing to their vulnerablity to food alterations, it is likely that specialists have been eliminated by permanent bottom trawling first (see Menge &

Sutherland 1987), subsequently replaced by generalistic species. Consequently, bottom trawling is responsible for the high level of trophic redundancy in the benthic system, and thus has created artificially enhanced community resistance (PUBLICATION II, e.g. McCann et al. 1998, Berlow 1999, Eggers & Jones 2000, McCann 2000).

The food web of the German Bight soft-bottom community is dominated by species that are trophic generalists. This results from the continuous trawling impact which selects against trophic specialists and towards trophic generalists, i.e. predators/scavengers that profit from the trawling-induced food subsidies and species feeding unselectively on detritus. Consequently, bottom trawling created artificially resistance of the community by mainly 'weak' trophic links between species and thus high trophic redundancy.

Bottom trawling not only selects towards trophic generalists, but also towards species comparably small in size, with short life cycles and high turnover rates (Figure 10b – d; PUBLICATION IV, PUBLICATION V, e.g. Menge & Sutherland 1987, Collie et al. 2000). These are lifestyle features that reduce vulnerability with respect to permanent disturbance by trawling and thus enhance overall system resistance (e.g. DeAngelis 1980, Jennings et al. 2001a, 2001b, Hiddink et al. 2006a, Duineveld et al. 2007).

The overall pattern of mainly 'weak' trophic interactions and thus of high species trophic redundancy has fundamental implications for the whole benthic food web structure. Ecosystems that are subjected to frequent/semi-continuous perturbations such as the German Bight show moderate to low biodiversity. This results from the 'physical' elimination of vulnerable and possibly specialised species (e.g. Jennings & Kaiser 1998, Blanchard et al. 2004, Callaway et al. 2007), the loss of top predators such as seabirds, marine mammals and fish (see Pauly et al. 1998, Wolff 2000, Pauly & Palomares 2005), and indirect elimination of species through the loss of habitat complexity (e.g. Riesen & Reise 1982, Briand & Cohen 1987, Thrush & Dayton 2002). Consequently, trophic complexity in highly trawled areas is comparatively low (PUBLICATION II), whereas trophic redundancy is high (PUBLICATION II, Figure 10a). The latter may be seen as a crucial buffer that secures sufficient resistance capacity to balance bottom-trawling pressure (insurance hypothesis, see PUBLICATION II, Naeem & Shibin 1997, Naeem 1998, Yachi & Loreau 1999).

Ecological theory predicts exactly such a food web structure, as well as high turnover rates of species for a system subjected to continuous disturbance (e.g. Menge & Sutherland 1987, Jennings et al. 2001b, Dunne et al. 2004, Hiddink et al. 2006a, Queirós et al. 2006), as manifest in terms of hydrodynamics and particularly long-term bottom trawling in the German Bight (see Kröncke et al. 1998, Clark & Frid 2001, Kaiser et al. 2002, Callaway et al. 2007). Accordingly, the benthic food web of my study area is dominated by small species with comparably low trophic elevation in abundance (Figure 10b, PUBLICATION IV). Large species with low trophic elevation and small species with intermediate trophic elevations constitute the major part of biomass (Figure 10c, PUBLICATION IV). The energy flow through the system, i.e. the trophic significance of species (indicated by species metabolism scaled abundance, see PUBLICATION V for details), is mainly driven by small species with intermediate trophic elevations (Figure 10d).

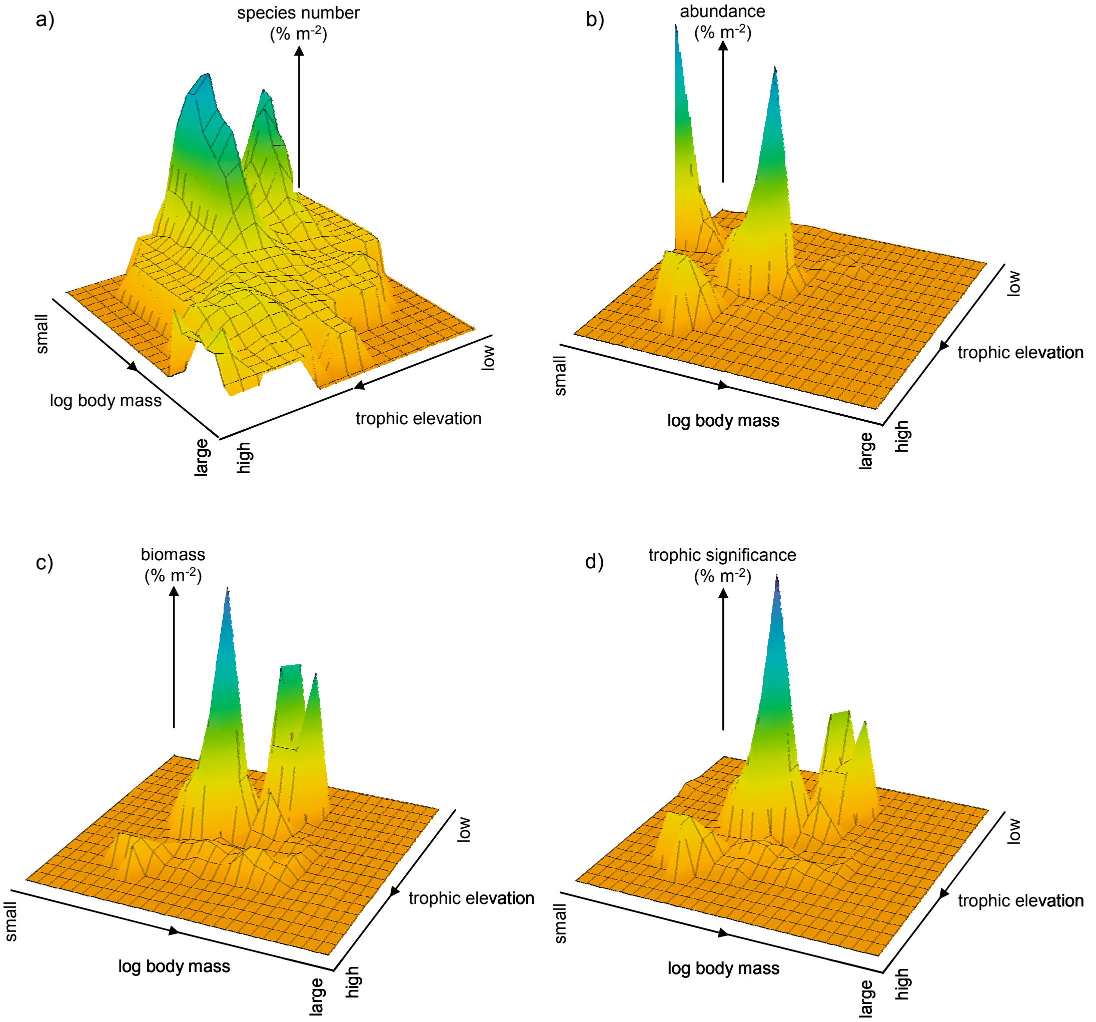


Figure 10: Distribution of (a) species number, (b) abundance, (c) biomass and (d) trophic significance as share (all in % with similar scale) with respect to trophic elevation and body mass of the macrozoobenthic species in the study area.

So far, there are no studies with comparable data to my German Bight example, i.e. that have determined trophic complexity and trophic redundancy with comparable parameters and at such a highly resolved scale. However, if the continuously disturbed German Bight system is taken as a reference point for a typical resistant system, then predictions can be made of how trophic complexity and redundancy should measure in systems of different settings. 'Persistent' systems characterised by low levels of disturbance, long-term constancy and consequently high biodiversity (e.g. the Antarctic system, coral reefs and kelp forests, e.g. Vitousek et al. 1997, Jackson et al. 2001, Fosså et al. 2002, Jacob et al. 2006) should have a higher trophic complexity, lower trophic redundancy and slower turnover rates. ‘Resilient’ systems that experience regularly albeit ‘random’ catastrophic disturbance events and subsequent recolonisation, and thus consequently comparably low biodiversity (e.g. the Baltic Sea system, e.g. Pearson & Rosenberg 1978, Arntz & Rumohr 1982, Nilsson & Rosenberg 2000, Bonsdorff 2006) should have lower trophic complexity and lower trophic redundancy but higher turnover rates. In ‘resilient’ systems such as the Baltic Sea, disturbances might not be bufferd by trophic redundancy owing to the comparably low biodiversity. This lack of buffering capacity is likely to be counterbalanced by system dynamics, i.e. a high turnover rate which shortens the recovery time after perturbations (e.g. DeAngelis 1980, Arntz 1981, Boesch & Rosenberg 1981, Begon et al. 1996).

Hence, ecosystem stability (resistance, resilience and persistence) is a function of the balance between specialised and generalistic species, the extent of community trophic complexity as well as trophic redundancy, and system dynamics. It remains to be seen to what extent this food-web structure of weak interactions, high trophic redundancy and the shift of energy flow pathways towards smaller species with high turnover rates secures sufficient resistance to balance bottom-trawling pressure.

Bottom trawling creates artificial resistance of the benthic food web: by mainly ‘weak’ trophic links between species, high trophic redundancy and energy flow based on small species with high turnover rates. These food-web properties guarantee maximum capacity of resistance and keep the main trophic pathways despite a continuously changing species inventory by frequent bottom trawling.

5.1.2 Response to trawling cessation

Observations of ‘real world’ recovery after cessation of trawling are scarce. Estimates of recovery rates are based on either experimental trawling or on the comparison of ‘lightly’ and ‘heavily’ trawled areas and the models derived thereof. These models predict recovery times of 100 days in terms of numerical abundance (Collie et al. 2000) and 1 – 3 years in terms of biomass and production (Hiddink et al. 2006b). However, soft-bottom monitoring studies indicate longer recovery times after perturbations (more than 3 years, e.g. Pearson & Rosenberg 1978, Arntz & Rumohr 1982, Collie et al. 2005, Smith et al. 2006, De Juan et al. 2007). Regarding these estimates, is there a chance to detect any signs of recovery after only 14 months of closure in a highly dynamic ecosystem such as the German Bight?

Obviously, there is, if one looks at the right parameters: Differences in the benthic community were identified by trophic parameters (PUBLICATION V).

The absence of physical sediment disturbance of fishing gear appears to be the principle cause: the biogeochemnisty changed, i.e. sedimentary organic compounds were lower in the non-trawled area (see PUBLICATION V). Accordingly, community trophic significance was lower, too, particularly owing to a lower trophic significance of the infaunal deposit feeder

Echinocardium cordatum. This species prefers sediments rich in organic content (Wieking & Kröncke 2003, Kröncke et al. 2004) and its population seems to be rather less affected by bottom trawling (Bergman & Hup 1992, Kaiser et al. 2006, Tillin et al. 2006, Duineveld et al. 2007).

The share of small interface feeders (e.g. *Owenia fusiformis*, *Spiophanes bombyx*) and deposit feeders (e.g. *Chaetozone* cf. *setosa*) in community energy flow increased distinctly after cessation of trawling (PUBLICATION V). There was, however, no evidence for a change in diet, although these species depend on high quality food particles (e.g. Kröncke et al. 2004, Wieking & Kröncke 2005). Therefore, we conclude that the absence of physical disturbance is the major driver of this change, as it allows for an increased settlement in these species (PUBLICATION V). Their stronger presence and thus stronger processing of sedimentary organic compounds appears to be partly responsible for biogeochemical changes in the sediment (*sensu* Brown et al. 2005). Analysis based on abundance data detected as well increased settlement in the non-trawled area, albeit with a lower statistical significance (see PUBLICATION IV).

Increased trophic elevation of deposit feeders such as *Pectinaria koreni*, *E. cordatum* and *Tellimya ferruginosa* (PUBLICATION V) is likely to be related to an altered sediment biogeochemistry, too. Trawling cessation leads to an increase in benthic microbial activity (Pusceddu et al. 2005) and subsequent biogeochemical alteration of the processed particulate organic matter (see PUBLICATION V for further details). This signal is passed on to the benthic primary consumers, especially to those feeding on refractory material such as deposit feeders.

The second cause for differences in the benthic community appears to be the absence of fishery-generated additional and artificial food sources, i.e. gear-induced mortality and discards. Particularly large and mobile trophic generalists profit from the easily accessible, comparably high trophic level food generated by trawling (e.g. Arntz & Weber 1970, Fonds & Groenewold 2000, Groenewold & Fonds 2000, Rumohr & Kujawski 2000). Accordingly, trophic elevations are expected to be lower in the non-trawled area and trophic analysis detected such alimentation shifts in the facultative predating/scavenging *Ophiura albida*, *Euspira pulchella* and *Scolelepis bonnieri* (PUBLICATION V, Nagabhushanam & Colman 1959, Kenchington et al. 1998). Surprisingly, there were no such shifts in large, mobile predators and scavengers that are known to benefit from the trawling generated food subsidies, such as *A. rubens*, *A. irregularis* and *L. holsatus* (PUBLICATION V). Obviously, these trophic generalists cover such a trophically wide prey range (e.g. Pimm & Lawton 1978, Cohen et al. 1993, Davenport & Bax 2002) that a fishery related shift in diet is not detectable in species trophic elevation. There is, however, a clear signal in trophic significance, which is distinctly lower in the non-trawled area (PUBLICATION V). The disappearance of trawling generated food sources may have forced these generalists to migrate from non-trawled to trawled areas (PUBLICATION V). Migration as response to trawling cessation seems to be the strongest signal. It was also identifiable with analysis based on species abundance and biomass (PUBLICATION IV), and already observed by Smith et al. (2006) and De Juan et al. (2007).

Trawling cessation led to (1) a lower trophic significance of the community, (2) higher relative numerical abundance and higher trophic significance of small interface feeders, (3) higher trophic elevation of deposit feeders, (4) lower trophic elevation of small facultative predators and scavengers and (5) a lower abundance and lower trophic significance of predators/scavengers. Most likely, a change in biogeochemistry owing to the absence of physical sediment disturbance and the loss of food generated by trawling are the major reasons for these changes.

After 14 month of fishery closure, we were neither able to detect changes in the distribution of trophic elevation among species, as were Jennings et al. (2001a), nor to identify a distinct regime shift with multivariate-community analysis (PUBLICATION IV, PUBLICATION V).

The lack of change in the distribution of trophic elevation, most likely, results from the benthic trophic resistance (PUBLICATION II, see Chapter 5.1.1). Decades of bottom trawling have created a highly artificial but trophically robust system (PUBLICATION II, PUBLICATION V), and a fishery closure of only 14 months is too short to cause significant changes in the food-web structure.

In terms of numerical measures, the results of PUBLICATION IV fit in the recent history of attempts to identify trawling impact on the benthic ecological functioning: Certain strategies, such as the analysis of changes in habitat complexity (e.g. Thrush et al. 2001, Thrush & Dayton 2002), low taxonomic or functional resolution (e.g. PUBLICATION IV, Blanchard et al. 2004, Tillin et al. 2006) or the concentration on purely numerical parameters (species number, abundance, biomass), apparently fail to capture subtle changes in highly dynamic ecosystems (see PUBLICATION IV, Queirós et al. 2006, Tillin et al. 2006). Particularly in small infaunal species, significant and consistent changes following trawling cessation are quite difficult to detect with numerical measures. Duineveld et al. (2007), for example, was not able to provide such evidence even 20 years after closure.

The results of this thesis (compare results of PUBLICATION IV and PUBLICATION V) indicate that species trophic characteristics, the principal lever of ecological functioning (e.g. May 1974, Cohen 1978, Pimm 1982), are a much better indicator of response to trawling cessation than species numerical measures. Obviously, the indirect effects of trawling, i.e. the alteration of biogeochemical composition of the sediment and trophic distortion of food input (bycatch, discards and gear-induced mortality) are – at least at timescales as short as here – more important than direct damage and mortality.

Is there any chance that without fisheries the benthos will return to a condition that resembles the pre-trawling ‘pristine’ state? For the foreseeable future such a return seems rather unlikely, because many decades of bottom trawling caused quite irreversible changes, such as the loss of habitat diversity (e.g. Riesen & Reise 1982, Auster & Langton 1999), and the significant impact of external factors such as pollution (e.g. Duineveld et al. 1991, Basford et al. 1993) and climate change (Kröncke et al. 2001, Lotze et al. 2005, Frid 2006) persists (see chapter 5.3). Large-scale cessation of trawling is likely to cause a benthic regime shift (*sensu* Amaro 2005, Allen & Clarke 2007, Van Nes et al. 2007) towards a high biomass-low turnover system, presumably with higher biodiversity (see Worm et al. 2006). A foreseeable chance for a large-scale fishery ban might be the numerous planned offshore windmill farms along the coasts (Petersen & Malm 2006). However, it is unpredictable what this benthic community will look like in terms of species inventory and food-web structure, and how long the process of a potential regime shift will take.

Trophic characteristics are better and more significant indicators of subtle responses to trawling cessation than numerical measures (species number, abundance, biomass), at least over short timescales as in this thesis.

After 14 months of closure, however, significant changes in the distribution of trophic elevation among species were not detectable. Decades of bottom trawling created a highly artificial but robust system, and a fishery closure of only 14 months is too short to cause significant changes in the food-web structure. A large-scale and long-term fishery ban is likely to cause a benthic regime shift towards a kind of ‘pre-trawling’ state, but this will require a very long time.

5.2 Other anthropogenic impacts on the zoobenthos

The major problem of human impacts is that they do not act in isolation, but may impose additive or synergistic effects upon the affected ecosystem (e.g. Kröncke et al. 1998, Sala et al. 2000, Duffy et al. 2007). A complete overview of all multi-factorial and particularly indirect effects of human impacts on the German Bight benthos is not within the scope of this thesis. Nevertheless, I will discuss some interactions and how they interfere with the benthic system (Figure 11). Moreover, some changes in the benthic community might cause feedback processes on ecosystem services and goods which will be discussed later (see Chapter 5.3).

First and foremost, the macrozoobenthic response to disturbances is a species specific one (e.g. Pearson & Rosenberg 1978, Boesch & Rosenberg 1981, Arntz & Rumohr 1982, Kröncke et al. 1998, Kröncke et al. 2001, this study). As the species is the evolutionarily derived basic entity of ecological functioning, alterations in species inventory affect the overall benthic system, i.e. its biomass distribution, productivity, and trophic structure (Figure 11, blue arrows).

Some human activities affect the benthic ecosystem on a local scale only (Figure 11). Artificial hard substrates such as sheet pile walls, wind turbines or oil rigs cause primarily physical sediment disturbance. They alter the hydrographical conditions which leads to a modification of the surrounding sediment (grain-size alteration, scour development), and consequently to a change in the species inventory of the adjacent soft-bottom fauna (PUBLICATION III, e.g. Davis et al. 1982, Nelson et al. 1994). At the same time, they provide a three dimensional habitat for hard-bottom species which enhance biodiversity locally (e.g. Petersen & Malm 2006), and which constitute an additional food input (e.g. Wolfson et al. 1979, Ambrose & Anderson 1990, Fabi et al. 2002). Not only hard-bottom predators might be attracted thereby, but also those of the surrounding soft-bottom community (PUBLICATION III, e.g. Posey & Ambrose 1994, Petersen & Malm 2006, Wilhelmsson et al. 2006). In view of hundreds of planned wind turbines, these locally restricted alterations might lead to hitherto unknown cumulative effects on a larger spatial scale (see PUBLICATION III for detailed discussion). However, the effect of the turbines on the environment may be outweighed by the fact that bottom trawling, the most serious impact on the benthos, will be banned within windmill farms.

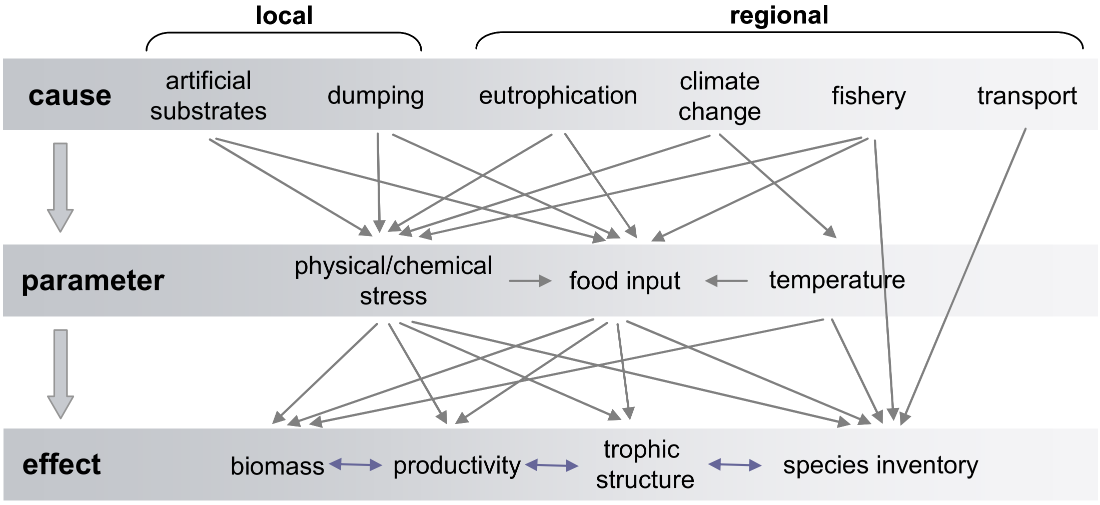


Figure 11: Simplified cause-and-effect chains of the most important anthropogenic impacts on benthic communities in the German Bight. Grey arrows indicate the different cause-parameter-effect chains; blue both-way arrows indicate indirect alterations of the benthic system by changes in species inventory (see text).

Dumping causes physical stress (burial, smothering, grain-size alteration) for the benthic community (e.g. Stronkhorst et al. 2003). In addition, sewage dumping affects the benthic fauna similar to eutrophication, i.e. organic enrichment of the sediment (see below, e.g. Rachor 1980, Mühlenhardt-Siegel 1981, Mühlenhardt-Siegel 1990). However, the introduction of sewage sludge in marine sediments has decreased over the last decades. Harbour-sludge dumping causes not only physical disturbance of the benthos, but might cause as well chemical contamination of the sediment which is passed to the benthos by e.g. feeding on detritus (e.g. Rosenberg 1977, Stronkhorst et al. 2003, Witt et al. 2004).

Eutrophication is the principal large scale anthropogenic impact on marine systems (Figure 11). It enhances the amount of nutrients and leads to increased primary production which is passed to the benthos by sedimentation (benthic-pelagic coupling, e.g. Tunberg & Nelson

1998, Kirby et al. 2007). Consequently, organic enrichment of the sediment initially causes an increase in benthic biomass (e.g. Pearson & Rosenberg 1978, Kröncke et al. 1998) and can lead to shifts in the trophic structure (e.g. Pearson & Rosenberg 1978, Wieking & Kröncke 2005, Kröncke 2006). In the last instance, such oversupply of organic matter can exhaust the aerobic degradation capacity of the benthic system, and induce mortality of species sensitive to oxygen deficiency (e.g. Pearson & Rosenberg 1978, Arntz & Rumohr 1982, Arntz & Rumohr 1986, Rachor 1990, Nilsson & Rosenberg 2000).

Climate change affects the benthic ecosystem primarily through alterations in the temperature regime and the hydrodynamical regime, i.e. frequency and strength of storms. Such changes favour more resistant species and consequently shift the species composition (e.g. Kröncke et al. 1998, Armonies et al. 2001, Kröncke et al. 2001, Schröder 2005, Frid 2006, Pörtner & Knust 2007). Secondary effects of climate change may become visible in the food regime: increased temperature may lead to (a) higher primary production (e.g. McQuatters-Gollop et al. 2007) and consequently affects the benthos similar to eutrophication, (b) a temporal delay in phytoplankton succession which causes lifecyle/food-resource mismatch (e.g. Beaugrand et al. 2003, Wiltshire & Manly 2004) and (c) higher inefficiency of food supply along the trophic hierarchy: increased temperature causes higher respiration rates of poikilothermal species which results in lower secondary production (e.g. Begon et al. 1996). As the current benthic system consists of mainly small species (see Chapter 5.1.1) with generally higher respiration rates, the effect of inefficient food supply might be additively amplified.

Introduction of alien species through long distance transport of larvae (ballast water) or adults (fouling organisms) by ships is, besides fishery impacts (see Chapter 5.1 for detailed discussion), the only other direct impact on the species inventory (Carlton & Geller 1993, Cohen & Carlton 1998). The overall effect of invaders depends on how they integrate into the community: they range from co-existence to extinction of indigenous species (e.g. Essink & Dekker 2002).

Anthropogenic impact does not only act on various spatial scales (Figure 11), but also on different time scales, i.e. long-term (e.g. climatic changes, artificial hard substrates), frequently (e.g. trawling) or comparably short-term (e.g. dumping). The severity of the effect on the benthic fauna depends on the strength and the frequency of the impact (e.g. Connell 1978). Trawling is the most frequent impact in the southern North Sea, but it does not act in isolation. Other human impacts and natural forces may enhance or dampen it, but such interactions are complex. At present, they are hardly assessable, albeit together they shape the present community characteristics (see Kröncke et al. 1998, Kröncke et al. 2001, Frid 2006). Especially in conjunction with indirect effects via biological interactions, anthropogenic interference leads to indirect and potentially unpredictable consequences in ecological functioning (see Chapter 5.3, e.g. Myers 1995, Duffy et al. 2007).

Different types of anthropogenic impact in the German Bight act on different temporal and spatial scales, although they do not act in isolation. Furthermore, although all disturbances affect primarily certain species, concurrently they affect the overall benthic system since species are the evolutionarily derived basic entity of ecological functioning. Accordingly, anthropogenic impacts impose additive or synergistic effects upon the German Bight ecosystem with indirect and potentially unpredictable consequences for ecosystem functioning.

5.3 Ecological implications

The severity of ecosystem changes results from the external forcing factors, natural and anthropogenic ones, their severity, and from the ecological traits an ecosystem has to buffer perturbation stress (e.g. Yachi & Loreau 1999, McCann 2000, Duffy et al. 2007). Hence, as species are the principle lever of ecological functioning, ecosystem changes are a result of the number and kinds of species which are lost or potentially added to the system (e.g. Boesch & Rosenberg 1981, Duffy 2003, De Ruiter et al. 2005).

The German Bight benthic system is affected by numerous natural (chapter 2.1) and anthropogenic perturbations (chapter 5.2). The complexity of this multi-factorial picture does not allow for an in-depth discussion of the whole setting. On the other hand, ecological alterations caused by fishery disturbance can not be treated in isolation, because other anthropogenic impacts impose additive and synergistic effects (see chapter 5.2). Nevertheless, bottom trawling is the most severe and most frequent impact in the southern North Sea, and it has caused a considerable loss of species and habitats over the last century (e.g. Riesen & Reise 1982, Callaway et al. 2007) with subsequent changes in ecological functioning (see chapter 5.1). Jackson et al. (2001) suggested that overfishing may often be a necessary precondition for other anthropogenic impacts such as eutrophication and invasion of species to occur.

In the following, I discuss the consequences of species loss on ecosystem services induced by fishery, and the potential species gain and its consequence for the benthic community that may arise from climate warming and species invasion.

Past and ongoing bottom trawling causes a decline in habitat complexity such as the loss of once common seagrass beds and natural reefs (Riesen & Reise 1982, Auster & Langton 1999). The loss of highly structured habitats leads to a loss of refuges (see Figure 12) and has a significantly negative influence on growth and survivorship of commercially valuable species (e.g. Briand & Cohen 1987, Watling & Norse 1998, Thrush & Dayton 2002). Moreover, overexploitation of mussel beds has led to a considerable loss of filter feeders and consequently to a deterioration of water quality (e.g. enhanced eutrophication, more toxic plankton blooms), subsequently affecting leisure, tourism and human well-being (see Riesen & Reise 1982, Vitousek et al. 1997, Jackson et al. 2001).

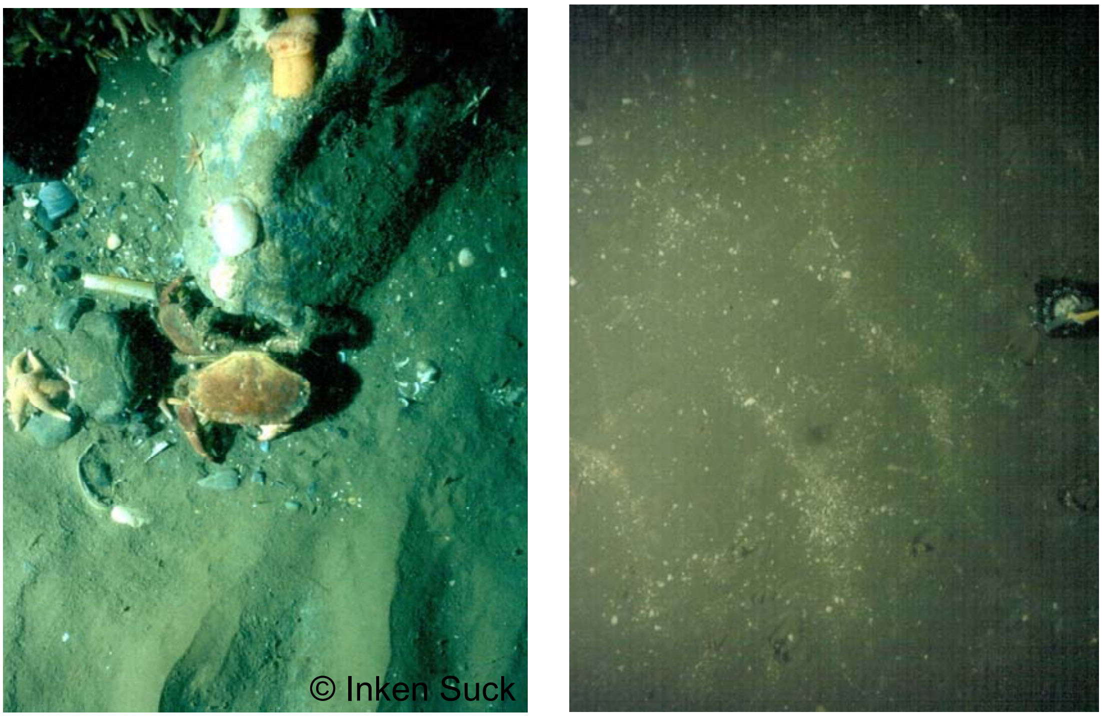


Figure 12. North Sea-bottom fotos: stones and sand-rippels providing a three-dimensional habitat (left side) and untextured surface caused by bottom trawling (right side); (scale: 0.75 m^2).

Bottom trawling causes a loss of high trophic level species. ‘Fishing down the food web’ characterises the long-term development of world fisheries: the shift from long-lived, large, high trophic level, piscivorous species towards short-lived, small, low trophic level species, owing to the seemingly unavoidable overexploitation of every target stock (see Pauly et al. 1998, Pauly & Palomares 2005). Extinction of high trophic level species can lead to unintended cascading effects along the food web hierarchy (e.g. Post 2002a, Bascompte et al. 2005). On the one hand, a decrease in piscivorous fish can lead to an increase in planktivorous pelagic fish stocks (direct positive effect). On the other hand, it can lead to a decrease in planktivorous pelagic fish because of missing ‘beneficial predation’, i.e. preying on other predators or competitors of the planktivorous fish species (indirect positive effect) (see Sih et al. 1985, Pauly et al. 2002, Morissette et al. 2006). Hence, overexploitation can indirectly lead to a loss of other valuable resources (e.g. Pauly et al. 1998, Frank et al. 2005) or to an overwhelming increase in other species, e.g. jellyfish (e.g. Mills 2001, Daskalov 2002). For example, the overexploitation of pelagic planktivorous fish (together with eutrophication) caused a burst of the invasive ctenophore *Mnemiopsis leidyi* in the Black Sea, not vice versa as generally believed (Gucu 2002): both species feed on phytoplankton and the decrease in planktivorous fish released the ctenophore from food competition.

Human interferences such as bottom trawling trigger directly or indirectly ecosystem processes through decimation, extinction of species or changes in species distribution. This impact on ecosystem processes is more obvious in hitherto pristine communities (e.g. Fosså et al. 2002, Hall-Spencer et al. 2002), but is continuing more subtly in already affected areas (see chapter 5.1). Therefore, ecological theory predicts that past, ongoing and forthcoming indirect and synergistic human impacts on ecological functioning will lead to a further reduction in services and goods (Naeem & Shibin 1997, Chapin III et al. 2000, Loreau et al. 2001, Dobson et al. 2006).

Forthcoming synergistic effects on the German Bight benthos may arise from climate change and increased species invasion. Over the last decades, climate warming has caused biogeographical shifts in several species (see Perry et al. 2005, Sims 2006). In the southern North Sea, the water temperature has risen by 1.1°C over the last 45 years (Wiltshire & Manly 2004), and concurrently, more southern species have been reported 'visiting' the North Sea (see Franke & Gutow 2004, Sims 2006, Wätjen 2007), a recent example is the above named ctenophore *Mnemiopsis leidyi* (Boersma et al. 2007, pers. communication K. Barz).

Whether invasive species establish successfully in an ecosystem depends on (a) the accessibility of the habitat, (b) the capability of the prevailing ecosystem to support the non-indigenous species (Vander Zanden et al. 2004, Reise et al. 2006) and (c) the potential competitive advantage of the invader over native species (e.g. Stachowicz et al. 2002b).

On the one hand, the German Bight is easily accessible via larval dispersal and migration through the natural Atlantic Ocean corridors (e.g. Reise et al. 2006), particularly since the inflow of Atlantic-water masses in the North Sea has increased over the last decades (e.g. Edwards et al. 2002, Beaugrand 2004). On the other hand, the German Bight is an invasion 'hot spot' because of intense transoceanic shipping traffic, and thus carriage of non-indigenous species by ship ballast water and hull fouling (e.g. Gollasch 1996, Ricciardi & Rasmussen 1998).

Ecological theory predicts that less diverse communities with low trophic complexity are more susceptible to invasions because of lower competition of invaders with native species for food and space, i.e. there might be more opportunities for an invader to establish successfully in the ecosystem (*sensu* Elton 1958, Stachowicz et al. 1999, Duffy 2003). The southern North Sea is a geologically very young sea (about 10 000 years, Becker et al. 1992) and not all species niches might yet be filled. Moreover, past and ongoing disturbances keep the German Bight system 'open' for invasion by the continuous loss of species and the consequent low trophic complexity (PUBLICATION II). A number of invaders have already established populations in the southern North Sea successfully (mainly since 1950, Gollasch 2006), most of them rather by integration into the prevailing community than by 'conquering' niches from local species (see Reise et al. 1999, Essink & Dekker 2002, Reise et al. 2006, Dannheim & Rumohr submitted).

Invasions might become, even more than today, a significant aspect of climate change on ecological functioning. For example, the interaction of overexploitation and climate warming is responsible for the dramatic decrease in North Sea cod (*Gadus morhua*) (Casini et al.

2005, Perry et al. 2005, Stige et al. 2006). In contrast, the abundance of grey gurnard (*Eutrigla gurnardus*) has increased, and the species occupies a trophic niche similar to that once occupied by cod (Floeter et al. 2005). The red mullet (*Mullus surmuletus*), a lusitanian species which has continuously expanded its range into the southern and western North Sea during the last fifteen years, can be expected to fill the 'empty' cod-niche, too, at least the niche of small cod (Wätjen 2007).

The current benthic community is able to resist permanent physical stress and adapt to an altered food regime (chapter 5.1 and 5.2), but it remains to be seen whether and to what extent the benthic species are able to adapt physiologically to higher temperatures (see example of eelpout (*Zoarces viviparus*) in Pörtner & Knust 2007). Invaders from the south are better adapted to higher temperatures, an important advantage over native species that becomes manifest e.g. by differential recruitment success (e.g. Stachowicz et al. 2002b, Diederich et al. 2005), and finally by successful establishment in the German Bight (see example of *Crassostrea gigas* – *Mytilus edulis* in Diederich et al. 2005, Nehls et al. 2006).

Currently, overexploitation and climate change are causing dramatic alterations in many coastal ecosystems resulting in changes in species composition (both through local extinctions as well as the introduction of new species) and, as a result, changes in the linkages between the different components of the food web (e.g. McCann et al. 1998, McCann 2000, Stachowicz et al. 2002a, Vander Zanden et al. 2004). Synergistic effects of expected food web shifts in combination with environmental changes may threaten marine ecosystem stability and recovery potential. This in turn may lead to significant and potentially irreversible changes in coastal ecosystem characteristics and services (e.g. Vitousek et al. 1997, Sala et al. 2000, Dobson et al. 2006).

The species inventory of a given ecosystem results from the interplay of environmental conditions, evolutionary adaptation and immigration of predisposed species. Accelerated environmental change might topple the delicate balance between selective and adaptive forces, when species elimination and replacement are out of synchrony, causing change or loss of ecosystem functioning. Understanding ecosystem change thus requires understanding of species response including differential responses of interacting species.

Human interferences such as bottom trawling directly or indirectly trigger the loss of species, and as a result, change ecosystem processes which will – finally – lead to a reduction in services and goods.

Overexploitation and climate change are causing dramatic alterations in many coastal ecosystems in species compositon and subsequent changes in the food web structure. This may lead to signifcant and potentially irreversible changes in coastal ecosystem characteristics and services. Accelerated environmental change might topple the current ecosystem stablilty properties, causing change or loss of ecosystem functioning.

5.4 Future challenges

This case study of the German Bight benthos demonstrates how strongly bottom trawling affects the trophic structure of the benthic system and that it will not return towards a pre-trawling “pristine” stage in the foreseeable future. In contrast, continuous climate warming (Edwards et al. 2002, Beaugrand 2004, Wiltshire & Manly 2004) and increased species invasion (e.g. Reise et al. 2006, Sims 2006) might put further pressure on the benthic community (see Vitousek et al. 1997, Kröncke et al. 1998, Sala et al. 2000, Duffy et al. 2007).

Hence, reducing trawling pressure in the southern North Sea is indispensable, not only in order to re-establish an ecosystem-compatible and sustainable fishery management that fulfils the increasing demand for marine services and goods (e.g. Pauly et al. 2002, Cury et al. 2005, Worm et al. 2006), but also for enhancing ecological ‘quality’ (higher biodiversity and higher trophic complexity) in the long term. Permanent and large marine protected areas with ‘no-take’ reserves at their core may be one way to achieve this goal. They are likely to cause a shift towards a high biomass-low turnover system, presumably with higher biodiversity (*sensu* Worm et al. 2006, Allen & Clarke 2007, Van Nes et al. 2007) and positive spillover effects such as an increase in fish populations in the surroundings (e.g. Murawski et al. 2000, Roberts et al. 2001). A forthcoming and rather ‘practial’ chance for conceivable long-term and large-scale closure might be the planned offshore windmill farms in the German Bight (Petersen & Malm 2006).

Although scientists and politicians agree that sustainability of fisheries can only be managed with a comprehensive ecological approach, the practial accomplishment is quite difficult, i.e. habitats and species differ in their sensivity to trawling impact (see Browman & Stergiou 2004, Dobson et al. 2006, Gray et al. 2006, Hiddink et al. 2007, this study). Hence, a central issue concerning sustainability is still the lack of knowledge on ecological functioning of coastal ecosystems (Cury 2004 in Browman & Stergiou 2004, Frid et al. 2006). In the public as well as in science, charismatic or economically important marine species still receive much more attention (Pinnegar et al. 2005, Dobson et al. 2006) than inconspicuous ones, albeit they may contribute much more to crucial ecological processes (Hall & Raffaelli 1993, Arntz et al. 1999, Jennings 2005). In order to develop ecologically meaningful management approaches at the ecosystem level, it is inevitable to better understand basic ecological functioning and stress response of the benthic system. Therefore, future research should focus on:

trophic properties as they offer reliable data for ecological changes, especially in highly dynamic coastal ecosystems such as the German Bight, because (a) they seem to be less affected by natural environmental variability than numerical measures (species number, abundance and biomass) and (b) a number of anthropogenic impacts alter, directly or indirectly, the food regime;

species sensivity to disturbances because (a) the species is the evolutionarily derived basic unit of ecological functioning, (b) seemingly functionally 'similar' species may differ in their response to perturbations and (c) every response of a system starts with the response of certain species. '*Do not classify! Look how organisms create, maintain and change their habitat!*' (Pearson 2007);

connections between occurrence, distribution and trophic properties of species, i.e. species share in total energy flow of a system and species trophic niche width; these parameters link ecological patterns to environmental processes and thus provide information on (a) community structure in terms of stability properties and (b) habitat characteristics and habitat distributions, e.g. essential feeding habitats. (c) The combination of (a) and (b) might be an initial step forward to 'design ecological rules' for marine protected areas, i.e. how they should be adjusted to regions and ecosystems (Frid et al. 2006).

Ecosystem functioning and the linkage between environmental patterns, anthropogenic disturbances and ecological processes will be the major challenge in future marine research (e.g. Hutchinson 1959, Polis & Strong 1996, McCann 2000, Dunne et al. 2002, Duffy et al. 2007). This is essential for developing ecosystem approaches for sustainable fishery management and to move beyond the case-by-case responding, i.e. focusing on the most recent symptoms of the problem, than rather understanding the intrinsic mechanisms (Jackson et al. 2001). For the time being, the uncertainties regarding synergistic effects of anthropogenic impacts and our prevailing ignorance of the details of ecological functioning (e.g. Myers 1995, Loreau et al. 2001, Duffy et al. 2007) suggest that we should handle coastal ecosystems as carefully as possible.

“*Only after the last tree has been cut down,*
only after the last river has been poisoned,
only after the last fish has been caught,
then will you find that money cannot be eaten.“
(Cree Prophecy)

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7 Literature

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8 Annex

List of all species occurring in the study area with corresponding nitrogen stable isotope ratio (δ^{15}N, ‰) and feeding guild (FG). DF = deposit feeder, DF/PS = DF and predator/scavenger, HV/PS = herbivore and predator/scavenger, IF = interface feeder, PS = predator/scavenger, PA = parasite, SF = suspension feeder, SL = sandlicker. * marks species whose average δ^{15}N values served as primary consumer (PC) base (see PUBLICATION II, PUBLICATION V). Numbers in parenthesis indicate δ^{15}N data source (see end of table).

Species	δ^{15}N (‰)	FG	Source of δ^{15}N
MOLLUSCA			
GASTROPODA			
Acteon tornatilis	11.52	PS	value *E. pulchella*
Cylichna cylindracea	11.52	PS	value *E. pulchella*
Turbonilla acuta	–	PA	no data, excluded from analyses
Vitreolina philippi	–	PA	no data, excluded from analyses
Euspira catena	11.52	PS	value *E. pulchella*
Euspira pulchella	11.52	PS	(1) direct measurement
Turritella communis	9.33	SF	(7)
Mangelia brachystomum	11.52	PS	value *E. pulchella*
Raphitoma linearis	11.52	PS	value *E. pulchella*
BIVALVIA			
Nucula nitidosa	8.34	DF	(7)
Thracia papyracea	8.34	DF	(7) value *Thracia convexa*
Corbula gibba	9.90	SF	(7)
Donax vittatus	9.33	SF	mean SF
Mactra stultorum	9.33	SF	mean SF
Spisula sp.	9.33	SF	value *S. subtruncata*
Spisula elliptica	9.33	SF	value *S. subtruncata*
Spisula subtruncata	9.33	SF	(7)
Tellimya ferruginosa *	10.00	DF	(1) direct measurement
Mysella bidentata	9.33	SF	mean SF
Ensis directus	9.56	SF	(9) value *E. siliqua*
Ensis ensis	9.56	SF	(9) value *E. siliqua*
Pharidae	9.71	SF	mean *E. directus*, *E. ensis* & *P. pellucidus*
Phaxas pellucidus *	10.01	SF	(1) direct measurement
Gari fervensis	9.33	SF	mean SF
Abra alba	8.34	DF	mean DF
Tellina fabula *	9.08	SF	(1) direct measurement
Chamelea gallina (7)	9.19	SF	(7)

List continued	$\delta^{15}N$ (‰)	FG	Source of $\delta^{15}N$
<u>**CEPHALOPODA**</u>			
Sepiola atlantica	15.61	PS	value *L. vulgaris*
Alloteuthis spp.	15.61	PS	value *L. vulgaris*
Loligo vulgaris (8)	15.61	PS	(8)
<u>**ANNELIDA**</u>			
<u>**POLYCHAETA**</u>			
Capitellida			
Capitella capitata	9.94	DF	value *N. latericeus*
Notomastus latericeus	9.94	DF	(7)
Magelona alleni	11.44	IF	mean IF
Magelona filiformis	11.44	IF	mean IF
Magelona johnstoni	11.44	IF	mean IF
Cirratulida			
Chaetozone cf. setosa	7.34	DF	(4) value *Tharyx acutus*
Opheliida			
Ophelia limacina	8.34	DF	mean DF
Scalibregma inflatum	8.34	DF	mean DF
Orbiniida			
Scoloplos armiger	7.70	DF	(4) value *Orbinia ornata*
Oweniida			
Owenia fusiformis	11.44	IF	(7)
Phyllodocida			
Aphrodita aculeata	15.51	PS	(8)
Glyceridae	10.89	PS	(7) value *Glycera* sp.
Glycinde nordmanni	10.89	PS	(7) value *Glycera* sp.
Goniada maculata	14.75	PS	(1) direct measurement
Goniadella bobretzkii	12.82	PS	mean *G. maculata* & *G. nordmanni*
Goniadidae	12.82	PS	mean *G. maculata* & *G. nordmanni*
Podarkeopsis helgolandica	10.24	PS	(4) value *Podarke obscura*
Nephtys spp.	13.29	PS	(1) direct measurement
Nephtys assimilis	13.29	PS	value *Nephyts* spp.
Nephtys caeca	13.29	PS	(7)
Nephtys cirrosa	13.29	PS	value *Nephyts* spp.
Nephtys hombergii	13.29	PS	(7)

List continued	**$\delta^{15}N$ (‰)**	**FG**	**Source of $\delta^{15}N$**
Nephtys longosetosa	13.29	PS	value *Nephyts* spp.
Eunereis longissima	13.56	DF/PS	(1) direct measurement
Pholoe baltica	10.72	PS	mean *Harmothoe extenuata* & *H. imbricata*
Eteone foliosa	10.04	DF/PS	(4) value *Eteone lactea*
Eteone longa	10.04	DF/PS	(4) value *Eteone lactea*
Eumida sanguinea	12.57	PS	mean PS polychaetes
Phyllodoce groenlandica	12.57	PS	mean PS polychaetes
Phyllodoce lineata	12.57	PS	mean PS polychaetes
Phyllodoce mucosa	12.57	PS	mean PS polychaetes
Phyllodoce rosea	12.57	PS	mean PS polychaetes
Phyllodocidae	12.57	PS	mean PS polychaetes
Eunoe nodosa	10.72	PS	(4) Mean *H. extenuata* & *H. imbricata*
Gattyana cirrosa	10.72	PS	(4) Mean *H. extenuata* & *H. imbricata*
Harmothoe glabra	10.72	PS	(4) Mean *H. extenuata* & *H. imbricata*
Malmgrenia marphysae	10.72	PS	(4) Mean *H. extenuata* & *H. imbricata*
Polynoidae	10.72	PS	(4) Mean *H. extenuata* & *H. imbricata*
Sigalion mathildae	10.72	PS	(4) Mean *H. extenuata* & *H. imbricata*
Sthenelais limicola	10.72	PS	(4) Mean *H. extenuata* & *H. imbricata*
Autolytus prolifer	12.57	PS	mean PS polychaetes
Streptosyllis websteri	11.44	IF	mean IF
Spionida			
Poecilochaetus serpens	11.77	IF	(1) direct measurement
Aonides paucibranchiata	11.44	IF	mean IF
Polydora pulchra	11.44	IF	mean IF
Scolelepis spp.	12.70	IF	value *S. bonnieri*
Scolelepis bonnieri	12.70	IF	(1) direct measurement
Scolelepis tridentata	12.70	IF	value *S. bonnieri*
Spio decoratus	11.44	IF	mean IF
Spio filicornis	11.44	IF	mean IF
Spio goniocephala	11.44	IF	mean IF
Spionidae	11.44	IF	mean IF
Spiophanes bombyx	12.26	IF	(1) direct measurement
Terebellida			
Pectinaria spp.	9.92	DF	value *P. koreni*
Pectinaria koreni *	9.92	DF	(1) direct measurement
Lanice conchilega	11.41	IF	(1) direct measurement

List continued	$\delta^{15}N$ (‰)	FG	Source of $\delta^{15}N$
ARTHROPODA			
CRUSTACEA			
Amphipoda			
Ampelisca brevicornis	5.87	SF	(5)
Ampelisca tenuicornis	5.87	SF	(5)
Amphilochus neapolitanus	8.34	DF	mean DF
Aora gracilis	6.29	DF	(4) *Microdeutopus gryllotalpa*
Argissa hamatipes	8.34	DF	mean DF
Atylus spp.	12.23	DF/PS	mean DF/PS
Atylus falcatus	12.23	DF/PS	mean DF/PS
Atylus swammerdami	12.23	DF/PS	mean DF/PS
Apherusa ovalipes	8.34	DF	mean DF
Caprellidae	12.23	DF/PS	mean DF/PS
Pariambus typicus	11.44	IF	mean IF
Phtisica marina	12.23	DF/PS	mean DF/PS
Siphonoecetes krøyeranus	11.44	IF	mean IF
Bathyporeia spp.	11.82	SL	value *Urothoe poseidonis*
Bathyporeia elegans	11.82	SL	value *U. poseidonis*
Bathyporeia guilliamsoniana	11.82	SL	value *U. poseidonis*
Bathyporeia tenuipes	11.82	SL	value *U. poseidonis*
Urothoe poseidonis	11.82	SL	(1) direct measurement
Microprotopus maculatus	12.23	DF/PS	mean DF/PS
Photis longicaudata	8.34	DF	mean DF
Jassa falcata	9.33	SF	mean SF
Leucothoe incisa	8.34	DF	mean DF
Acidostoma obesum	13.00	DF/PS	(5), (10) mean *Anonyx* sp., *Orchomene gerulicorbis*, *O. chevrieux*
Lysianassidae	13.00	DF/PS	(5), (10) mean *Anonyx* sp., *Orchomene gerulicorbis*, *O. chevrieux*
Orchomene nana	13.00	DF/PS	(5), (10) mean *Anonyx* sp., *Orchomene gerulicorbis*, *O. chevrieux*
Megaluropus agilis	9.33	SF	mean SF
Abludomelita obtusata	8.34	DF	mean DF
Perioculodes longimanus	11.82	SL	value *U. poseidonis*
Pontocrates altamarinus	8.34	DF	mean DF
Pontocrates arenarius	8.34	DF	mean DF
Synchelidium maculatum	8.34	DF	mean DF
Stenothoe marina	9.33	SF	mean SF
Cumacea			
Bodotria scorpioides	8.34	DF	mean DF
Iphinoe trispinosa	8.34	DF	mean DF
Diastylidae	11.44	IF	mean IF

List continued	**$\delta^{15}N$ (‰)**	**FG**	**Source of $\delta^{15}N$**
Diastylis bradyi	11.44	IF	mean IF
Diastylis laevis	11.44	IF	mean IF
Diastylis rathkei	11.44	IF	mean IF
Eudorella truncatula	11.44	IF	mean IF
Pseudocuma longicornis	11.44	IF	mean IF
Pseudocuma similis	11.44	IF	mean IF
Decapoda			
Callianassa spp.	8.34	DF	value *C. subterranea*
Callianassa subterranea	8.34	DF	(7)
Callianassa tyrrhena	8.34	DF	value *C. subterranea*
Cancer pagurus	15.01	PS	(8)
Corystes cassivelaunus	14.11	PS	(7)
Crangon allmani	13.31	PS	(8)
Crangon crangon	14.29	PS	(1) direct measurement
Crangonidae	13.80	PS	mean *C. crangon* & *C. allmani*
Philocheras bispinosus	13.80	PS	value Crangonidae
Philocheras trispinosus	13.80	PS	value Crangonidae
Galathea spp.	12.23	DF/PS	mean DF/PS
Ebalia cranchii	12.61	PS	(8)
Ebalia tumefacta	12.61	PS	value *E. cranchii*
Hyas sp.	12.23	DF/PS	mean DF/PS
Macropodia sp.	12.23	DF/PS	mean DF/PS
Macropodia rostrata	12.23	DF/PS	mean DF/PS
Pagurus bernhardus	11.96	PS	(1) direct measurement
Pandalus montagui	12.61	PS	(8)
Pisidia longicornis	13.12	PS	mean PS decapods
Liocarcinus spp.	12.77	PS	mean *L. holsatus* & *L. depurator*
Liocarcinus arcuatus	12.77	PS	mean *L. holsatus* & *L. depurator*
Liocarcinus depurator	12.21	PS	(8)
Liocarcinus holsatus	13.33	PS	(1) direct measurement
Processa spp.	11.71	PS	(8) value *P. canaliculata*
Processa modica	11.71	PS	(8) value *P. canaliculata*
Processa nouveli holthuisi	11.71	PS	(8) value *P. canaliculata*
Thia scutellata	13.12	PS	mean PS decapods
Upogebia deltaura	9.33	SF	(7)
Mysidacea			
Gastrosaccus spinifer	11.44	IF	mean IF
Tanaidacea			
Tanaissus lilljeborgi	8.34	DF	mean DF

List continued	**$\delta^{15}N$ (‰)**	**FG**	**Source of $\delta^{15}N$**
CHELICERATA			
Pantopoda			
Achelia echinata	12.03	HV/PS	(3) value *Ascorhynchus abyssi*
Nymphon brevirostre	12.03	HV/PS	(3) value *A. abyssi*
Nymphon gracile	12.03	PS	(3) value *A. abyssi*
Anoplodactylus petiolatus	12.03	PS	(3) value *A. abyssi*
ECHINODERMATA			
Asteroidea			
Asterias rubens	14.10	PS	(1) direct measurement
Astropecten irregularis	13.63	PS	(1) direct measurement
Echinoidea			
Echinocyamus pusillus	11.82	SL	value *U. poseidonis*
Psammechinus miliaris	12.31	DF/PS	(8)
Echinocardium cordatum *	8.88	DF	(1) direct measurement
Ophiuroidea			
Acrocnida brachiata	11.44	IF	value *A. filiformis*
Amphiura filiformis	11.44	IF	(7)
Amphiuridae	8.34	IF	value *A. filiformis*
Ophiothrix fragilis	10.81	SF	(8)
Ophiura albida	13.15	PS	(1) direct measurement
Ophiura ophiura	13.01	PS	(8)
Ophiuridae	12.32	PS	mean *O. fragilis*, *O albida* & *O. ophiura*
CHORDATA			
OSTEICHTHYES			
Gadiformes			
Gadus morhua	14.62	PS	(2)
Merlangius merlangus	15.93	PS	(2)
Trisopterus luscus	16.94	PS	(9) value *T. minutus*
Trisopterus minutus	16.94	PS	(9)
Ciliata mustela	15.11	PS	mean PS pisces
Perciformes			
Ammodytes tobianus	14.34	PS	(9) value *A. marinus*
Hyperoplus lanceolatus	15.09	PS	(2)

List continued	**$\delta^{15}N$ (‰)**	**FG**	**Source of $\delta^{15}N$**
Callionymus lyra	15.91	PS	(2)
Callionymus reticulatus	15.91	PS	(2) value *C. lyra*
Pomatoschistus minutus	15.19	PS	(1) direct measurement
Mullus surmuletus	15.45	PS	(2)
Pholis gunnellus	15.11	PS	mean PS pisces
Echiichthys vipera	15.11	PS	mean PS pisces
Pleuronectiformes			
Arnoglossus laterna	14.71	PS	(2)
Limanda limanda	15.20	PS	(2)
Microstomus kitt	14.49	PS	(2)
Platichthys flesus	15.57	PS	(2)
Pleuronectes platessa	14.56	PS	(2)
Buglossidium luteum	15.39	PS	(2)
Solea solea	18.02	PS	(9)
Scorpaeniformes			
Agonus cataphractus	15.11	PS	mean PS pisces
Myoxocephalus scorpius	13.00	PS	(2)
Liparis liparis	12.37	DF/PS	(5)
Chelidonichthys gurnardus	15.25	PS	(2)
Chelidonichthys lucerna	15.25	PS	value *C. gurnardus*
Syngnathiformes			
Entelurus aequoreus	12.07	DF/PS	(6) Mean *Syncnathus abaster* & *S. typhle*
Syngnathus rostellatus	12.07	DF/PS	(6) Mean *S. abaster* & *S. typhle*
Others			
Anthozoa	13.92	PS	(1) direct measurement
Edwardsia spp.	11.44	IF	mean IF
Branchiostoma lanceolatum	9.33	SF	mean SF
Cerianthus lloydi	11.44	IF	mean IF
Phoronis sp.	9.33	SF	mean SF
Nemertini	15.14	PS	(1) direct measurement

$\delta^{15}N$ data sources:

(1) Direct measurement
(2) Mintenbeck K. unpublished data
(3) Bergmann M. unpublished data

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