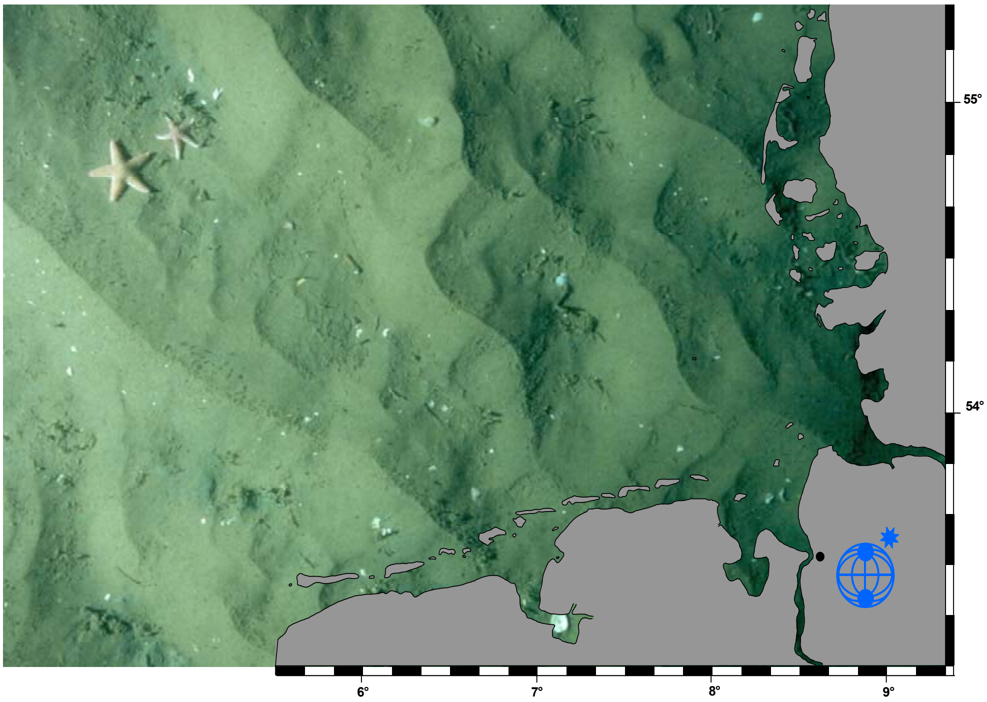
Community dynamics and development of soft bottom macrozoobenthos in the German Bight (North Sea) 1969 - 2000

Dynamik und Entwicklung makrozoobenthischer Weichbodengemeinschaften in der Deutschen Bucht (Nordsee) 1969 - 2000



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

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

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Bremen 2003

Aus dem
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2. Gutachter: Dr. R. Knust

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Acknowledgements

Zusammenfassung

Um die Langzeitentwicklung und die interannuelle Variabilität sublittoraler makrozoobenthischer Weichbodengemeinschaften der Deutschen Bucht zu untersuchen, wurden vier Dauerstationen fortlaufend während der letzten 35 Jahre beprobt. Interannuelle Variabilität und mögliche Langzeittrends wurden anhand von Frühjahrsproben analysiert. Die Umgebung der Stationen wurde 1998 intensiv beprobt, um die räumliche Variabilität der benthischen Gemeinschaften dieser Gebiete beurteilen zu können. Diese Daten wurden außerdem genutzt, um die nötige Probenzahl für eine angemessene Erfassung der benthischen Gemeinschaften abzuschätzen. Gleichzeitig wurde die Abhängigkeit der Gemeinschaftsparameter (Artendichte, Äquität, Ähnlichkeit etc.) von der Probengröße untersucht, da diese bei Felddaten von theoretischen Voraussagen abweicht.

Eine ausreichende Charakterisierung der lokalen Gemeinschaften kleiner homogener Gebiete für Langzeituntersuchungen kann bei einer Standartprobengröße von fünf 0.1 m² van Veen Greifern angenommen werden. Da die größte Zunahme der Genauigkeit der Erfassung der Fauna durch die ersten fünf Greifer erreicht wird, wird diese Probengröße als praktischer Kompromiss akzeptiert, um die wichtigsten Gemeinschaftstrends zu dokumentieren. Für eine Analyse der Populationsdichte einzelner Arten sollten zehn oder mehr Greifer genommen werden. Die vorliegenden Ergebnissen dienen als Grundlage für Empfehlungen für ein Monitoring von Weichboden-Makrozoobenthos der Nordsee.

Die benthischen Gemeinschaften an den Dauerstationen zeigen eine große interannuelle Variabilität sowie Veränderungen auf einer annähernd dekadischen Skala. In Übereinstimmung mit für die Nordsee dokumentierten großräumigen Systemveränderungen, änderten sich auch die Zusammensetzung der benthischen Gemeinschaften zwischen den 70er, 80er und 90iger Jahren. Die Übergänge der Perioden sind nicht durch deutliche Veränderungen gekennzeichnet, sondern spiegeln eher graduelle Veränderungen von Artenzusammensetzung und Dominanzstruktur wider.

Die zeitliche Entwicklung benthischer Gemeinschaften verläuft in verschiedenen Gebieten der Nordsee ähnlich, und scheint eine Folge klimatischer und ozeanographischer Einflüsse zu sein. Die lokale Entwicklung ist allerdings ein Ergebnis lokaler Umweltvariabilität und biologischer Interaktionen, die sich zwischen verschiedenen Gebieten unterscheiden. Da jede Station eine deutlich andere Bodenfauna aufweist, unterscheidet sich auch die Entwicklung der Gemeinschaften.

Um mögliche klimatische, ozeanographische und anthropogene Einflüsse abzuschätzen, wurde die Entwicklung der benthischen Gemeinschaften mit verschiedenen Umweltdaten korreliert (NAO Index; Wassertemperatur, Wind, Salinität und Nährstoffkonzentrationen bei Helgoland; Elbabflussmengen). Die deutlichste Veränderung von Umweltfaktoren ist die zunehmende Tendenz des NAOI mit den damit verbundenen höheren Wintertemperaturen und der zunehmenden Frequenz von Stürmen in der Deutschen Bucht. Die während der 70er Jahre zunehmende Phosphatkonzentration nahm in den späten

80ern wieder ab, während die Stickstoffkonzentration zumindest bis in die mittleren 90er Jahre weiterhin zunahm.

Die Entwicklung der benthischen Gemeinschaften zeigt an allen Stationen eine deutliche Korrelation mit dem NAOI. Die dramatischsten Veränderungen folgten den strengen Wintern von 1970, 1979, 1986 und 1996, mit einer Abnahme der Artenzahlen und Organismendichte an allen Stationen. Die flacheren Feinsand- (FSd) und Schlick- (Slt) Stationen sind durch starke interannuelle Schwankungen charakterisiert, und die Situation nach strengen Wintern unterscheidet sich hier nicht so deutlich von anderen Jahren, wie an den tieferen Schlicksand- (SSd) und "Weiße Bank"- (WB) Stationen.

Ein Einfluss von Eutrophierung lässt sich aus den Korrelationen ableiten, die zwischen Nährstoffkonzentrationen und der Entwicklung der benthischen Gemeinschaften an den Stationen der inneren Deutschen Bucht (SSd und Slt) gefunden wurden. Diese deuten auf eine enge bentho-pelagische Kopplung hin. In Verbindung mit ungünstigen hydrographischen Verhältnissen begünstigt Eutrophierung auch das Auftreten von bodennahem Sauerstoffmangel, der zu einer Reduzierung oder einem Absterben des Makrozoobenthos führen kann. Auswirkungen eines einzelnen Sauerstoffmangelereignisses wurden an der Station WB beobachtet. Die relativ arme benthische Gemeinschaft an der Schlick-Station kann als ein Ergebnis häufigerer Sauerstoffmangelereignisse angesehen werden.

Die Entwicklung der Gemeinschaften von Slt und FSd ist auch mit der Häufigkeit von Stürmen korreliert, die durch starke Wellenbewegungen eine Störung der Sedimente verursachen können. Das Vorherrschen kleiner opportunistischer Arten an der Feinsand-Station mag in den instabilen Sedimenten begründet sein. Die ehemalige Verklappung von Dünnsäure an der Feinsand-Station und von Klärschlamm östlich der Schlick-Station zeigte keine deutlichen Auswirkungen auf die benthischen Gemeinschaften. Auswirkungen der Bodenfischerei auf die Bodenfauna wurden in zahlreichen Studien nachgewiesen, wegen fehlender detaillierter Informationen zur lokalen Fischereiintensität an den Dauerstationen sind diese allerdings anhand der vorliegenden Daten nicht belegbar.

Die Hauptfaktoren, die die Entwicklung der benthischen Gemeinschaften beeinflussen, sind biologische Interaktionen sowie Klima, Nahrungsangebot und das Störungsregime. Die häufigsten Störungen sind extrem kalte Winter, Sauerstoffmangel und Störungen der Sedimente während starker Stürme oder durch Bodenfischereigeräte. Besonders an den flacheren Stationen sind die Bodengemeinschaften an häufige Störungen angepasst und eine Erholung nach lokalen Störungen kann sehr schnell erfolgen. Die "normale" Gemeinschaftszusammensetzung spiegelt in diesem Fall eher das Störungsregime wider (bezüglich Art, Intensität und Häufigkeit), als eine "reife" Gemeinschaft.

Eine klare Unterscheidung der Auswirkungen von Klima, Eutrophierung, Verschmutzung oder Bodenfischerei ist kaum möglich, nicht nur da für verschiedene Faktoren ähnliche Auswirkungen vorausgesagt werden, sondern auch weil die beobachteten Veränderungen ein Ergebnis der synergistischen Effekte aller Faktoren darstellen.

Summary

In order to examine the long-term development and the interannual variation of offshore macrozoobenthic soft-bottom communities of the German Bight, four stations have been sampled continuously over the last 35 years. Interannual variability and possible long-term trends were analysed based on spring-time samples. The vicinities of the stations were extensively sampled in 1998 to evaluate the spatial variability of the benthic communities around the stations. These data were also used to estimate the number of grabs needed for an appropriate description of the benthic communities and to investigate the sample-size-dependencies of community descriptors (species density, evenness, similarity, etc.) based on real data, which differ from theoretical predictions.

A sufficient characterisation of a local community of small homogeneous areas for long-term studies may be assumed with a standard number of five replicate 0.1 m² van Veen grabs. Because the largest increase of the precision of estimates is reached by the first five grabs, this sample size is used as a practical compromise to detect the main trends. However, ten or more grabs are desirable for an analysis of single species population densities. Based on the present results, some recommendations are derived for offshore monitoring of North Sea soft-bottom makrozoobenthos.

Benthic communities at the sampling stations show a large interannual variability combined with a variation on a roughly decadal scale. In accordance with large-scale system shifts reported for the North Sea, benthic community transitions occurred between roughly the 1970ies, 80ies and 90ies. The transitions between periods are not distinctly marked by strong changes but rather reflected in gradual changes of the species composition and dominance structure.

The *timing* of changes in communities is similar between different parts of the North Sea and seems to be a result of climate and oceanographical features. However, the *local* community development is mainly a product of *local* environmental variation and biotic interactions, and both differ between areas. As each station represents a clearly distinct benthic fauna, the nature of the community changes differs.

To evaluate possible climatic, oceanographic and anthropogenic influences, the benthic community development was correlated to various environmental data sets (NAO index; water temperature, wind, salinity and nutrient concentrations at Helgoland; Elbe river runoff). Most notable changes of environmental factors are the increasing tendency of the NAOI with its consequences on higher winter temperature and the increasing frequency of storms observed in the German Bight. An increasing concentration of phosphate during the 1970ies was reversed in the late 80ies, while nitrogen concentrations continued to increase at least until the mid-1990ies.

The development of the benthic communities at all stations shows clear correlations to the NAOI. The most dramatic changes of the communities followed the severe winters of 1970, 1979, 1986 and 1996, when reductions in species number and abundance were discernible at all stations. The shallower "Fine Sand" (FSd) and "Silt" (Slt) stations are characterised by larger interannual changes, and the situation following severe winters is not as clearly different from other years as it is the case at the deeper "Silty Sand" (SSd) and "White Bank" (WB) stations.

An influence of eutrophication can be inferred from a high number of correlations found between nutrient concentrations and the benthic community development at the stations in the inner German Bight (SSd and Slt). These hint towards a coupling of the benthic and planktonic system. However, in combination with unfavourable hydrographic conditions, eutrophication also favours the occurrence of benthic hypoxia, leading to a reduction or elimination of macrobenthos. Only at WB an indication of effects of a distinct hypoxic event was observed on a single occasion. The relatively poor benthic community at Slt can be seen as a result of frequent hypoxic episodes.

The community development especially at Slt and FSd is also correlated to the frequency of storms, which may create a physical disturbance of the sediment by wave erosion. The dominance of small opportunistic and mostly mobile worms at FSd may result from unstable sediments. No obvious effects of the former dumping of acid-iron wastes at the FSd station and of sewage sludge east of the Slt station were evident for the benthic communities. Bottom trawling has been shown to have strong impacts on benthic organisms, but, because of the lack of detailed information about the local fishing intensity at the stations, trawling effects can not be proven from the present data.

The main factors affecting benthic community development are biotic interactions as well as climatic conditions, food supply and the disturbance regime. The most common forms of disturbances are extremely cold winters, hypoxia following algal blooms in stratified waters, and physical disturbance of the sediment by turbulent wave erosion during strong storms or by demersal fishing gear. Especially at the shallower stations, the communities are adapted to frequent disturbances, and a recovery following localised disturbances can be very quick. The "normal" community composition in this case reflects the general disturbance regime (in terms of type, intensity and frequency) rather than a "mature" community.

A clear distinction between the effects of climate, eutrophication, pollution or bottom trawling is hardly possible, not only because various factors are predicted to produce similar effects, but also because the observed changes are a result of the synergistic effects of all factors.

1. Introduction

Because of its mostly sessile character and its ability to "integrate" environmental influences over longer time scales, the macrozoobenthos is commonly regarded as a good indicator for environmental impacts (Underwood 1996) as well as for long-term changes in the ecosystem (Kröncke 1995). It is - especially in shallow shelf seas - an integral part of the system with major importance in the remineralisation and transformation of deposited organic matter (Josefson et al. 2002) and as the main food resource of demersal fishes (Reid 1987).

Soft bottom macrozoobenthic communities of the North Sea have been studied since the beginning of the 20th century. Several types of communities have been defined, their distribution being mainly determined by sediment type and water depth (Petersen 1914; Hagmeier 1925; Stripp 1969; Glemarec 1973; Salzwedel et al. 1985; Eleftheriou & Basford 1989; Kuenitzer et al. 1992; Craeymeersch et al. 1997; Rachor & Nehmer 2003). Comparisons of the results from these large-scale investigations revealed that the spatial distribution of these communities has remained relatively constant, while major differences in community composition occurred (Salzwedel et al. 1985; Kröncke 1992; 1995; Rumohr et al. 1998; Kaiser & Spence 2002). Over the 20th century, benthic communities in large parts of the North Sea generally show 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 (Duineveld et al. 1987; Rachor 1990; Kröncke 1992; 1995; Witbaard & Klein 1993; Rumohr et al. 1998).

An interpretation of the observed differences between temporally separated studies as long-term changes is problematic because marine ecological systems are subject to large variability on various time scales. Seasonal, interannual and multidecadal temporal patterns are commonly observed not only on local scales but even for whole ocean basins. Probably the most famous and drastic example of climate-induced changes of ecosystems is the El Niño Southern Oscillation (ENSO) in the Pacific Ocean. Alterations of the atmospheric circulation result in changes of the trophic system with dramatic implications on all trophic levels on an ocean-wide scale (Arntz & Fahrbach 1991). These fluctuations with periodicities of 3-10 years are embedded in multidecadal regime shifts at a period of approximately 50 years (Chavez et al. 2003). Although with less extreme biological effects, similar temporal pattern have also been observed in the North Atlantic and the North Sea. Water temperature and salinity of the North Atlantic were found to fluctuate with periods of 3-4, 6-7, 10-11, 18-20 and 100 years, which could be related to astronomical periodicities (Gray & Christie 1983). The dominant signal of the interannual variability in the atmospheric circulation over the North Atlantic is the North Atlantic Oscillation (NAO; Hurrell 1995). It has a cyclical component of 7.9 years and influences the temperature but also the current regime of the North Atlantic and the North Sea (Tunberg & Nelson 1998). These climatological variations have far-reaching repercussions on the ecosystem of the North Sea.

Parallel fluctuations to those of climate were found across several trophic levels from phytoplankton over zooplankton and fish up to seabirds (Aebisher et al. 1990). Recruit numbers of different fish species in the North Sea are strongly correlated to the NAO index (Philippart et al. 1996; Dippner 1997) with some indications for long-term fluctuations with a period of up to 50 years, paralleled by fluctuations of zooplankton (Russell 1973). Major shifts of the North Sea system have also been attributed to inflows of Atlantic waters that also depend on the current regime in the North Atlantic and finally atmospheric circulation (Lindeboom et al. 1994; Edwards et al. 2002). Changes in sublitoral benthic communities have also been related to the NAO, mediated by changes in water temperature and altered hydrodynamics (Tunberg & Nelson 1998; Kröncke et al. 2001; Carpentier et al. 1997; Tunberg & Nelson 1998).

Part of the climatic influences on benthic communities is explained by indirect effects via alterations of phytoplanktonic primary production (Buchanan 1993; Josefson et al. 1993; Frid et al. 1996; Pearson & Mannvik 1998; Tunberg & Nelson 1998; Kröncke et al. 2001). Changes in the phytoplankton community composition may change the trophic structure of an ecosystem and result in a different amount and quality of organic material arriving at the sea floor (Sommer et al. 2003). Changes in benthic communities may in turn alter zooplankton communities especially via the influence of meroplanktonic larvae on the planktonic food web (Lindley et al. 1995). Besides indirect effects on the food web, extreme climatic conditions also affect benthic communities of shallower areas directly and may even appear as "natural disturbances" such as cold winters (Ziegelmeier 1964; 1970; Dörjes et al. 1986; Kröncke et al. 1998; Armonies et al. 2001) or sediment transport by strong gales (Rachor & Gerlach 1978).

Apart from climatic factors, anthropogenic influences like eutrophication and pollution or demersal trawling have been made responsible for major changes in the North Sea ecosystem.

Nutrient concentrations in the German Bight have increased during the 20th century, with a significant increase in the N:P-ratio especially in the last two decades (Hickel et al. 1997). Eutrophication has caused major changes in the planktonic communities (Reid et al. 1990) and has consequently been made responsible for changes in benthic communities caused by the increased supply of organic matter (Pearson et al. 1985; Rachor 1990; Buchanan 1993).

In combination with warm, calm weather periods, eutrophication increases the risk of oxygen deficiencies in bottom waters with strong and sometimes catastrophic effects for benthic communities (Rachor 1977; Arntz 1981; Arntz & Rumohr 1986; Niermann et al. 1990; Heip 1995). Depending on its physical conditions, almost every local system responds differently to eutrophication (de Jonge et al. 2002).

Bottom trawling has been held responsible for persistent alterations of benthic communities with a decrease of large, long-lived species and an increase of small opportunists (Kröncke 1995; Rumohr et al. 1998; Frid et al. 1999). These effects are, however, similar to those attributed to eutrophication. Changes in eutrophication are also often coupled to climatological trends (Richardson & Cedhagen 2001). A distinction between the consequences of eutrophication, demersal fishery and climate changes is therefore very difficult at present (Rachor & Schröder 2003).

Although similar trends in selected aspects of benthic community dynamics have been observed at different locations, local conditions determine the actual community composition of smaller areas and may lead to asynchronous fluctuations of local population densities (Gray & Christie 1983; Remmert 1991). These local differences complicate an interpretation of correlations between fauna and large-scale environmental factors but may in the long run be useful for a distinction of causal relationships. A comparison of various localities with similar faunal communities but slightly different environmental conditions may allow inferences on the relative importance of, and possible interactions between factors.

In order to examine the long-term development and the inter annual variation of the main offshore macrozoobenthic soft bottom communities of the German Bight, four stations have been sampled continuously over the last 35 years (Rachor & Salzwedel 1975; Rachor & Gerlach 1978; Rachor 1980). The vicinities of these stations were extensively sampled in 1998 to evaluate the spatial variability of the benthic communities around the stations and to test for possible large-scale spatial patterns in the areas. These data are also used to estimate the number of grabs needed for an appropriate description of the benthic communities and to investigate the sample-size-dependency of community descriptors based on real data, which may differ from theoretical predictions.

The objective of this study is to describe the development of benthic communities at the permanent sampling stations during the last 30 years and to relate it to climatic, oceanographic and anthropogenic influences. An analysis of the temporal and spatial variability of the benthic communities at these stations forms the basis for an evaluation of the current sampling regime.

Against the background of previously published correlations between environmental variables and benthic communities, the following hypotheses shall be addressed by the analysis of the data at hand:

- Benthic communities in the German Bight have undergone distinct changes during the last 30 years of the 20th century.
- Environmental parameters, both natural and anthropogenic, have also changed during this period.
- If large-scale factors like climatic fluctuations are the main influencing factors, the temporal development of the benthic communities at the four stations should run in parallel.
- Direct climatic influences should be more pronounced in shallow habitats. Deeper waters of the North Sea have a more constant temperature regime, and wind induced sediment transports are less common than in shallow areas.
- Eutrophication and pollution effects should be most pronounced in the inner German Bight, while being less important in the outer reaches.
- Extreme environmental conditions (temperature, storms, oxygen deficiencies) may act as disturbances with profound effects on the temporal development of benthic communities.
- Organisms and communities of shallower habitats adapted to high short-term variability should be less influenced by long-term variations.

2. The German Bight (North Sea)

A short description of the abiotic conditions may serve as background information to understand the living conditions of the benthic fauna in the German Bight. More details on the whole North Sea as a large marine ecosystem can be found in Lozan et al. (Lozán et al. 1990; 2003) and Ducrotoy et al. (2000) or the "Quality Status Report 2000 – Region II Greater North Sea" (OSPAR Commission 2000) and references cited therein.

2.1 Topography

The North Sea is a semi-enclosed shallow sea on the north-western European continental shelf. With a mean depth of only 90 m, it covers an area of 750 000 km² (Ducrotoy et al. 2000; OSPAR Commission 2000). Surrounded by land on three sides, it is open towards the North Atlantic Ocean in the northwest. In the southwest the English Channel forms another connection to the Atlantic Ocean and in the east the Skagerrak a connection to the Baltic Sea. In its present form, the North Sea is a geologically very young sea. During the last glaciation 15 000 years ago, the main part of today's sea bottom was land. Many of its main topographic features are remnants from this time (Becker et al. 1992). The river Elbe cut a deep valley in the older sediments and created the presently still recognisable Pleistocene Elbe valley. It runs from the modern river mouth of the Elbe in north-westerly direction and still represents the deepest part of the German Bight (Figge 1981). The stony and gravely areas east of it represent end-moraines from the ice-age (Pratje 1951). After the regression of the glaciation about 10 000 years ago, the sea level rose and reached roughly its present level about 2 000 years ago (Becker 1990). The water depth of the North Sea increases from South to North. In most of the area of the German Bight, i.e. the south-eastern part of the North Sea enclosed by the East- and North-Friesian coasts, the water depth is less than 40 m. Only in the "Helgoländer Tiefe Rinne" and in the outer reaches of the Pleistocene Elbe valley the water depth reaches up to 60 m.

2.2 Climate

The climate of the North Sea region is strongly influenced by the North Atlantic Oscillation (NAO), a periodic change in the large-scale pressure system measured by the sea surface pressure difference between Lisbon, Portugal and Reykjavik, Iceland. It determines the strength of prevailing westerlies and ocean surface currents, leading to alternations of strong continental influences and generally milder oceanic influences (Hurrell 1995). During the past two decades, exceptional climatic conditions have been recorded in the North Sea area. A series of exceptionally cold winters followed by particularly mild winters were accompanied by high salinities and an increased storminess (Becker et al. 1997). The recently higher wind speeds have affected water circulation (Ducrotoy et al. 2000).

2.3 Hydrography

The North Sea is an extremely dynamic system subjected to many different influences causing a high regional and seasonal variability (Niermann et al. 1990). The main import of Atlantic water occurs in the North between the Shetlands and Norway as well as between the Orkneys and the Shetlands and less than 10 % in the South through the English Channel (Becker 1990). The main water export runs through the Norwegian trench along the Norwegian coast. This results in a long-term main water transport in an anti-clockwise gyre. The mean flushing time for the whole North Sea has been estimated at 1-1.5 years (Otto et al. 1990). The actual dynamic conditions are mainly the result of wind-induced and tidal currents (Lee 1980). Fresh water enters the North Sea via the various rivers, from the Baltic Sea and by atmospheric precipitation. About half of the fresh water input is compensated by evaporation. These proportions are, however, not constant, and years with stronger Atlantic influences are followed by years with stronger continental influences (Becker 1990). The oceanographic conditions of the North Sea – temperature, salinity and circulation – are strongly coupled to the NAO (Becker 2003).

The German Bight is mainly influenced by two water bodies: The outer reaches, especially the bottom waters in the Pleistocene Elbe valley, are mostly under the influence of the "central southern North Sea water" (NSW). It originates from Atlantic water and is characterised by a high salinity of more than 34 PSU and a low concentration of pollutants (Becker et al. 1992). The water masses of the areas closer to the coast and of the inner German Bight are named "continental coastal water" (CCW). The CCW is a mixture of Atlantic water from the English Channel with the river discharges from Rhine, Meuse, Ems and, in the eastern and northern parts of the German Bight, also from Elbe and Weser. This mixed water is much more variable in its temperature (annual surface temperature variation up to 24 °C) and is characterised by a much lower and more variable salinity (30 ± 1-3 PSU) than the NSW (Becker et al. 1992).

With the fresh water, the rivers also transport large amounts of fine sediments and of nutrients and pollutants, either in dissolved form and adsorbed to sediment particles, to the North Sea. A large proportion of the particulate input from Elbe and Weser is deposited in the inner German Bight south of Helgoland, but especially the very fine fractions can also be transported over larger distances. The high input of nutrients allows in the coastal area and the inner German Bight especially in spring a very high primary production leading to an increased deposition of organic matter (Bauerfeind et al. 1990; Colijn et al. 1990). A large proportion is deposited directly in the inner German Bight or imported into the Wadden Sea (Van Beusekom & de Jonge 2002), but fine material is also transported in mainly northern direction and deposited in areas with lower current speeds.

Especially the discharges of Elbe and Weser create a relatively regular haline stratification in the inner German Bight, because the lighter fresh water from the rivers floats on the more saline and therefore denser North Sea water. In conjunction with a warming of the surface waters a pronounced thermo-haline stratification often develops in summer that extends from the river mouths in north-westerly direction up to the outer reaches of the German Bight (Goedecke 1968; Becker et al. 1992). Under normal conditions the water masses in the relatively shallow area of the German Bight are well mixed by wind induced and tidal currents and the thermo-haline stratification does not persist long. In periods of calm and warm weather it may, however, persist for longer periods and prevent an exchange of oxygen between surface and bottom waters. In combination with a high input of organic matter and its decomposition, this situation may lead to a marked decrease of the oxygen content of the bottom waters. Low oxygen concentrations of less than 4 mg/l have been recorded in the German Bight in 1981, '82, '83, '89 and '94 (Rachor & Albrecht 1983; Westernhagen et al. 1986; Frey 1990; Niermann et al. 1990; Van Beusekom et al. 2003). First indications of oxygen deficiencies were reported by Rachor in 1977 (Rachor 1977).

The mean tidal range in the inner German Bight amounts to about 2.4 m and tidal currents in open waters reach 60 – 100 cm/s and more (Reineck et al. 1968; Becker 2003). The residual current runs in an anti-clockwise direction and transports the water masses of the inner German Bight in northern direction with a long term mean of 5 cm/s (Becker et al. 1992). Water bodies entering the North Sea at the Orkneys reaches the German Bight after about 1.2 years and the time needed for a total local replacement of the water in the southern North Sea amounts to about 0.2 years (Becker 1990). The mean flushing time of the German Bight is about 33 days (10 – 56 days) (Lenhart & Pohlmann 1997).

More detailed descriptions about the oceanographic conditions of the North Sea can be found in Becker (1990; 2003) and Otto et al. (1990).

2.4 Sediments

Surface sediments of the sea bottom are mostly Holocene fluvio-glacial sands mixed with silt and coarser sediments (Caston 1979). Detailed sediment maps of the German Bight have been presented by Gadow & Schäfer (1973) and Figge (1981). A map of the sediment distribution in the German Bight compiled from several sources by Salzwedel et al. (1985) is shown in Fig. 2.4.1.

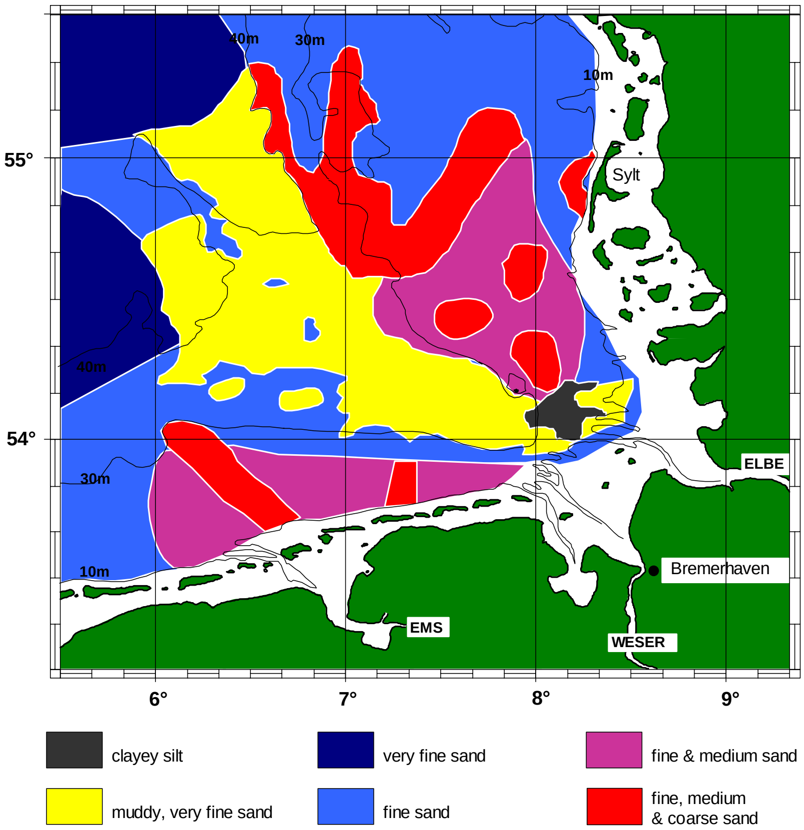

Fig. 2.4.1: Distribution of surface sediments in the German Bight. (modified after Salzwedel et al. 1985)

The sedimentation of suspended matter depends on the current speed and on turbulences. During storms and high wave heights, sediments may be re-suspended in shallow areas and transported to other areas (Becker et al. 1992). At low current speeds near the bottom, even fine material is deposited, especially in the deeper areas and in depressions like the Pleistocene Elbe valley. This led to an accumulation of up to 15 m of fine-grained sediments in the Pleistocene Elbe valley. The actual sedimentation rate in this area is not exactly known, but estimated to a mean of approximately 10 cm per 100 years (Eisma 1981).

2.5 Benthic fauna

The benthic communities of the North Sea are presumably amongst the most intensively studied communities of the world. The concept of benthic faunal communities characterised by dominant species and connected to water depth and sediment structure was developed here by Petersen (1914). Since then, the macrozoobenthos of the various parts of the North Sea has been described in numerous publications (summarised in Glemarec 1973; Kingston & Rachor 1982). Petersen's concept was refined by Remane (1940) and Thorson (1957). While they classified the communities according to the dominant species, Jones (1950) differentiated between areas according to environmental conditions with temperature and sediment as the main determinants. The annual variation in bottom water temperature was used by Glémarec (1973) to divide the North Sea area into three "étages" within which the distribution of benthic fauna was determined by sediment composition. The southern North Sea including the German Bight belongs to the "infralittoral étage" with a water depth of less than 60 m and temperature variations of more then 10 °C. This division has been mainly supported by the international "ICES North Sea Benthos Survey" in 1986 (Duineveld et al. 1991; Kuenitzer et al. 1992; Heip et al. 1992), although the differentiation was shifted to slightly different depth contours (100, 70, 50 and 30 m instead of 100 and 60 m by Glémarec). Temperature and food supply have been identified as main factors influencing the distribution and structure of the faunal communities (Kuenitzer et al. 1992). The spatial distribution of these factors results from water depth and coastal distance, current regime and the different water masses. The latter two factors are decisive for the distribution of the bottom sediments. Therefore the distribution of bottom fauna communities of the North Sea can be delineated according to water depth and sediment type (Duineveld et al. 1991; Kuenitzer et al. 1992). A detailed investigation for the area of the German Bight from 1975 has been produced by Salzwedel et al. (1985 Fig. 3.2.1).

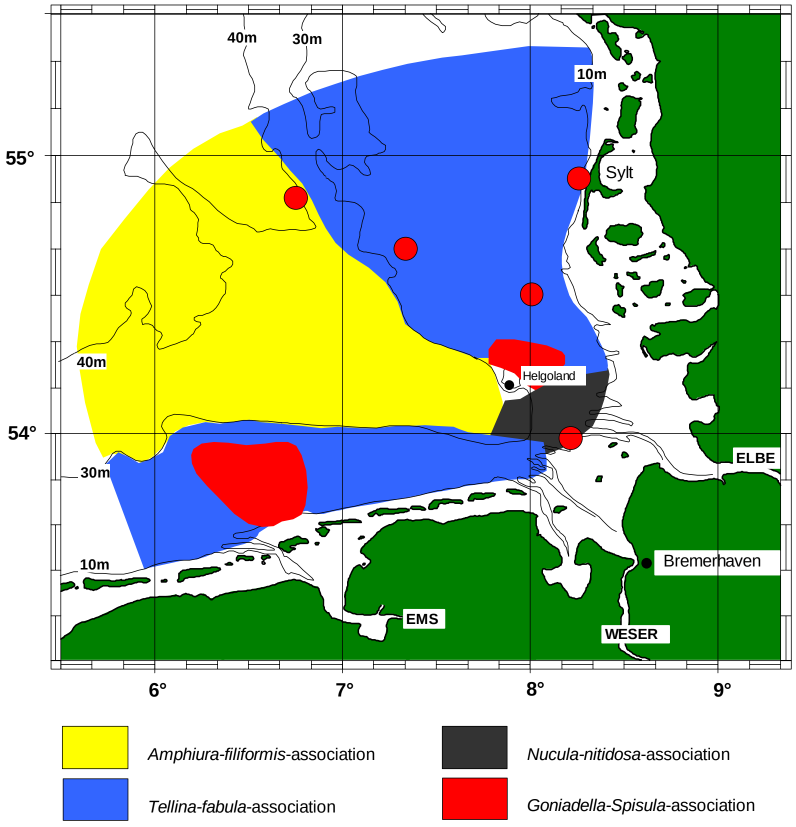

Fig. 2.5.1: Spatial distribution of benthic macrofauna associations in the German Bight 1975. (modified after Salzwedel et al. 1985)

The distribution of the benthic associations described by Salzwedel et al. (1985) agrees largely with the results of earlier investigations of smaller parts of the German Bight (Hagmeier 1925; Stripp 1969; Dörjes 1977). Based on the more detailed investigation of the whole German Bight and new analytical methods, the borders between the communities were altered slightly, and the associations were renamed. Results from more recent studies agree mostly with the associations delineated by Salzwedel et al. (Duineveld et al. 1991; Kuenitzer et al. 1992; Rumohr et al. 1998; Rachor & Nehmer 2003). Four main associations are generally distinguished:

- The *Nucula-nitidosa*-association of silty sediments and silty sands between 13 and 35 m depth. It is characterised by the bivalve *Nucula nitidosa* and the cumacean *Diastylis rathkei* (*Abra-alba*-community sensu Hagmeier 1925).
- The *Amphiura-filiformis*-association of very fine to silty sands in 34 – 45 m depth. It is characterised by the brittle star *Amphiura filiformis*, the polychaetes *Pectinaria auricoma* and the gastropod *Cylichna cylindracea* (*Echinocardium-filiformis*-community sensu Hagmeier 1925). This association is similar to the *Nucula-nitidosa*-association and was joint with the latter by Jones (1950) while all other authors separated them (Hagmeier 1925; Remane 1940; Thorson 1957).
- The *Tellina-fabula*-association of fine and medium sands in 13 – 31 m depth. It is characterised by the polychaete *Magelona papillicornis* (*M. mirabilis, M. johnstoni*), the bivalve *Tellina fabula (Fabulina f.)* and the amphipod *Urothoë grimaldii* (*U. poseidonis*) (*Venus-gallina*-community sensu Hagmeier 1925).
- The *Goniadella-Spisula*-association of coarse sands to gravel in 14 – 29 m depth. The characteristic species are the polychaetes *Goniadella bobretzkii,* the archiannelid *Polygordius appendiculatus* and bivalves of the genus *Spisula* (parts of the *Venus-gallina*-community sensu Hagmeier 1925).

The borders between the benthic associations are strongly correlated to the distribution of sediment types. The exact borders as delineated in Fig. 2.5.1 should however rather be seen as approximate and deliberate lines. Especially the delineation between the Nucula-nitidosa-ass. and the Amphiura-filiformis-ass. may be influenced by temporal changes in the communities and therefore differ between authors (Salzwedel et al. 1985; Rachor & Nehmer 2003). In reality the transition between the associations is normally represented by a gradient rather than an abrupt change.

The extensive literature on North Sea benthos, related ecological processes, long-term changes from various sub-regions and possible influences was reviewed by Kröncke (1995) and Kröncke & Bergfeld (2001).

3. Methods

3.1 Long term stations

Samples were taken at four locations in the German Bight ("stations") that were chosen to represent the main offshore soft bottom communities of the area within typical environmental conditions (Tab. 3.1.1, Fig. 3.1.1). At the three stations around Helgoland ("Slt", "SSd" and "FSd") sampling began in 1969 while the station "WB" in the outer reaches of the German Bight was added in 1981. A yearly sampling in spring has been carried out until today. Additional sampling in other times of the year was common in the early years and data are available. Samples from summer or autumn have been taken only occasionally during later years, but samples have not been analysed yet.

Tab. 3.1.1: Position, depth and sediment type of the permanent sampling stations.

Station	**Position** Latitude	 Longitude	**Depth** [m]	**Sediment type**	**Md Grain size**	**% Silt & Clay < 63µm**
Slt	54° 03.00’ N	8° 05.00’ E	23	silt	~ 70 µm	~ 40 %
FSd	54° 22.50’ N	7° 37.00’ E	26	fine sand	~ 180 µm	< 1 %
SSd	54° 01.00’ N	7° 49.00’ E	36	silty sand	~ 83 µm	~ 25%
WB	55° 00.00’ N	6° 30.00’ E	42	silty sand	~ 82 µm	~ 25%

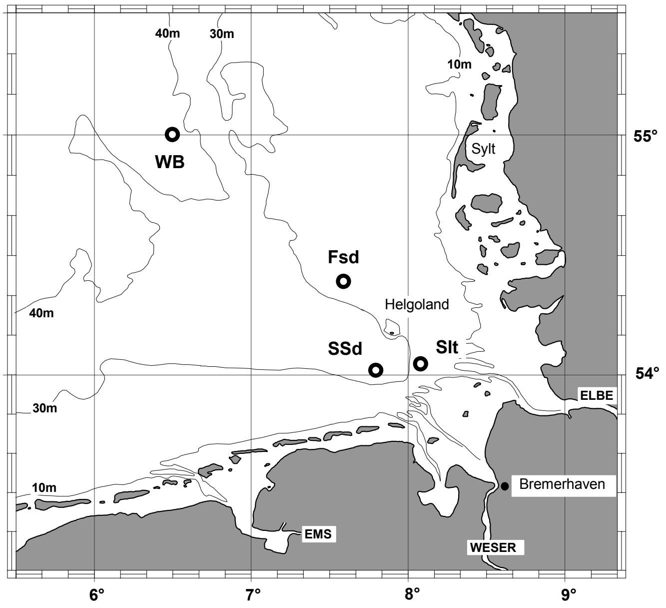

Fig. 3.1.1: Locations of the permanent sampling stations in the German Bight.

The shallowest Silt-station "Slt" is located in 23 m depth in front of the river mouths of Elbe and Weser (Fig. 3.1.1). Sediments consist of black and soft silt with a median grain size around 70 µm and about 40% silt and clay (Tab. 3.1.1). The benthic community represents a typical *Nucula-nitidosa*-association sensu Salzwedel et al. (1985). Until 1980, sewage sludge from Hamburg had been disposed about 4.5 nm east of this station (Rachor 1982).

The "FSd"-station is located at the centre of a former dumping area about 15 nm north-west of Helgoland (Fig. 3.1.1) where acid-iron wastes from TiO_2-production had been discharged from 1969 to 1989 (Rachor & Dethlefsen 1976; Rachor 1972; Rachor & Gerlach 1978). It is named after its typical sediment of homogeneous fine sand with a median grain size of 180 µm and a silt and clay content of less than 1 % (Tab. 3.1.1). The water depth is 26 m and the benthic community is a typical example of the *Tellina-fabula*-association sensu Salzwedel et al. (1985).

The Silty-Sand-station "SSd" is situated south of Helgoland in the old Pleistocene Elbe River valley at 36 m depth (Fig. 3.1.1). Sediments consist of silty fine sands with a median grain size of about 83 µm and a silt and clay content of about 25 % (Tab. 3.1.1). The benthic community here is a shallow type of the *Amphiura-filiformis*-association found in the German Bight at more than 30 m depth (Salzwedel et al. 1985). Located at the western boundary of the muddy area in the inner German Bight, it contains also elements of the *Nucula-nitidosa*-association of silty sediments.

The deepest station "WB" lies about 60 nm west of the island of Sylt and about 20 nm east of the White Bank (Fig. 3.1.1), which is also responsible for the station's name. It is located near the eastern slope of the old Pleistocene Elbe River valley in 42 m water depth. Sediments are similar to those found at SSd and consist of silty fine sands with a median grain size of about 82 µm and a silt and clay content of about 25 % (Tab. 3.1.1). The benthic community at WB is a deeper and more characteristic variant of the *Amphiura-filiformis*-community (Salzwedel et al. 1985) than that at SSd.

3.2 Benthos data

Quantitative data on the macrozoobenthic communities are based on samples taken by bottom grabs.

3.2.1 Sampling methodology

For the long-term series, the most often used sample size consisted of five 0.1m² van-Veen grabs (vV) per station, resulting in a total sampled area of 0.5 m². The sampling protocol was not always constant over the whole time span at all stations. During the early years until 1985, a lighter standard van-Veen grab was used. As this gear showed a low penetration depth especially in sandy sediments, occasionally larger van-Veen grabs of

0.2, 0.4 or 0.5 m² were employed. At FSd and SSd the light vV was complemented by a 0.017 m² Reineck box corer (RBC) that had a much deeper penetration depth, usually in a combination of two vV's plus six RBC's from 1976 to '89. On a few occasions, some other sampling gears were employed e.g. van-Veen grabs of 0.05 or 0.4 m² area or a large 0.056 m² Box-corer. From 1986 onwards, a new modified warp-rigged van-Veen grab with sieve-covered windows on the upper side and a larger weight (Dybern et al. 1976; Rumohr 1999) was used, resulting in a reduced bow-wave when approaching the bottom and a deeper penetration depth especially in sandy sediments. Details on the available data and the gear type used can be found in the annex A.2.

Either data from five 0.1 m² van-Veen grabs or from a combination of two vV's with six Reineck box corers are available for most years.

In July 1976, a large number of samples were taken at the FSd-station while the ship was anchored. Data from a total of 16 vV plus 25 RBC were used to evaluate the effect of a combination of vV's and RBC's on the results regarding species number, diversity, organism density and inter-samples similarity. Monte-Carlo simulations were based on 10000 permutated samples consisting of random combinations of five vV's or of combinations of two vV's plus six RBC's.

The variable methodologies require careful consideration of the quality of data extracted from the database for any analytical question. Details on sampling dates, the respective sampling gear, the number of replicates and the quality (see paragraph 3.2.3) of the available data are listed in the table in the annex A.2.

3.2.2 Sample processing

Samples were sieved on board on 0.5 mm round-hole sieves and fixed (and stored) in buffered 4% formalin. In the laboratory, samples were stained with rose bengal to facilitate sorting.

Organisms were identified to species level as far as possible, counted and weighted (wet weight). Methods in general followed the ICES and HELCOM recommendations for sampling benthos and treatment of samples (Rumohr 1999). Taxonomic groups not adequately sampled by these methods (Nematoda, Foraminifera), colonial (Hydrozoa) and mostly pelagic (Calanoida, Chaetognatha) organisms were excluded from the data analysis. Juvenile and damaged specimens were classified to the lowest level where confident identification was possible. Nemertines, Plathelminthes, Oligochaetes were not identified further. A few rare species with difficult identification were combined at genus or family levels. All densities are reported as organisms per 0.1 m² (one grab sample) unless specified otherwise.

Identification of organisms for newly analysed samples was based on the following literature:

Crustacea: Lincoln 1979; Dauvin & Bellan-Santini 1988; Myers & McGrath 1991; Stephensen 1940; Jones 1976; Holdich & Jones 1983; Isaak & Moyse 1990; Isaak et al. 1990; Moyse & Smaldon 1990; King 1974; Mauchline 1984; Naylor 1972; Sars 1894; Sars 1900

Polychaeta: Hartmann-Schröder 1996; Petersen 1998; Fauvel 1923; Fauvel 1927; Hilbig & Dittmer 1979

Echinodermata: Moyse & Tyler 1990; Webb & Tyler 1985; Lieberkind 1928

Mollusca: Tebble 1966; Jones & Baxter 1987; von Cosel et al. 1982; Graham 1988; Thompson & Brown 1976; Hayward 1990; Hayward et al. 1990; Poppe & Goto 1991; Poppe & Goto 1993; Ziegelmeier 1957; Ziegelmeier 1966; Luczak & Dewarumez 1992

Others groups: Broch 1928; Ryland 1990; Manuel 1988; Pax 1928; Cornelius et al. 1990; Gibbs 1977

(References are listed separately under "References II"). During earlier years not all of these in part new releases were available and in some cases older editions were used.

Biomass data were not recorded in most of the previously existing records.

3.2.3 Data sources

For the three stations Slt, SSd and FSd data from 1969 until 1987 were with few exceptions available from the original laboratory protocols. For the FSd station, spring data were available until 1991. Parts of these data were published before (Rachor 1977; 1980; 1982; 1990; Rachor & Salzwedel 1975; Rachor & Gerlach 1978; Rachor & Bartel 1981; Rachor et al. 1982; Heuers 1993). Data for later years until 2000 were obtained by analysis of stored samples as far as available and by continuation of the sampling. All data for station WB, starting from 1981, were obtained by analysis of stored and newly taken samples. Before 1974 only one value per sampling date is available in most cases, as grab samples were pooled either on board or in the laboratory and data were only reported for the pooled sample. Since 1975, raw data as abundances per sample are mostly available. Biomass data are available for WB since 1981 and from 1988 for all stations (newly analysed samples).

All data were entered in a specially developed database (Annex A.3) and checked for quality and consistency over time (see following paragraph).

3.2.4 Data quality control

All data entered into the database were checked by comparing printed reports with original data sheets. Data were checked for inconsistencies in identification over time and doubtful identifications re-identified from stored samples as far as available. Original identification and comments were kept in the "remark" field of the respective database entry.

A serious source of error for long term analyses as well as for comparisons of data from different sources are taxonomic difficulties. The simplest possible error source are synonyms of scientific names, resulting from the use of different identification literature or from changes of the scientific nomenclature. Over the course of the last 30 years, several species were renamed, some of them even several times. The problem of synonyms was overcome by the construction of a specific taxonomic database ("DB99_Species"), linking all synonyms to one single valid scientific name. This species database contains all species recorded in the German Bight during the long-term investigations, from large spatial studies covering the whole area and from selected literature (a detailed description can be found in annex A.4).

Using this table during the extraction of the data from the database, the result will be free from synonyms. It can also be used to extract data at a higher systematic level such as genus, family, order or the like. Less simple is the case of taxa that were determined with differing precision (species, genus or family) as well as of species that were newly described, lumped or split. For specific data sets containing such problems, the respective species were combined at the next higher reliable systematic level, which can be assumed to be consistent within the respective data set. These cases are not treated automatically, as other subsets with e.g. a restricted time span may not contain dubious cases and do not require species lumping with its associated loss of information.

For a large number of samples, only certain taxonomic groups had been identified. Other samples consist only of one or two grabs (Annex A.2). The status of the data is recorded for each sample separately, stating whether the analysis of the sample was complete or if only some major groups had been analysed. Additionally the data status is recorded for each station, allowing an easier identification of those sampling occasion with a sufficient number of adequately analysed samples.

3.2.5 Data selection for the long-term study

The analysis of temporal changes in the benthic communities is based on a reduced set of data. Just like the number of species, similarity calculations are influenced by the sample size (see chapter 4.2.5). Analyses based on any kind of similarity calculations should therefore be based on samples of the same size wherever possible.

From each year one sampling date from spring (preferably early April) was selected where the most reliable data were available. As far as possible, samples of five 0.1m² van-Veen grabs were preferred, but alternative samples (e.g. two vV plus six RBC) had to be accepted especially for SSd and FSd-stations for certain years.

Whenever appropriate data from April were not available, the date closest to April with appropriate data was chosen (selected data are marked in annex A.2). All data were standardized to abundances per m². In cases were different grab types were combined, a weighted arithmetic mean density was calculated.

3.2.6 Spatial sampling

The sampling for the long term series was intended always to take place at the same location. Bad weather conditions and less accurate positioning systems in earlier times (e.g. DECCA) probably often only allowed much less precise positioning than today. If some kind of spatial structure or gradient was present in the area, a deviation from the exact position could result in different results for benthic communities. An minimum accuracy of ± 0.5 nm can be assumed at all times.

To asses the possible effect of deviations from the exact sampling position, 21 van-Veen grabs were taken in the vicinity of the centre position of all four permanent stations in April 1998 (Tab. 3.2.1). The area covered by the spatial sampling was chosen to cover all possible deviations from the centre position even under unfavourable conditions. Samples at 1 nm from the centre were included to asses further spatial variation in the area.

Tab. 3.2.1: Date and time of spatial sampling and weather conditions.

		Time		Wind			
Station	**Date**	**from**	**to**	**Main direction**	**Mean speed [m/s]**	**Bft.**	**Mean temperature**
WB	21.04.1998	8:01	15:05	S	4.1	3	8.7 °C
FSd	23.04.1998	6:01	11:38	E	10.1	5 (-6)	10.6 °C
SSd	25.04.1998	8:01	14:00	SW	5.3	3-4	10.4 °C
Slt	25/26.04.1998	15:15	19:40	E	3.4	2	8.5 °C

Five samples were taken at the centre position for the long term programme. Additionally each two samples were taken at a distance of 0.5 and 1.0 nm in all four directions (Fig. 3.2.1).

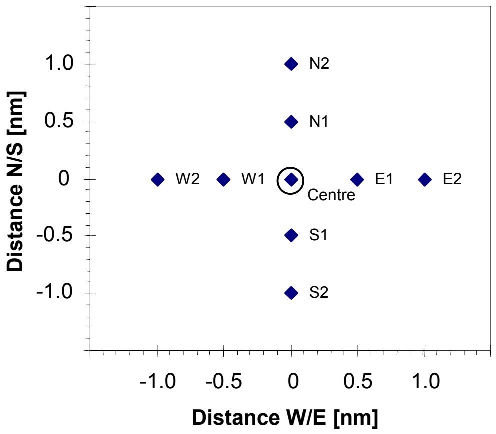

Fig. 3.2.1: Locations of the sampling positions around the permanent stations ("Centre").

One sample from FSd had to be disregarded due to inappropriate fixation resulting in a total of 20 samples for this station. Samples were collected by a 0.1 m² modified van-Veen grab (see chapter 3.2.1), sample processing followed the procedures described in chapter 3.2.2.

3.3 Environmental data

Several environmental data sets were used in the analysis of correlation between environmental regime and benthic communities.

Climatic data from October 1966 until June 2001 were obtained from Deutscher Wetterdienst (DWD) for all weather stations along the North Sea and Baltic Sea coast with 4 to 24 values per day. From these data, modal wind direction, minimum, mean and maximum wind speed and air temperature were calculated per day. For the analyses in the present study, data from a weather station located at Helgoland were used, as this station is closest to the four investigated benthos stations and it best reflects the offshore weather. The weather-station is situated in the southern harbour of Helgoland at ten metres above the ground without higher structures in the vicinity that could influence wind measurements (DWD, pers. comm.).

Water temperature and salinity, nutrients and phytoplankton data have been continuously recorded by the Biologische Anstalt Helgoland (BAH). Samples have been taken at the "Helgoland Reede" station (54°11'18"N 7°50'00"E) between the main island and the dune island since 1962 on every weekday (Hickel et al. 1997). Data were kindly supplied by K. Wiltshire, P. Mangelsdorf and S. Janisch (partly unpublished; Data archived in the information system PANGAEA – Network for Geological and Environmental Data, http://www.pangaea.de). Unfortunately the phytoplankton data from Helgoland are subject to several methodological errors and thus are currently not yet usable for an analysis of the phytoplankton development in the German Bight (K. Wiltshire, pers. comm.).

The water discharge of the river Elbe at km 537 is recorded daily from 1960 to 2000, was kindly provided by Eggert (2002) (http://www.dgj.de/servlet/IbMenu).

The "North Atlantic Oscillation Index" (NAOI) summarizing the main climatic features over Northern Europe was provided by the Climate Analysis Section, NCAR, Boulder, USA, Hurrell (1995) (http://www.cgd.ucar.edu/~jhurrell/nao.html). It is available on a monthly, seasonal or annual basis from 1865 until 2000 and as winter-index (Dec – Mar) from1864 until 2002.

3.4 Analytical methods

The community structure, spatial distribution and temporal development of the benthic organisms is summarised and compared by various univariate and multivariate indices and statistics:

3.4.1 Indices

All diversity and similarity indices are calculated from formulas as stated in Krebs (1998) and Legendre & Legendre (1998) unless specified otherwise.

Univariate statistics were calculated using STATISTICA vers. 5.5 (StatSoft Inc. 2000), multivariate analyses based on PRIMER 5 software vers. 5.2.2 (Primer-e 2000). Indices and *p*-value adjustment were calculated by custom written Excel Visual-Basic-modules.

3.4.1.1 Spatial distribution & variability

3.4.1.1.1 Univariate statistics

The variability of any measure can be expressed by the ratio between the standard deviation (SD) and the mean ($\bar{x}$), which is called *coefficient of variation* (CV = $SD/\bar{x}$) (Elliott 1977). It is independent of the sample size and invariant to linear extrapolations. It can however not be used to classify the type of spatial distribution of organisms.

One of the oldest and simplest measures of dispersion is the ratio between variance and mean ($s^2/\bar{x}$) of local organism densities. It ranges from 0 for uniform distribution over 1 for random distribution to its maximum which equals the total number of organisms in the sample (Krebs 1998). Values larger than 1 indicate an aggregated distribution. The variance-to-mean ratio is however problematic, as any data transformations may change this ratio. When a simple multiplication with a fixed factor is applied, the square of this factor will affect the variance, while the mean is only affected by the simple factor. An extrapolation to densities per m² may often result in an interpretation of aggregated distribution for nearly all species. The variance-to-mean ratio should thus only be applied to raw data. Another serious concern was raised by Hurlbert (1990) who showed that several non-random pattern can lead to a variance-to-mean ratio of 1. Other measure of dispersion may be used to overcome these problems.

The spatial distribution of the organisms can be tested by Morisita's index of dispersion I_d (Morisita 1962).

$$I_d = n\left[\frac{\sum x^2 - \sum x}{\left(\sum x\right)^2 - \sum x}\right] \qquad \text{(eq. 3.1)}$$

where n = number of samples
Σx = sum of organisms

It has the advantage of having a known sampling distribution and the statistical significance of non-randomness can be tested (Krebs 1998). This procedure is simplified by the standardisation of this index to a range of –1 to 1 by Smith-Gill (1975). After the calculation of I_d, two critical values M_u and M_c are calculated:

$$M_u = \frac{\chi^2_{.975} - n + \Sigma x}{(\Sigma x) - 1} \quad \text{and} \quad M_c = \frac{\chi^2_{.025} - n + \Sigma x}{(\Sigma x) - 1} \qquad \text{(eq. 3.2 \& 3.3)}$$

where $\chi^2_{.975}$ = value of Chi-square distribution with (n-1) d.f. with 97.5% of the area to the right
n = number of samples
Σx = sum of organisms

Then the standardised Morisita index I_p is calculated by one of the following formulas:

If $I_d \geq M_c > 1$:
$$I_p = 0.5 + 0.5 * \left[\frac{I_d - M_c}{n - M_c}\right] \qquad \text{(eq. 3.4)}$$

If $M_c > I_d \geq 1$:
$$I_p = 0.5 * \left[\frac{I_d - 1}{M_c - 1}\right] \qquad \text{(eq. 3.5)}$$

(The term "M_u" given in Krebs (1998) is a mistake, and must read "M_c" (Smith-Gill 1975))

If $1 > I_d > M_u$:
$$I_p = -0.5 * \left[\frac{I_d - 1}{M_u - 1}\right] \qquad \text{(eq. 3.6)}$$

If $1 > M_u \geq I_d$:
$$I_p = -0.5 + 0.5 * \left[\frac{I_d - M_u}{M_u}\right] \qquad \text{(eq. 3.7)}$$

In this standardised form, I_p-values larger than 0.5 indicate a significantly clumped distribution, values around 0 a random distribution and values lower than –0.5 a significantly more even distribution (Krebs 1998).

3.4.1.1.2 Multivariate statistics

The multivariate variance is measured by the average similarity between all pairs of samples and its coefficient of variation (CV). The higher the similarity between two samples from an area, the lower the multivariate spatial variability within the community. Similarities however are not independent random variables (Clarke & Warwick 1994), thus usual statistical procedures can not be applied to test the significance of differences. The mean and CV can however be used for purely descriptive purposes.

Comparisons of the variability of two samples is only valid if both samples have the same mean or, in case both samples have different means, if it is known that the variability does not systematically depend on the mean (Krebs 1998). The same applies to similarity measures. The exact relation between mean similarity and its variance is an inherent property of the chosen similarity index and is at present unknown. Comparisons of the *variability* of similarities of several groups are strictly only valid if all groups have the same *mean* similarity. Comparisons of the CV across groups of different mean similarity are likely to be valid if the similarity measure changes linearly. The Bray-Curtis-similarity is one of the few similarity indices that show this linear behaviour (Bloom 1981). This should allow a comparison of the variability of similarities even between groups of differing mean similarity.

3.4.1.2 Diversity

Besides purely quantitative descriptions in terms of organism density and biomass, several measures of diversity in the wider sense are the most common attributes used to describe biological communities. These include the simple species number, evenness or dominance indices and various "diversity" indices combining aspects of species richness and evenness. A combination of these measures is meant to summarise the main information about the numerical community structure. Most of these measures are affected by sample size. This dependency is investigated as a background information for the long-term study and to estimate the minimum sample size necessary for a reliable value without excessive variability.

Species number

The simplest aspect of diversity is the *number of species* present (S). The total number of species in a benthic community is however mostly not possible to determine. The number of species found is strongly dependent on the sampling effort. The species number should thus always be related to the respective sample size, and comparisons should only be made between samples of the same size. For quantitative investigations, this sample size relates to a standard sampling effort (e.g. sampled area, resp. number of grabs) and is termed *species density*.

The number of species per unit area is termed *species density*. The number of species relative to the number of organisms is called *species richness* (Gotelli & Colwell 2001). The total number of species found in an area is termed *species spectrum.*

Noting the strong dependence between sample size and species number, Sanders (1968) proposed to calculate the *expected number of species* for a given (smaller) number of organisms drawn randomly from the existing sample ($E(S_n)$). The corrected formula for this "rarefaction" given by Hurlbert (1971) is:

$$E(S_n) = \sum_i \left[1 - \frac{\binom{N-N_i}{n}}{\binom{N}{n}} \right] \qquad \text{(eq. 3.8)}$$

where N = total number of organisms in the collection
N_i = number of organisms in species i
n = number of organisms chosen for standardisation ($n \leq N$)

In this case the species number is related to the number of organisms and called *species richness* (Gotelli & Colwell 2001). Rarefaction assumes a random distribution of the organisms in space. This includes a random distribution within each species and independence between the species. In practise, most species' distributions are clumped and there may be positive as well as negative associations between the species. The larger these violations of the assumption of randomness, the larger will be the overestimation of the number of species by the rarefaction method (Krebs 1998).

When a sufficient number of samples is available, sample-based species accumulation curves can be constructed by Monte-Carlo computer simulations of the number of species in relation to the number of samples (Gotelli & Colwell 2001). These represent an unbiased presentation of the expected (=mean) number of species for a given sample size and with an empirical confidence interval around this mean. The sample size can be interpreted not only in terms of number of samples or the respectively sampled area (*sp. density*), but also in terms of mean number of organisms (*sp. richness*).

Evenness

Evenness indices summarise the dominance structure of the community. Maximum evenness is reached when all species are present in equal densities. The higher the numerical dominance of a few species, the lower the evenness. Probably the most common measure of evenness is Pielou's J' (Pielou 1966):

$$J' = \frac{H'}{H_{\max}} = \frac{H'}{\log_2(S)} \qquad \text{(eq. 3.9)}$$

It relates the observed heterogeneity to the maximum possible diversity (heterogeneity), which is reached when all species are equally abundant ($H'_{max}=\log_2(S)$).

Although theoretical studies have suggested other indices as preferable (Smith & Wilson 1996), a comparison of sample size dependence and variability of various evenness indices using real data from the spatial sampling identified J' as the least variable measure. Results on the sample size dependence of J' and its variability are presented in the results chapter, details on the results from other indices and their comparison go beyond the scope of the present study and shall be presented in a forthcoming publication.

Heterogeneity

The concept of heterogeneity combines the aspects of species richness and evenness into a single measure.

Based on information theory, the Shannon-Wiener index (Shannon & Weaver 1963) was first applied in ecology by Margalef (1958).

$$H' = -\sum_i p_i \log_2(p_i) \qquad \text{(eq. 3.10)}$$

where $p_i = n_i / N$
n_i = abundance of species i
N = total number of organisms

It measures the uncertainty about the species identity if one more organisms were to be collected from the respective community (in bits per organism). In theory it can reach very high values, but for biological communities H' does not seem to exceed 5.0 (Krebs 1998).

As its unit (bit) is a rather hard to interpret, Hurlbert (1971) and Hill (1983) recommended the use of its exponential form $N_1=2^{H'}$ instead. This index has the more readily understandable unit of species (Santos & Bloom 1983). The exponential transformation does expand the range and may pronounce especially differences between highly diverse communities (Gray 2000). As this is a simple monotone transformation of H', it does not affect the outcome of comparisons or nonparametric statistical tests. In practise, H' is still the most often applied form of this index of diversity. To enhance comparability to published results, it is used throughout this study.

Although several authors have suggested other indices as preferable (Hurlbert 1971; Hill 1973; Krebs 1998), the choice of index has to rely on the interpretability of the results. A comparison of sample size dependence and variability of various diversity indices using real data from the spatial sampling identified H' as the least variable measure. Results on the sample size dependence of H' and its variability are presented in the results chapter, details on the results from other indices and their comparison go beyond the scope of the present study and shall be presented in a forthcoming publication.

3.4.1.3 Multivariate similarity

All community attributes mentioned above do only describe the numerical structure of the community, but do not include any information about the species identities, which seems a rather crucial aspect for community comparisons. Multivariate methods have shown to be more powerful in detecting small changes in biological communities than univariate methods (Warwick & Clarke 1991; Clarke & Warwick 1994; Legendre & Legendre 1998). The combination of the species identities and of the dominance structure is what makes quantitative similarity indices such a powerful tool for community comparisons.

One of the most widely used measures of similarity is often called “*Bray-Curtis-similarity*” which was earlier proposed by Motyka (1947) and attributed to H. Steinhaus (Legendre & Legendre 1998). Species absent in both samples are not considered in the calculation of similarities.

$$BC = \frac{2 * \sum_i \min(x_{ia}, x_{ib})}{\sum_i (x_{ia} + x_{ib})} = 1 - \frac{\sum_i |x_{ia} - x_{ib}|}{\sum_i (x_{ia} + x_{ib})} \qquad \text{(eq. 3.11)}$$

where x_{ia} = abundance of species *i* in sample *a*

For the sake of sticking to the most common name and reducing the confusion about index names, I will nevertheless retain the term *Bray-Curtis-similarity* (BC). Bray & Curtis (1957) calculated the similarity based on proportions, thus similarity measure used in their often cited paper is in fact Renkonen's (1938) *Percentage similarity*, as the authors noted themselves.

With the sum of differences in its denominator, the BC index is strongly dominated by the presence of single large differences and transformations are recommended to reduce this influence (Field et al. 1982). A 4th root data transformation prior to the calculation of similarities removes the excessive influence of the dominant species and distributes the weight more evenly between all members of the community (Field et al. 1982). Many similarity indices like e.g. the Bray-Curtis-index are invariant to linear scaling of the data like e.g. calculations of densities per m². This property is maintained if square root or fourth root transformations are applied (Field et al. 1982), but it is lost if logarithmic transformations are applied.

In a comparison of the properties of various (dis-) similarity indices, the *Bray-Curtis-similarity* with a fourth root transformation was chosen for the further analyses of the present study as it produced the least variable and most consistent results. Results of the sample size dependence of the BC are presented here, details on the results from other indices, transformations and their comparison go beyond the scope of the present study and shall be presented in a forthcoming publication.

3.4.2 Multivariate analytical procedures

In analyses of ecological communities, the assumption of independent variables (species or environmental factors) is not realistic. Organism densities are often influenced by biological interactions and environmental factors are often correlated amongst themselves. Studying multidimensional data sets using univariate statistics however assumes this independence. Only multivariate methods taking the dependence of the variables into account can properly analyse the whole story when dependencies exist (Legendre & Legendre 1998). This may be one of the main reasons why multivariate analyses have proven to be more powerful in detecting changes in ecological communities than various univariate methods (Clarke & Warwick 1994).

3.4.2.1 MDS

Nonmetric Multidimensional Scaling (MDS) (Kruskal 1964) is used to represent the multivariate similarities between samples in a reduced number of dimensions. It is based on an association matrix containing the (dis-) similarities between all pairs of samples. A MDS-plot represents as much of the information contained in the underlying association matrix in the specified number of dimensions as possible. The quality of this representation is measured by the "stress"-value (Kruskal 1964). The lower this value, the better the presentation. A high stress-value indicates a higher dimensionality of the data (Clarke & Warwick 1994) and is typical for samples which do not contain a clear structure (Rumohr et al. 2001).

Consecutive MDS-plots based on the same association matrix and with the same stress-value may differ, because of problems with the placement of samples which are not closely related to the other samples in the plot. Such point will be located at the periphery of the plot, more or less at random and probably at different borders in consecutive iterations of the same analysis (Bob Clarke cited as pers. comm. by Gamito & Raffaelli

1992). With other ordination methods such a principal component analysis (PCA) or correspondence analysis (CA or DCA), such points may be positioned in the first two axes amongst the other points with which they have no affinity, while being separated on higher axes. The variation seen in the MDS plots may as such be more informative with regard to the affinities of such samples (Gamito & Raffaelli 1992).

In order to avoid misinterpretation of the position of single years relative to the whole time-series, a minimum of ten 2D plots based on the same similarity matrix with the same minimal stress were compared amongst each other and to 3D solutions. Only those results were interpreted that were consistent with all 2D and 3D solutions. In doubtful cases the results were confirmed by inspection of the similarity matrix.

3.4.2.2 Cluster Analysis

Like MDS, this analysis works with any type of similarity measure. Hierarchical cluster procedures join samples consecutively to produce groups that maximise the similarity within the groups and at the same time the distinction of the groups. The result is usually presented as dendrogram. The appearance of this plot is strongly influenced by the clustering procedure applied. As the similarity between single samples remains untouched, the pairs with the highest similarity are usually the same for all procedures. The way these are joined can however differ largely. Out of the large number of procedures described (Clifford & Stephenson 1975; Legendre & Legendre 1998) the "Group average" clustering is the preferred standard procedure. It joins two groups by evaluating the mean similarity between the samples from both groups. It is not as much prone to the "chaining"-effect as the "Single linkage" procedure nor to an artificial formation of distinct clusters (as possible with "Complete linkage") (Field et al. 1982 & own unpublished results). In cases where several groups are rather similar or even overlapping, "Complete linkage" may provide additional (and possibly clearer) information to facilitate the decision of where to draw the line between the groups.

3.4.3 Statistical tests

3.4.3.1 Comparison of univariate measures

Statistical significance of differences between two means of univariate measures were tested using the *U*-test (Mann & Whitney 1947). This rank sum test does not rely on assumptions of normality and homogeneity of variances. It only assumes an ordinal scale. It is known to be one of, if not the most powerful nonparametric alternative to a two-sample t-test. In some cases with few observations, it may even be more powerful (Zar 1996). With $n > 20$, U quickly approaches a normal distribution, while for small n the actual value of U is compared to all possible values with the given number of observations in both samples by a permutation test.

Box & Wisker plots are used for a graphical presentation of differences between groups of samples (Tukey 1977). In the form used here, it displays the median, the 25th and 75th percentiles and the range of values excluding extremes. Extreme are values that are more than 1.5 times the interquartile range larger than the 75th percentile or smaller than the 25th percentile (displayed as separate dots). A "notch" around the median indicates the 95% confidence interval of the median (McGill et al. 1978).

3.4.3.2 Correlations

Throughout this study, regressions are used for graphical representation of trends in data, while associated statistics are only used as indications of uncertainty without using them for statistical inference. Linear regression is strictly speaking only valid under the assumptions of normality of residuals and homogeneity of variance over the range of the independent variable. This is often not the case in ecological data sets and confidence intervals and coefficients of determination are not statistically valid. Statistical inference is therefore accomplished by the robust nonparametric Spearman's rank-correlation coefficient ρ (rho). It does not rely on assumptions about the distribution of the data or linearity of the correlation. It tests for monotonic correlations and is based on ranks and thus only requires ordinal data.

3.4.3.3 Smoothing of time series

Most time series presented here are shown without smoothing methods, because these would suppress any short-term effects caused by disturbance. However, for the development of benthic communities, these disturbances are considered one of the most important factor. The only exception is the presentation of the long-term (1864 – 2002) development of the NAOI, which is presented with a low-pass filter, analogue to the presentation from Hurrel (1995). This low-pass filter represents a weighted running mean over seven years with weights of 1, 3, 5, 6, 5, 3 and 1.

3.4.3.4 Multivariate differences

The statistical significance of multivariate differences between two groups is tested by the ANOSIM procedure, a permutation test based on Clarke's *R* statistic (Clarke & Warwick 1994). Clarke's *R* measures the relation between the mean rank similarities within each group $\bar{r}_W$ and the mean rank similarity between both groups $\bar{r}_B$:

$$R = \frac{\bar{r}_B - \bar{r}_w}{M/2} \quad \text{(eq. 3.12)}$$

where $M = \frac{n(n-1)}{2}$ the total number of similarity-ranks in the test

$\bar{r}_W$ = mean rank similarities within each group

$\bar{r}_B$ = mean rank similarity between both groups

When *R* equals 1, all similarities within the groups are larger than those between samples from different groups. *R* = 0 indicates no differences while negative values indicate the need to verify the homogeneity of the samples. Large negative values of *R* do occur when either or both groups contain outliers, or when two different states are found in both groups (Chapman & Underwood 1999). As *R* may be small but still significantly different from zero, the probability of falsely rejecting the null-hypothesis of *R* = 0 is calculated by a permutation test (Clarke & Warwick 1994).

3.4.3.5 Comparing multivariate pattern between stations

To test for a similar multivariate pattern in two sets of samples, a rank correlation is calculated between the two similarity matrices based on either data set. In case of a similar temporal development of the communities, there will be a significant correlation between the similarity matrices. The calculated correlation is compared to results from randomly permutated samples to test for statistical significance (Clarke & Warwick 1994; Primer routine RELATE). This correlation can only be calculated for years when data from both stations are available. A correlation indicates a similar temporal development, e.g. similar periods of relative stability and similar points of change, but does not imply a parallel population development for species present at both stations.

3.4.3.6 Multivariate Mantel correlograms

Multivariate Mantel correlograms are used to describe the temporal and the spatial autocorrelation of species assemblages. Multivariate *temporal* autocorrelation describes the similarity of samples in dependence on the time span between the sampling dates (Legendre & Legendre 1998), in this case for the long term series in years. In the presence of temporal autocorrelation, samples from consecutive years or separated by only a few years are more similar than samples separated by longer periods. Temporal correlograms are used to identify cyclical developments as well as long term trends. Multivariate *spatial* autocorrelation describes the similarity of samples in dependence on the spatial distance between the sampling sites (Somerfield & Gage 2000). In the presence of spatial autocorrelation, samples from sites located closer together are more similar than samples separated by longer distances. Spatial correlograms can be used to identify geographical patterns in community composition as well as large scale gradients.

Multivariate Mantel correlograms are based on an association matrix containing the pair-wise (dis-)similarities between the samples and a second corresponding matrix of temporal or geographical distances. The latter one is used to construct several model matrices. The distances are split into classes and one matrix is constructed for each class, each containing code 1 for those distances that belong to the respective distance class and zeroes in the remaining fields. A Spearman's rank correlation is calculated between the association matrix and each of these model matrices and the statistical significance tested by a permutation test (Mantel-test (Mantel 1967), Primer routine RELATE). As this involves as many statistical tests as there are distance classes, the *p*-values are adjusted for multiple testing by a sequential adjustment procedure for multiple testing (Legendre & Legendre 1998). The correlations are plotted against distance classes and significant correlations are marked. Correlations for the largest class(es) commonly involve very few values and should be disregarded.

3.4.3.7 Multiple statistical test

Statistical test procedures generally results in an error probability "*p*" indicating the probability that a null-hypothesis is falsely rejected. When several test are computed simultaneously, the overall error probability becomes much larger than the nominal error probability α accepted for the single test. The simplest way to account for this effect is to adjust the calculated *p*-values by the number of tests carried out (k) by the *Bonferroni*-correction $p' = k*p$. As this procedure is overly conservative, a much more powerful procedure is Holm's adjustment (Holm 1979): After ordering the *p*-values to an increasing series p_i with i running from 1 to k, each p_i-value is replaced by $p_i' = (k - i + 1)*p_i$. When proceeding from $i = 1$ to k, every value which is smaller than its predecessor is augmented to the larger value, resulting in a monotonously increasing series (Legendre & Legendre 1998). This procedure is also valid for non-independent tests (Wright 1992). An even more powerful procedure only applicable to *independent* tests was proposed by Hochberg (1988). Only the last step differs from Holm's procedure: proceeding this time from $i = k$ to 1, if an adjusted value is larger than its predecessor, it is diminished to the lower value. With this method, no adjusted *p*-values can be larger than the largest unadjusted *p*-value or exceed 1 (Legendre & Legendre 1998). By using either of these adjustments, the overall error probability is preserved.

3.4.4 Analysis of spatial variability

Spatial variability in organism density between samples taken in any one area may be of two different types: systematic and random variability. Systematic variability includes spatial autocorrelation up to larger scale gradients across the whole area. Random variability results from natural random variance, a patchy distribution of the organisms at a scale smaller than the distance between sampling positions.

Systematic variability

Total organism density, species density, diversity and evenness were tested for possible gradients in either N/S or W/E direction by Spearman's rank correlation to the geographical position. Probabilities were adjusted for each station separately for testing two axes by Hochberg's procedure to preserve the 5% error-level for each parameter.

To test for multivariate spatial autocorrelation or a possible gradient in the community, multivariate Mantel correlograms were constructed. As gradients only present in a single direction may pass unnoticed in all-directional correlograms (Legendre & Legendre 1998), unidirectional correlograms were computed separately for the North-South axis and the West-East axis. Similarities were calculated using Bray-Curtis index and fourth root transformed data. Geographical distances were split into 5 classes corresponding to the main distances implied by the sampling scheme (Tab. 4.6.2):

Tab. 3.4.1: Distance class for Mantel-correlograms.

Class	[nm]	[m]	Class centre
1	**0 – 0.25**	**0 – 463**	**0 nm**
2	**0.25 – 0.75**	**463 – 1389**	**0.5 nm**
3	**0.75 – 1.25**	**1389 – 2315**	**1.0 nm**
4	**1.25 – 1.75**	**2315 – 3241**	**1.5 nm**
5	**1.75 – 2.25**	**3241 – 4167**	**2.0 nm**

Random variability

The spatial variability of univariate variables is measured by the coefficient of variation [CV] (McArdle et al. 1990). The spatial distribution of the organisms is evaluated by the variance-to-mean ratio and tested by the standardised Morisita index of dispersion I_p (chapter 3.4.1.1.1). The average Bray-Curtis similarity between all pairs of samples (fourth root transformed organism densities) and its CV is used as measure of multivariate variability.

3.4.5 Samples size dependence

Even if gradients or spatial autocorrelation were detectable in the benthic community, all samples taken within the assumed area of sampling are replicate samples from the respective community including its natural spatial variability. To asses the number of grabs necessary to adequately describe the benthic community, the statistics used for the community description are plotted against the sample size.

The variability of the mean number of organisms and biomass per m² is estimated for a cumulative number of pooled samples by a bootstrap procedure using re-sampling *with* replacement to preserve a correct estimate of variance (Manly 1997). Error bars indicate the standard deviation of the values calculated from different samples sizes. For single grabs this is the ordinary standard deviation (SD). For larger samples it represents the standard deviation of the *mean* density per m² calculated from two, three or more grabs and is thus equivalent to the standard error of the mean (SE). As most measures are not normally distributed, these statistics can not be used to construct a confidence interval (C.I.). An empirical C.I. around the mean is determined that includes 95% of all permutation values. The precision of the estimated mean is expressed as the ratio between the size of the empirical C.I. and the mean.

The species density, diversity (H') and evenness (J') (see chapter 3.4.1.2) are compared regarding their sample size dependence. Values for cumulative number of pooled grabs are calculated by re-sampling *without* replacement. Variance estimates are thus slightly negatively biased (Manly 1997). For samples containing more than half the total number of samples the decrease in variance is influenced by the decreasing number of possible permutations and should be interpreted with caution. This drawback has to be accepted because the number of species in a pooled sample is a function of the number of *distinct* samples contained. Selecting e.g. 20 samples *with* replacement will result in a pooled sample containing almost always less than 20 distinct samples. Therefore the resulting number of species should be attributed to the actual number of *distinct* grabs contained. For this reason all diversity calculations are done by re-sampling *without* replacement as all of them are influenced by the species richness to a certain extend.

An adequate sampling can be assumed at the point where the average similarity between two samples of the same size does not increase remarkably with a further increase in sample size. This can be graphically presented in a self-similarity or similarity area curve (Weinberg 1978; Kronberg 1987; Streever & Bloom 1993). If a community is adequately reflected by a certain sample size, the similarity between samples will be high and the variability of the similarities will be low. The smaller this variability, the smaller the differences that can be detected between communities (or their temporal changes).

Similarity matrices were calculated for increasing numbers of pooled randomly chosen samples *without* replacement. This procedure assures that no similarities were computed between pooled samples containing the same grab in both samples and that all grabs were included in the matrices to an equal extend. For each pooling level, random pooling and calculation of the similarity matrix was repeated until 10 000 similarity values were obtained.

Because of the unknown frequency distribution of similarity indices, an empirical confidence interval around the mean is determined that includes 95% of all permutation values. This interval represents the range where 95% of all values for the respective sample size are to be expected.

All permutation and bootstrap procedures were calculated using 10000 replications as far as possible. Calculations are carried out by custom written Excel Visual-Basic-modules.

3.4.6 Temporal community development

Similarities between years were calculated as Bray-Curtis-Similarity of fourth root transformed densities per m². Based on this similarity matrix, cluster analysis using group average clustering was applied to identify major groups. Temporal development was represented on two dimensional nonmetric MDS plots with consecutive years connected by lines. This implies that the position of every year is interpreted in relation to the remaining years. Data points that are very different from the rest are positioned in a somewhat arbitrary position on the edge of the plot by the MDS (Gamito & Raffaelli 1992). In order to avoid misinterpretation of the position of single years, a minimum of ten 2D plots based on the same similarity matrix with the same minimal stress were compared amongst each other and to 3D solutions. Only those results were interpreted that were consistent with all 2D and 3D solutions.

3.4.7 Environmental influences

The relation between the community development and environmental conditions was investigated by correlating the similarity matrix based on the benthos data to distance matrices based on combinations of environmental factors:

- The North Atlantic Oscillation index (NAOI) as Winter-NAOI and annual NAOI.
- Mean and minimum water temperature during Winter (Dec. – Mar.) and mean and maximum water temperature during summer (Jul. – Sep.).
- The frequency of strong winds with ≥ 7 Bft (≥ 28 kn) separated for westerly (NW,W,SW) and easterly directions (NE,E,SE) and summed over all directions. The number of days with a mean wind speed of 7 Bft. or more were summed over the windy season from September until March preceding the benthos sampling.
- Mean salinity and concentrations of PO_4, DIN and SiO_4 at Helgoland as well as Elbe total river runoff were calculated per year (from April of the preceding year to March before the benthic sampling).

A Spearman's rank correlation was calculated between the similarity matrix based on the faunal data (4th root transformed, Bray-Curtis similarity) and the similarity matrix calculated from the set of environmental data (untransformed data, Normalised Euclidian distance). To identify the best explaining variables from the whole set of environmental data, the calculation of this correlation was repeated for all combinations of up to three variables including a time lag of up to three years (Primer BIOENV-routine: Clarke & Warwick 1994). The largest correlations are selected and tested by a permutation test. Only combinations of two factors are listed that yield a higher correlation than the best single factor. Combinations of three factors are only considered if they result in a higher correlation than the best two factors.

A selection of the highest observed correlations increases the risk of erroneously accepting accidental correlations. Most of the highest correlations are statistically significant if tested singly by permutation tests, but these tests are not formally valid as the presented correlations are the highest of a great number of possible (combinations of) factors. A formally valid Bonferroni-correction of the error level may be too conservative as this reduces the significance of possibly influential factors simply because of the number of additional and possibly irrelevant factors tested. As an alternative, a series of 1000 variables of random numbers was created and the observed *R* for real factors compared to the highest values obtained from a correlation between these random variables and the benthos data. The percentage of random variables that yield higher correlations than the tested factor is indicative of the error probability. All correlations larger than the largest correlation of any random factor can be assumed significant at an error level of < 0.1%.

4. Results

4.1 Precision of sampling position

Several influences lead to an unknown distance between the actual position of the grab at the sea bottom and the position recorded by the ship's positioning-system. Today, the position is usually recorded by a Differential Global Positioning systems (DGPS; ± 3-4 m) to two decimal minutes (± ~10 m in the German Bight). The distance between GPS-antenna and the suspension of the grab amounts to about 10 m in case of the FS Heincke used for the present sampling. The unavoidable drift of the vessel and the grab may cause the wire of the grab to descend from the suspension at an angle of up to about 20° (pers. observation), adding another 10 to 17.5 m of uncertainty at water depth of 20 to 40 m. Considering all these influences, a more conservative estimate of the precision of the recorded GPS-position would be between ± 20 m to ± 40 m depending on water depth and weather conditions.

Under offshore conditions in the North Sea it is hardly possible to manoeuvre the ship to exactly the desired position at exactly the moment when the sampling gear touches the bottom. Depending on the strength and direction of wind and currents, this results in a median distance between the desired position and the position recorded at the moment of sampling at the sea floor of 89 to 152 m (Fig. 4.1.1; total median 101 m).

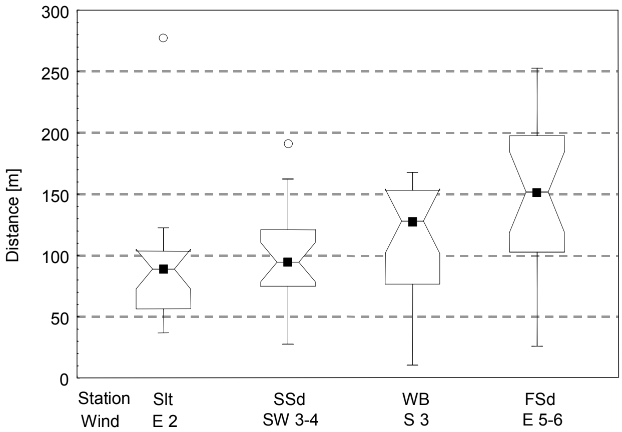

Fig. 4.1.1: Distance between the desired position (= 0) and recorded position at the time of sampling for separate stations in 1998; main wind direction and force in Bft. as recorded during the sampling.

Weather conditions during this cruise were not exceptional, ranging between 2 and 6 Bft. from various directions (subscripts in Fig. 4.1.1).

4.2 Spatial variability

As background information for the interpretation of the long-term variability, the spatial variability of the benthic communities at the four sampling stations is assessed from the extensive sampling conducted in April 1998 (Chapter 3.2.6; Tab. 3.2.1).

4.2.1 Spatial structuring

Within each station, there is a high variability of the grabs, but no clear structuring. A distinction of groups or spatial gradients is not possible. At all station the similarity between the five grabs from the centre station is about equal to that between grabs from other positions. Some pairs of grabs taken at the same position are quite close together, but other pairs are widely spread (Fig. 4.2.1; each grab is represented by a letter denoting the geographical direction from the centre and a number indicating the distance e.g. S1 ≈ 0.5 nm and S2 ≈ 1.0 nm south of centre position).

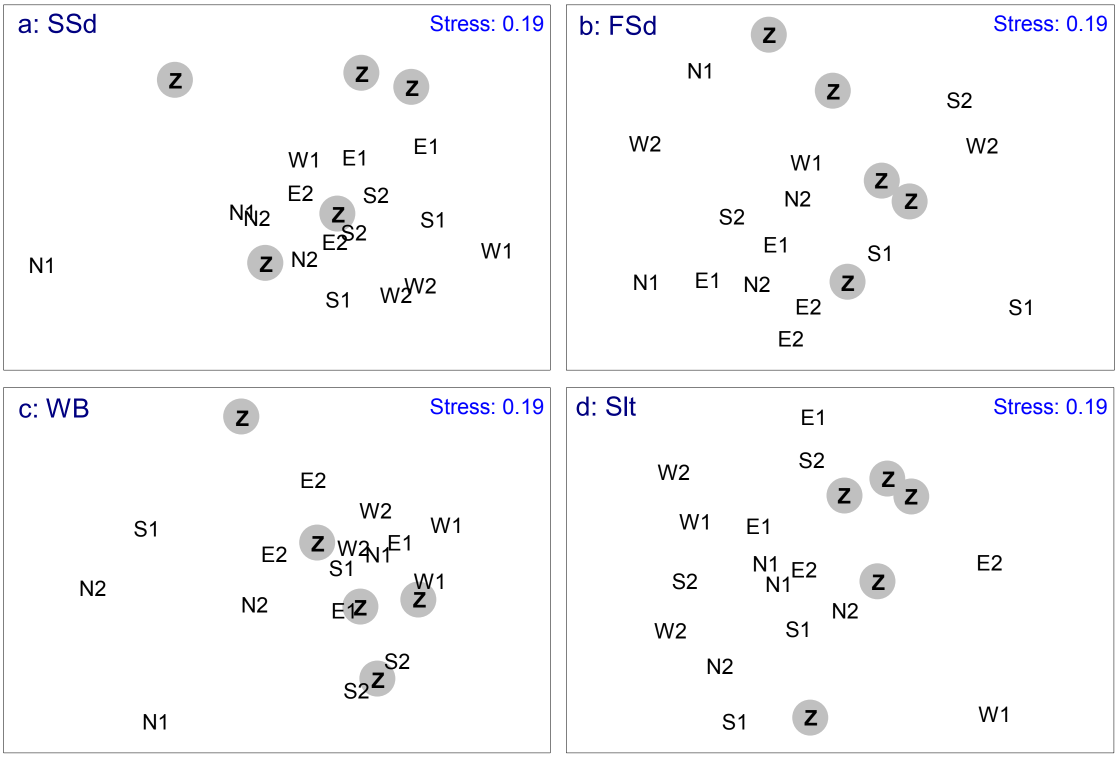

Fig. 4.2.1: MDS plots of separate stations: Bray-Curtis-similarity of 4^{th} root transformed densities from single grabs. Labels as in Fig 4.1.1, with two grabs per position. Samples from the centre position (z) are marked.

The “centre” grabs (Z) are not tightly clustered in the middle of the group, but at least some of them often take a very prominent position. Grabs positioned at the periphery of the plot are mostly paired with central ones. The geographically outer positions (W2, N2 etc.) are not further separated than more central ones (W1, N1 etc. or Z).

Pooling pairs of samples from the same position to reduce the sampling error yields no further structure in MDS or cluster analysis (not shown).

4.2.1.1 Gradients

The spatial sampling was designed to detect spatial differences in the benthic communities within the vicinity of the four permanent stations. These differences may by found as a higher similarity between the benthic community at geographically closer sampling positions (spatial autocorrelation) or as larger scale gradients in the community composition mainly in N-S or W-E direction.

4.2.1.1.1 Community composition

To detect spatial autocorrelation or gradients in the species composition and community structure, a multivariate analysis was based on inter-sample similarities. In the presence of spatial autocorrelation or gradients, the similarity of samples taken closer together should be larger than the similarity of samples taken further apart. This was tested by multivariate Mantel Correlograms (Fig. 4.2.2).

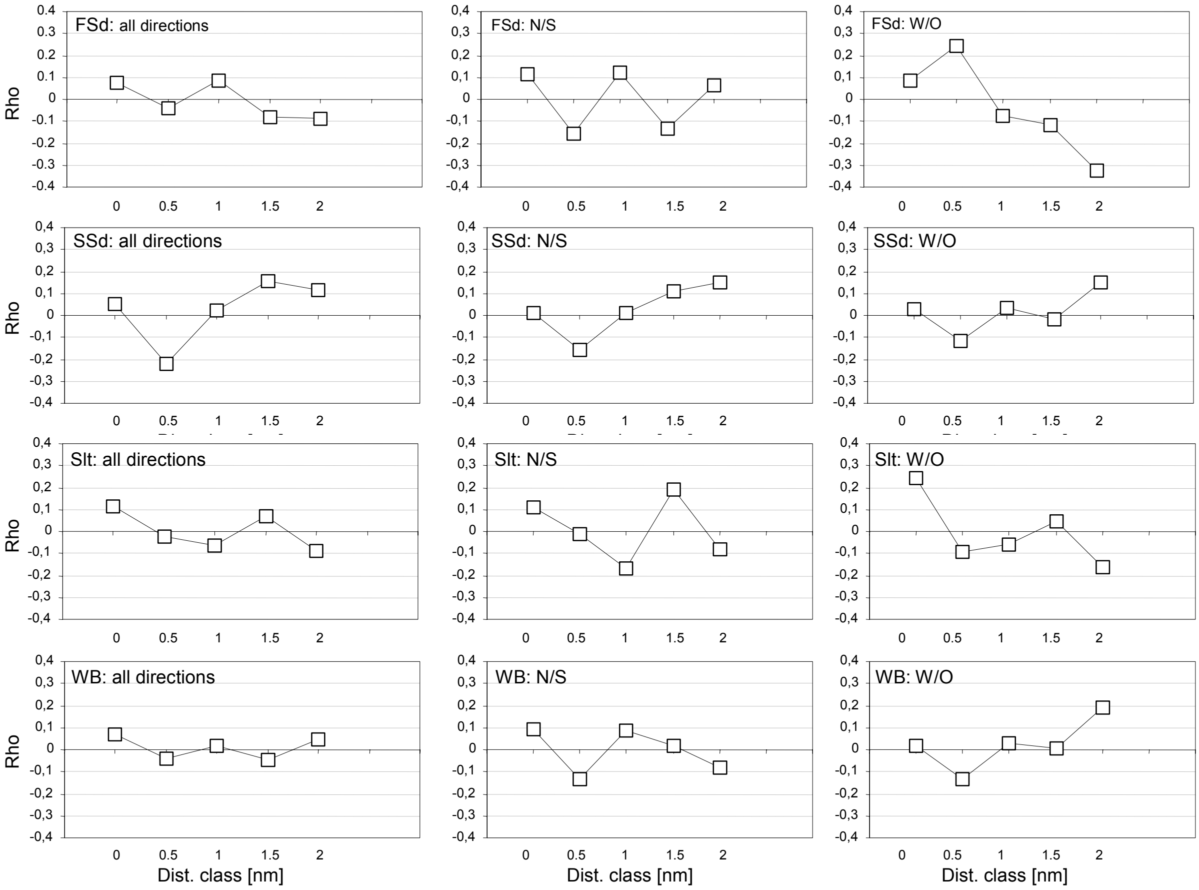

Fig. 4.2.2: Mantel-correlograms based on Spearmans rank correlation between BC-similarity (4th root) and geographical distance classes as listed in Tab 3.4.1 (chapter 3.4.4).

None of the correlograms indicated any statistically significant spatial autocorrelation or gradient. Most correlograms show a positive correlation for the first class and a negative at class 2 (or 3). This may indicate a patch size of less than 0.25 nm. At FSd the two smallest classes show a positive correlation while larger classes are negatively correlated indicating a (non-significant) gradient in W-E direction.

As no significant correlation between the similarity of the samples and the geographical distance between sampling positions can be found, no spatial structuring of the benthic community is detectable at the scale of the present sampling grain, interval and extend (sensu Wiens 1989).

4.2.1.1.2 Sum parameter

To test for the presence of gradients in univariate community descriptors, Spearmans rank correlations were calculated between sum parameters (*N, S, J', H'*) and latitude resp. longitude. At three stations Slt, SSd and WB no correlation of any parameter with geographical position was detectable (Tab. 4.2.1). All variation is attributed to a patchy distribution of the communities.

Tab. 4.2.1: Spearmans rank correlation between sum parameter and latitude or longitude. Significant correlations (α=0.05) are printed in bold, only adjusted *p*-values < 0.2 are given in brackets (corrected by Hochberg's procedure for 2 tests per parameter and station); S: Species per 0.1 m^2; N: Organisms per 0.1 m^2; J': Pielou's evenness index; H': Shannon-Wiener's diversity index.

	SSd		**Slt**		**FSd**		**WB**	
Parameter	**Lat.**	**Lon.**	**Lat.**	**Lon.**	**Lat.**	**Lon.**	**Lat.**	**Lon.**
S	-0.12	0.04	-0.06	-0.17	**0.68** $^{(0.02)}$	**0.68** $^{(0.02)}$	-0.14	-0.27
N	-0.22	-0.20	0.25	-0.40	0.27	0.29	-0.29	-0.09
J'	0.17	0.21	-0.17	0.31	0.12	0.62 $^{(0.07)}$	0.19	0.22
H'	0.00	0.20	-0.36	0.31	**0.60** $^{(0.04)}$	**0.59** $^{(0.04)}$	-0.01	0.15

The only station where a correlation of some parameters with geographical position was detectable was the FSd-station. Here the species density and consequently *H'* increased with latitude as well as with longitude (Tab. 4.2.1). The samples taken east and north of the centre position had a higher species density than the western and southern samples (Fig. 4.2.3). Eastern samples also showed a higher evenness (*J'*) and consequently also higher diversity (*H'*), although these correlations were only significant at 0.1 error-level.

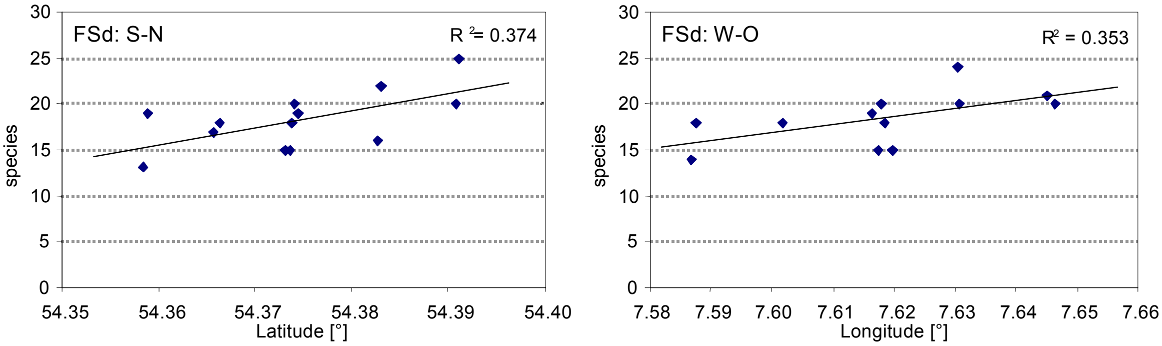

Fig. 4.2.3: Correlation of species density ($0.1m^{-2}$) with geographical position:
a: Longitude W→E x-axis in degrees East;
b: Latitude S→N x-axis in degrees North.

The calculated *p*-values are only valid for each separate station. Considering the fact that two correlations for four stations and thus eight significance test were calculated per parameter, the overall error rate is much higher than the values indicated in Tab. 4.2.1. If the *p*-values are adjusted for this multiple testing, only the correlation between latitude and the number of species at FSd remains significant at 10%-level.

4.2.2 Benthic community composition

Although several species occur at more than one stations, each station represents a clearly distinct type of benthic community.

4.2.2.1 SSd

The benthic community found in 1998 at SSd resembles the shallower *Nucula-nitidosa*-association of silty sediments with aspects of the deeper *Amphiura-filiformis*-association of silty sands (Salzwedel et al. 1985). It has a considerably higher overall density of organisms and a higher species density than at Slt and FSd, accumulating to a total of 60 species in 21 grabs. 18 species occur in densities above one per grab and several of the more abundant species have a standard deviation (SD) of density which is lower than the mean (Tab. 4.2.2). Nevertheless all of the dominant species exhibit a clumped distribution including the polychaetes *Nephtys hombergii*. Only species with mean densities below two per grab are characterised by a random distribution.

Tab. 4.2.2: SSd: numerically dominant species with a mean density > 1 /grab (0.1 m^2). Mean density and wet weight per m^2; SD: standard deviation; CV: coefficient of variation; s^2/Ø: variance/mean-ratio; I_p: standardized Morisita index of dispersion, values indicating significantly (α=0.05) clumped distribution are printed in bold.

Species	**Presence %**	**Wet Weight [m^{-2}]**			**Density [m^{-2}]**			**s^2/Ø**	**I_p**
		Mean	**SD**	**CV**	**Mean**	**SD**	**CV**		
Total		**200.6**	**96.5**	**0.48**	**1096**	**308**	**0.29**	8.66	**0.50**
Nucula nitidosa	100%	2.3	1.1	0.49	176	112	0.64	7.18	**0.51**
Ophiura albida	100%	21.0	8.1	0.38	133	57	0.43	2.46	**0.50**
Abra nitida	100%	3.3	2.3	0.70	131	72	0.55	3.99	**0.50**
Ophiuridae juv.	76%	0.4	0.4	1.01	83	67	0.81	5.48	**0.51**
Nephtys hombergii	100%	7.0	3.2	0.46	81	38	0.47	1.82	**0.50**
Scalibregma inflatum	95%	1.5	1.8	1.20	69	60	0.86	5.11	**0.51**
Mysella bidentata	90%	0.2	0.1	0.69	60	48	0.79	3.78	**0.51**
Lanice conchilega	100%	19.6	18.2	0.93	59	52	0.88	4.59	**0.51**
Phoronis spp.	86%	0.1	0.0	0.66	46	37	0.81	3.01	**0.51**
Notomastus latericeus	76%	12.8	12.2	0.96	34	33	0.99	3.30	**0.51**
Pholoe minuta	81%	0.1	0.1	1.08	22	22	0.99	2.13	**0.50**
Montacuta ferruginosa	76%	0.2	0.2	1.10	20	22	1.09	2.42	**0.51**
Echinocardium cordatum	86%	78.1	85.2	1.09	17	11	0.69	0.80	-0.19
Callianassa subterranea	67%	0.1	0.1	1.06	14	13	0.96	1.27	0.19
Ampelisca brevicornis	67%	0.1	0.2	1.33	12	12	1.05	1.31	0.22
Eudorella truncatula	57%	0.0	0.2	3.66	12	14	1.21	1.73	**0.50**
Spiophanes bombyx	62%	0.0	0.1	2.15	12	12	1.02	1.23	0.16
Thyasira flexuosa	62%	0.1	0.1	1.76	10	10	0.93	0.90	-0.09

In terms of biomass, *Echinocardium cordatum* dominates the community with 38.9 %, followed by *Ophiura albida* (10.4 %), *Lanice conchilega* (9.8 %) and *Notomastus latericeus* (6.4 %). The remaining species have a mean wet weight below 10 g/m^2.

4.2.2.2 WB

The benthic community sampled at WB in 1998 may be seen as a deeper and more characteristic variant of the *Amphiura-filiformis*-community (Salzwedel et al. 1985) with a total of 68 species found in 21 grabs. It is strongly dominated by its main characteristic species, the brittle star *Amphiura filiformis* occurring in very high densities (Ø 1939 /m^2; ± 1319 SD). The other species are less abundant, only four other species occur with more than 5 organisms per grab, and a total of 16 species occurs in mean densities above 1.0 per grab. Despite the high mean density, the abundance of *A. filiformis* is relatively variable with a significantly clumped spatial distribution and a coefficient of variation (CV) of 0.68. Compared to the remaining species this is however a rather low variability and only two species show a similarly relatively low CV, the bivalve *N. nitidosa* and the gastropod *Euspira pulchella,* although both have a rather low density. Ten out of the dominant 16 species show a significantly clumped distribution, while only Nemertini and *N. hombergii* have a random distribution.

Tab. 4.2.3: WB: numerically dominant species with a mean density > 1 /grab (0.1 m²). Mean density and wet weight per m²; SD: standard deviation; CV: coefficient of variation; s²/Ø: variance/mean-ratio; I_p: standardized Morisita index of dispersion, values indicating significantly (α=0.05) clumped distribution are printed in bold.

Species	**Presence %**	**Wet Weight [m^{-2}]**			**Density [m^{-2}]**			**s²/Ø**	**I_p**
		Mean	**SD**	**CV**	**Mean**	**SD**	**CV**		
Total		**90.7**	**53.9**	**0.59**	**2557**	**1579**	**0.61**	97.51	**0.51**
Amphiura filiformis	100%	26.9	4.6	0.91	1939	1319	0.68	89.81	**0.51**
Mysella bidentata	90%	0.1	0.1	1.06	109	107	0.98	10.52	**0.52**
Euspira puchella	95%	0.1	0.1	1.23	69	44	0.64	2.85	**0.50**
Echinocardium cordatum	95%	37.5	32.2	0.86	59	49	0.83	4.05	**0.51**
Nucula nitidosa	100%	1.4	1.7	1.19	53	30	0.56	1.66	0.46
Scoloplos armiger	90%	0.2	0.4	1.61	43	56	1.29	7.18	**0.53**
Pholoe minuta	76%	0.0	0.0	1.12	30	31	1.02	3.20	**0.51**
Ophiura albida	43%	1.0	1.9	1.96	29	74	2.58	19.05	**0.65**
Cylichna cylindracea	76%	0.1	0.1	0.95	26	21	0.81	1.69	0.49
Nephtys hombergii	90%	3.6	3.2	0.89	22	16	0.71	1.11	0.08
Leptosynapta inhaerens	62%	1.1	1.8	1.61	16	17	1.08	1.82	**0.50**
Nemertini indet.	71%	2.1	4.3	2.04	14	12	0.84	1.02	0.01
Callianassa subterranea	57%	0.0	0.0	1.30	11	12	1.08	1.34	0.24
Eudorella spp.	52%	0.1	0.1	1.76	11	14	1.32	1.91	**0.50**
Harpinia antennaria	57%	0.0	0.0	1.59	10	14	1.30	1.76	**0.50**
Trachythyone elongata	57%	0.3	0.7	2.17	10	12	1.18	1.40	0.28

Although its mean wet weight is much lower than at SSd and FSd, the density of *E. cordatum* is higher at WB and it dominates the biomass of the community with 41.3 %. Second to this, *A. filiformis* accounts for another 29.7 % of the mean weight. All other species have a low mean biomass at WB and the total wet weight is only half of that at SSd and FSd and only a fifth of that found at Slt.

4.2.2.3 Slt

The benthic community found in 1998 at the Slt station is a typical *Nucula-nitidosa*-association sensu Salzwedel et al. (1985) dominated by its characteristic bivalve *N. nitiosa* accounting for an average 35 out of the mean total 60 individuals per grab. In 21 samples 33 species were found, 9 of them in densities above 10 m^{-2} (Tab. 4.2.4). All of these species except the *Nephtys hombergii* have a significantly clumped distribution. The variation in the densities is rather high, 6 out of the 9 species have a SD which is larger than the mean. Only the three most abundant species *N. nitida*, *Ensis directus* and *N. hombergii* have a CV below one.

Tab. 4.2.4: Slt: numerically dominant species with a mean density > 1 /grab (0.1 m^2). Mean density and wet weight per m^2; SD: standard deviation; CV: coefficient of variation; s^2/Ø: variance/mean-ratio; I_p: standardized Morisita index of dispersion, values indicating significantly (α=0.05) clumped distribution are printed in bold; * characteristic species.

Species	**Presence %**	**Wet Weight [m^{-2}]**			**Density [m^{-2}]**			**s^2/Ø**	**I_p**
		Mean	**SD**	**CV**	**Mean**	**SD**	**CV**		
Total		**452.1**	**261.0**	**0.58**	**597**	**368**	**0.63**	22.68	**0.51**
*Nucula nitidosa**	100%	19.4	18.0	0.93	350	317	0.91	28.80	**0.52**
Ensis directus	95%	314.1	226.6	0.72	39	31	0.77	2.37	**0.50**
Nephtys hombergii	90%	1.4	1.2	0.88	38	21	0.56	1.17	0.12
Phoronis spp.	57%	<0.1	<0.1	1.52	31	45	1.44	6.50	**0.54**
Ophiura ophiura	76%	6.1	8.8	1.43	28	33	1.17	3.87	**0.52**
Mysella bidentata	76%	0.2	0.2	1.26	27	27	1.04	2.86	**0.51**
Echiurus echiurus	67%	77.2	98.9	1.28	17	25	1.49	3.68	**0.53**
Bylgides sarsi	57%	0.8	1.3	1.49	14	22	1.58	3.44	**0.53**
Ophiuridae juv.	43%	0.1	0.2	2.47	13	25	1.86	4.60	**0.55**

In terms of biomass, *Ensis directus* absolutely dominates the community (69.5 %), followed by *Echiurus echiurus* accounting for another 17.1 % of the total biomass. All other species together only sum up to 13.4 % of the biomass.

4.2.2.4 FSd

At FSd the community in 1998 is a typical example of the *Tellina-fabula*-association sensu Salzwedel et al. (1985). 15 out of a total of 50 species have mean densities above one per grab, and the variation especially of some of the more abundant species is relatively low with a CV around 0.5. Nevertheless also here most species exhibit considerable variations in densities with the SD equal to or often larger than the mean. Consequently the spatial distribution of 9 out of 15 species is significantly clumped. Although here in lower densities, *N. hombergii* again has a near random distribution like another relatively common polychaete, *Scoloplos armiger* and most of the less abundant species.

Tab. 4.2.5: FSd: numerically dominant species with a mean density > 1 /grab (0.1 m^2). Mean density and wet weight per m^2; SD: standard deviation; CV: coefficient of variation; s^2/Ø: variance/mean-ratio; I_p: standardized Morisita index of dispersion, values indicating significantly (α=0.05) clumped distribution are printed in bold; characteristic species for the *Tellina-fabula*-ass. (after Salzwedel et al. 1985) are marked by an asterisk.

Species	**Presence %**	**Wet Weight [m^{-2}]**			**Density [m^{-2}]**			**s^2/Ø**	**I_p**
		Mean	**SD**	**CV**	**Mean**	**SD**	**CV**		
Total		**197.7**	**119.7**	**0.61**	**667**	**157**	**0.25**	3.70	**0.50**
*Tellina fabula**	100%	14.3	8.9	0.62	178	90	0.51	4.59	**0.50**
*Magelona mirabilis**	100%	0.3	0.2	0.64	63	34	0.54	1.84	**0.50**
Scoloplos armiger	100%	1.0	0.6	0.61	52	21	0.40	0.84	-0.15
Ophiuridae juv.	90%	0.2	0.2	1.18	40	40	0.99	3.96	**0.51**
Montacuta ferruginosa	80%	0.5	0.4	0.88	32	28	0.87	2.42	**0.51**
Lanice conchilega	85%	5.9	9.4	1.59	31	46	1.46	6.69	**0.54**
Eumida spp.	70%	0.1	0.1	1.14	28	33	1.19	3.97	**0.52**
*Urothoe poseidonis**	70%	0.1	0.1	1.34	25	31	1.23	3.81	**0.52**
Phoronis spp.	45%	0.1	0.2	3.27	22	48	2.14	10.33	**0.60**
Bathyporeia elegans	75%	0.0	0.0	0.97	20	16	0.77	1.21	0.14
Echinocardium cordatum	90%	149.3	112.4	0.75	17	10	0.61	0.63	-0.35
Bathyporeia guilliamsoniana	70%	0.1	0.1	0.95	16	17	1.04	1.74	**0.50**
Goniada maculata	75%	0.3	0.3	0.92	15	15	0.98	1.44	0.30
Ophiura albida	60%	1.7	3.1	1.87	12	14	1.13	1.59	0.40
Nephtys hombergii	60%	1.8	3.0	1.66	11	11	0.99	1.12	0.08

In terms of biomass, *Echinocardium cordatum* dominates the community with 75.4 %, followed by *Tellina fabula* (7.2 %) while all of the other species have a mean biomass below 10 g/m^2.

4.2.3 Precision of quantitative sum parameters

The communities at the four stations differ not only in the species spectrum but also in total density and biomass (Tab. 4.2.6). The highest overall densities were found at WB, but with a high variability (CV = 0.61). This variability is similar at Slt (CV = 0.63), the station with the lowest total density of organisms of all four stations.

Tab. 4.2.6: Total density of organisms and biomass.
Mean values per m² ± SD and CV; N: number of organisms;
WW: wet weight; WW_{red}: wet weight excluding large species (see text).

	N		**WW**		**WW_{red}**	
Station	mean ± SD	CV	mean ± SD	CV	mean ± SD	CV
SSd	1096 ± 308	0.29	200.6 ± 96.5	0.48	111.0 ± 60.0	0.54
FSd	667 ± 157	0.25	197.7 ± 119.7	0.61	48.4 ± 37.6	0.78
WB	2557 ± 1579	0.61	90.7 ±53.9	0.59	53.2 ± 38.7	0.73
Slt	597 ± 368	0.63	452.1 ± 261.0	0.58	39.4 ± 44.6	1.13

At FSd the total densities are not significantly higher than at Slt (results of pairwise statistical tests in the annex Tab. A.5.1); but the variability of the mean density is much lower (CV = 0.25). The mean density at SSd is significantly higher than that at FSd, although less than half as high as at WB, but the variability is nearly as low as at FSd.

Total biomass estimates also differ widely between stations. The total wet weight at Slt (452 g/m²) is almost five times higher than at WB (91 g/m²), while in terms of total density of organisms it is just the other way around (Tab. 4.2.6). The total biomass at SSd and FSd is with about 200 g/m² intermediate between these extremes, but the variability is lower at SSd (CV = 0.48) than at FSd, where it is similar to that at Slt and WB with a CV around 0.6.

The large range of total biomass estimates is mainly a result of the distribution of very large species like the irregular sea urchin *Echinocardium cordatum*, the large bivalve *Ensis directus* and the echiurid *Echiurus echiurus* (Tab. 4.2.2 – 4.2.5). Large species are often inadequately sampled by a 0.1 m² van Veen grab because they live deeper in the sediment and/or are often widely dispersed. In the present data these include the above mentioned species plus single specimens of the sea star *Asterias rubens*. Excluding these species from the calculation of total wet weight strongly reduces the standard deviation of the mean biomass estimate (Tab. 4.2.6). At the same time it reduces the mean biomass even more strongly than its variance. This results in an increase of the CV of the biomass estimate at all stations. This effect is strongest for smaller samples and for the stations where these species account for a large proportion of the biomass like at Slt (Tab. 4.2.4, Tab. 4.2.6).

4.2.3.1 Sample size influence on density

The variability of the estimates of total density decreases with increasing sample size, but the 95% confidence interval (C.I.) is at most stations asymmetrical about the mean. The CV still seems suitable to compare the relative variability between the stations, but as a normal distribution is clearly not given, the size of the empirical C.I. is used as measure of precision instead. The total density estimates e.g. at SSd may range between 500 and 1800 ind./m^{-2} if calculated from single grabs, while a combination of five grabs would yield estimates between 800 and 1300 ind./m^{-2} (Annex, Fig. A.6.1).

Fig. 4.2.4 shows the relation between sample size and the precision of the estimated mean density as expressed by the ratio between the empirical confidence interval (C.I.) and the mean. At FSd and SSd the size of the C.I. is smaller than the mean for two grabs already while four to five grabs yield a C.I. smaller than half the mean. At Slt and WB a sample of five grabs is barely enough to achieve a C.I. as large as the mean while more than 20 grabs would be necessary to reach a C.I. of half the size of the mean. For these two stations a sample of ten grabs would result in a C.I. of bout 70% of the mean.

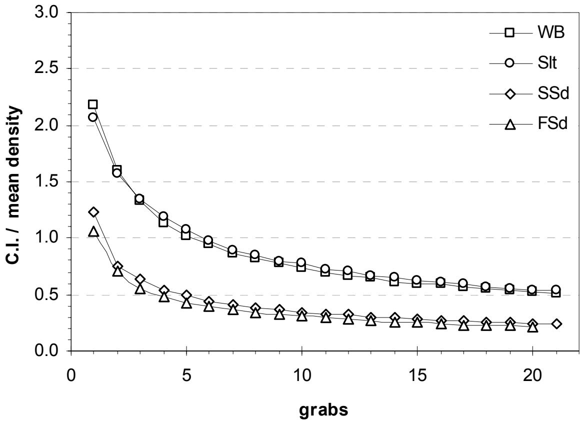

Fig. 4.2.4: Precision of mean total density of organisms (empirical C.I./mean) in relation to sample size.

For all stations, the gain in precision is most pronounced within the first three to five grabs while sample sizes above ten grabs yield only minor improvements of the precision.

4.2.3.2 Sample size influence on biomass

Just like for density estimates, the 95% C.I. of the mean biomass is at most stations asymmetrical about the mean (Annex, Fig. A.6.2). and the size of the empirical confidence interval (C.I.) is used as measure of precision.

The precision of the biomass estimate is at most stations very similar to the precision of the density estimate at Slt and WB. Five to six grabs are needed for a C.I. as large as the mean while ten grabs yield a C.I. of about 70% of the mean (Fig. 4.2.5 a). A C.I. of half the size of the mean is reached with more than 20 grabs. The variance of the wet weight is smaller at SSd where the C.I. is smaller than the mean with four grabs already, while 15 grabs would be enough for a C.I. of half the size of the mean (Fig. 4.2.5 a).

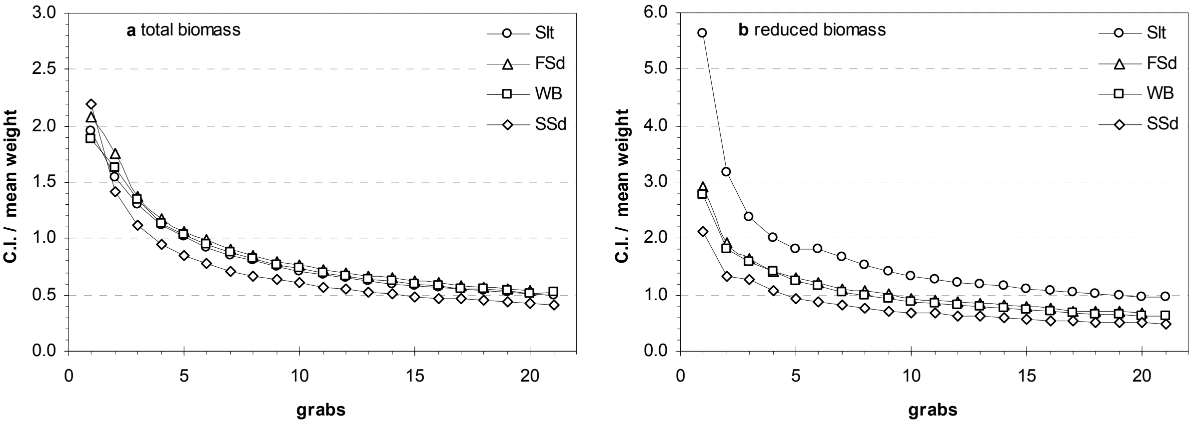

Fig. 4.2.5: Precision of mean biomass estimates per m² (empirical C.I./mean) in relation to sample size. a: total biomass; b: excluding large species (observe different y-scale).

The lower spatial variability in total wet weight as indicated by the lower CV at SSd (Tab. 4.2.6) seems to be rather an artefact of the inadequate description of variability by the SD as seen by the size of the empirical C.I., which is for single grabs in relation to the mean density even slightly larger than at the other stations (Fig. 4.2.5 a). A higher precision at SSd is only apparent for larger sample sizes. For all stations, the gain in precision of mean biomass estimates is most pronounced within the first three to five grabs while sample sizes above ten grabs yield only minor improvements of the precision.

The exclusion of the large species reduces the precision of the estimate of the mean biomass for all stations. At SSd five grabs are needed for a C.I. of the same size as the mean, ten grabs are needed at FSd and WB while 20 grabs are needed at Slt (Fig. 4.2.5 b). A C.I. of half the size of the mean is only reached at SSd at a sample size of 20 grabs but not at the other stations.

Apart from the reduction of the relative precision mentioned above, the reduction of the biomass by the exclusion of large species strongly increases the skewness of the distribution. While the lower edge of the empirical C.I. is for most stations close to the mean minus one SD, the upper edge is mostly larger than the mean plus two SD, especially at smaller sample sizes (Annex, Fig. A.6.3).

4.2.4 Community structure and sample size influences

The communities at the four stations differ not only in their species spectrum, total density and biomass but also in community structure. With a total number of 60 species found, SSd has the highest species richness (S_{1000} = 49 spp.) as well as species density (S = 22.6 spp./ 0.1 m²). Combined with the high evenness of 0.83 (J'), this results in the highest value for H' of 3.72 (Tab. 4.2.7).

Tab. 4.2.7: Species density, diversity and dominance.
Total S: total number of species per station; $E(S)_{1000}$: rarefaction no. of spp. per 1000 ind.; Mean values ± SD: S_{1000}: empirical no. of spp. per 1000 ind.; S: number of species per grab (0.1 m²); J': Pielou's evenness index; H': Shannon-Wiener diversity index.

Station	**Total S**	**$E(S)_{1000}$**	**S_{1000}**	**S**	**J'**	**H'**
SSd	60	49.5	49.3 ± 2.2	22.6 ± 3.4	0.83 ± 0.03	3.72 ± 0.27
FSd	50	46.9	46.9 ± 1.2	18.6 ± 3.1	0.83 ± 0.06	3.48 ± 0.36
WB	68	42.3	40.1 ± 4.4	20.7 ± 5.4	0.43 ± 0.10	1.83 ± 0.39
Slt	33	30.0	30.0 ± 2.1	9.9 ± 3.0	0.70 ± 0.18	2.20 ± 0.51

At FSd the total number of species (50 spp.) and the species richness are lower. The significantly lower species density results in a significantly lower value of H', while the evenness values for FSd and SSd are the same (Tab. 4.2.7; results of pairwise statistical tests in Tab. A.5.1 Annex).

The total number of 68 species found at WB is the highest of all stations, but the species richness (S_{1000} = 40 spp.) is even lower than that at FSd (Tab. 4.2.7). The species density (21 spp./0.1 m²) is intermediate between those from SSd and FSd but the differences are not significant (Tab. A.5.1 Annex). The extremely low evenness however results in the lowest diversity of all stations (H' = 1.83; Tab. 4.2.7).

In terms of total species number, species richness and species density, Slt is clearly the poorest of the four stations (Tab. 4.2.7). The evenness is lower than at FSd and SSd, although this difference is not significant because of the high variability of the evenness values at Slt, but it is significantly higher than at WB. Therefore the diversity as measured by H' is at Slt significantly lower than at FSd and SSd but significantly higher than at WB (statistical results in Tab. A.5.1 Annex).

The variability of the diversity measures (here S_{1000}, S, J' and H') is at all stations lower than the variability of the quantitative measures (Tab. 4.2.6 vs. Tab. 4.2.8). All diversity measures are more variable at Slt and WB and less variable at FSd and SSd (Tab. 4.2.8). This difference is most pronounced for J' and consequently also H'.

Tab. 4.2.8: Coefficient of variation (CV) of diversity measures:
S_{1000}: species richness; S: species density;
J': Pielou's evenness index; H': Shannon-Wiener diversity index.

Station	**S_{1000}**	**S**	**J'**	**H'**
SSd	0.04	0.15	0.02	0.07
FSd	0.03	0.17	0.06	0.10
WB	0.11	0.26	0.25	0.21
Slt	0.07	0.30	0.26	0.23

The low variability of the S_{1000} estimate in comparison to the variability of S, J' and H' is slightly misleading, because especially at stations with a lower density of organisms (FSd and Slt) it is based on a large number of grabs, while the other estimates are based on the variability of single grabs.

4.2.4.1 Sample size influence on species number

The number of species rises steeply with the sample size (Fig. 4.2.6). The increase in species number is most pronounced for the first three to five grabs, but continues very steadily up to the total number of grabs.

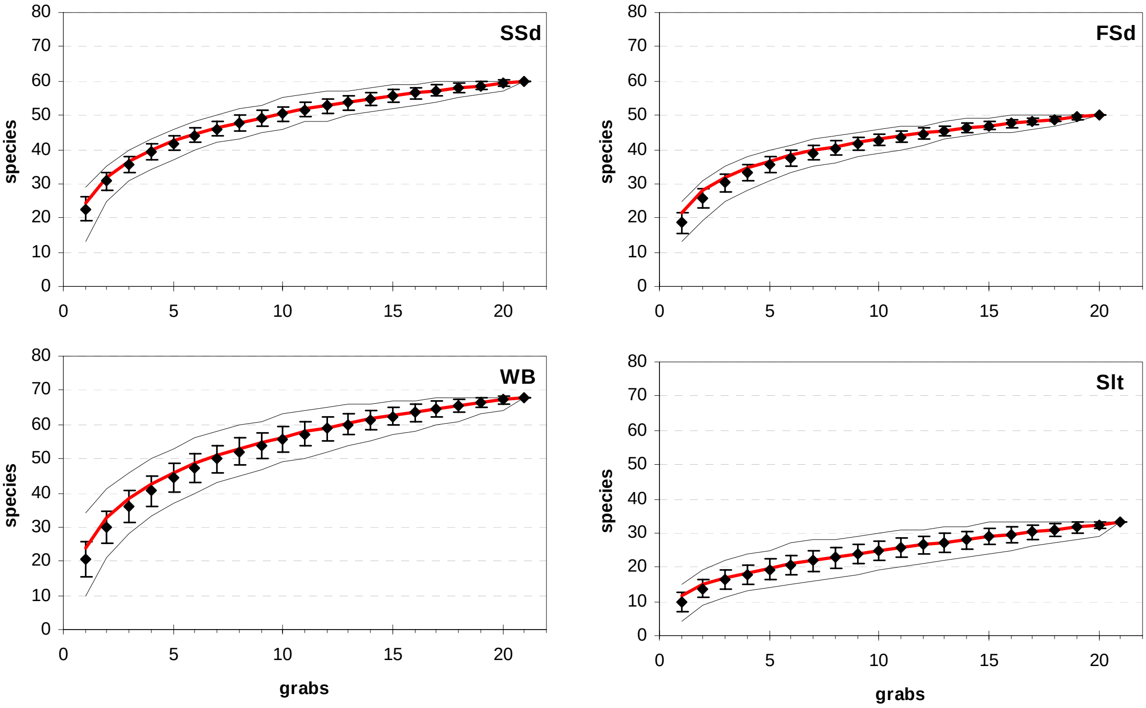

Fig. 4.2.6: Number of species (± SD) in relation to grab number or area (*"species density"*) . Outer lines delineate the empirical 95% confidence interval; red line represents rarefaction curve.

At FSd the number of species rises from a mean of 19 per single grab to 50 species found in all 20 grabs combined. At SSd it rises from 23 to 60 species in 21 grabs. The mean species number per grab at WB with 21 species is intermediate between these two but it rises up to 68 species in 21 grabs. Species density is lowest at Slt, rising from 10 per grab to a total of 33 species in 21 grabs.

Depending on the order of combination of the grabs, the total number of species found at any one station may be reached with less than the total number of grabs taken. The maximum number of species is reached by the upper 95% limit between 15 and 17 grabs (Fig. 4.2.6, "k_S" in Tab. 4.2.9). The continuing rise of the species accumulation curves indicates that the community contains more species. Even if e.g. 17 grabs may have yielded the total number of species contained in this data set, the 18th or later grab is likely to contain some additional species. The mean number of species and the upper 95% limit are thus negatively biased above this sample size. The upper end of the curve should therefore be treated with caution, as the true mean number of species for these sizes is probably higher.

The empirical species accumulation curve is very similar to the rarefaction curve (Fig. 4.2.6). Only at small sample sizes the species density calculated by rarefaction is higher than the empirically determined value.

Variability of species density estimates

The standard deviation of the species number clearly declines with increasing sample size at FSd and WB only (Fig. 4.2.7 a). At Slt and SSd it initially declines up to three to five grabs, but then remains constant up to half the maximum sample size. With more than half of the grabs pooled, the number of possible combinations strongly declines, causing in itself a decreasing variability. The further decrease is at least partly an artefact and should be disregarded.

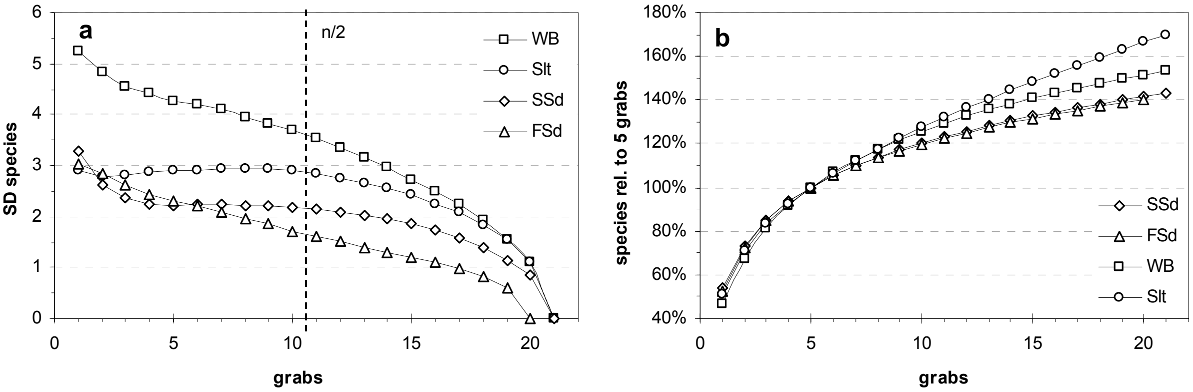

Fig. 4.2.7: a: Standard deviation of the number of species in relation to sample size;
b: The percentage of species found in 5 vV-grabs relative to sample size.

Comparing the *relative* number of species found in smaller samples to that found in the standard program of five grabs, the differences between the communities nearly disappear, especially for smaller sample sizes (Fig. 4.2.7 b).

In single grabs an average of 47 – 54% of the species found in five grabs are obtained, while three grabs yield 81 – 85% of the species. A larger sample size of ten grabs would yield between 20 and 27% more species that five grabs. With the small differences between the in other terms quite different communities, it seems adequate to use these percentages to adjust the species numbers for the long term series and account for the sometimes differing number of grabs, at least when the numbers are between 3 and 7 grabs (0.3 – 0.7 m²). For example three vV's at WB contain 81.2% of the species found in five vV's. The 56 species found in three vV's in 1987 at WB are therefore standardised to 69 species/0.5 m² (see Fig. 5.4.16).

Species richness

There is a large difference in the absolute density of organisms between the stations. Bringing all data to a common ordinate of organisms, the curve from SSd is the uppermost throughout, followed by FSd, WB and Slt as the lowest (Fig. 4.2.8).

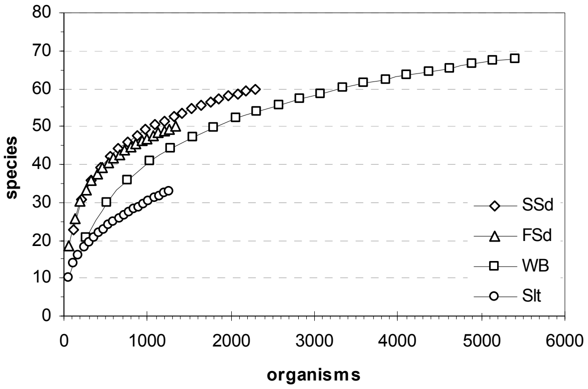

Fig. 4.2.8: Number of species at all four stations in relation to the number of organisms (*"species richness"*). Each point represents one sample.

This is reflected by the number of species per 1000 organisms, with 49 species at SSd, 47 at FSd, 40 at WB and 30 species at Slt (Tab. 4.2.9).

Additional species per grab

A common indicator for sufficient sampling is the number of additional species *ΔS* found in the k^{th} sampling unit with respect to *k*-1 units (here grabs). It differs widely between the communities and e.g. the fifth grab may still yield between 1.5 (Slt) and 3.8 (WB) expected additional species (Fig. 4.2.9).

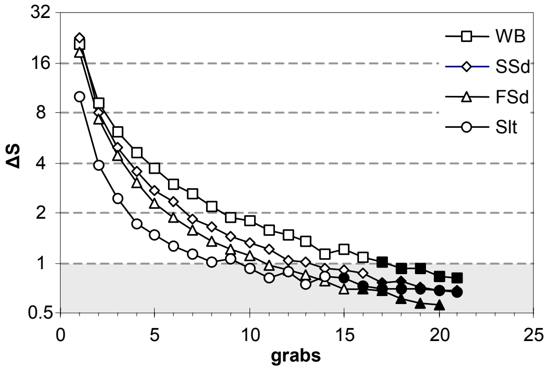

Fig. 4.2.9: Additional number of species per grab (ΔS). Filled symbols indicate that the upper 95% limit has reached the maximum number of species at the respective sample size (Fig. 4.2.6; see text).

The point where each additional grabs yields less than two additional species is reached between four (Slt) and nine (WB) grabs while nine to more than 17 grabs are needed to yield less than one additional species per grab ($k_{\Delta 1}$, Tab. 4.2.9; Fig. 4.2.9)

Tab. 4.2.9: Species densities for large number of grabs. S_{max}: total number of species in all grabs combined; N: total number of grabs; k_S: minimum number of grabs reaching S_{max}; $k_{\Delta 1}$: minimum number of grabs with ΔS < 1 (ΔS: expected additional number of species for k grabs with respect to k-1 grabs). * indicates that $k_{\Delta 1} > k_S$ and the real $k_{\Delta 1}$ may be larger.

Station	S_{max}	N	k_S	$k_{\Delta 1}$
Slt	33	21	15	9
FSd	50	20	16	11
SSd	60	21	17	14
WB	68	21	17	(18)*

At WB the number of additional grabs needed to yield less than one expected additional species $k_{\Delta 1}$ is higher than the minimum number of grabs containing S_{max} species (k_s). Because the number of species at this pooling level may be biased and the variance is underestimated, the true $k_{\Delta 1}$ for WB may be higher.

4.2.4.2 Sample size influence on evenness

Mean evenness estimates by Pielou's J' systematically decrease with samples size at all stations (Fig. 4.2.10). At SSd they decrease from 0.83 for single grabs to 0.77 for five grabs. For larger sample sizes J' decreases slowly to 0.71. Mean values for FSd are very similar while the variability of J' is slightly larger. The largest range in values is found at Slt where evenness values range between 0.37 and 0.92 (Ø 0.69) for single grabs. The decrease in variability with increasing sample size is slow, leaving a range of between 0.44 and 0.75 (Ø 0.58) for five grabs. Even an increase to ten grabs leaves a considerable range of between 0.46 and 0.64 (Ø 0.54). Larger values are influenced by the decrease in possible permutations and may underestimate the true variance. WB has the lowest evenness values decreasing from 0.43 for single grabs to 0.34 for five and more grabs, with an intermediate variability.

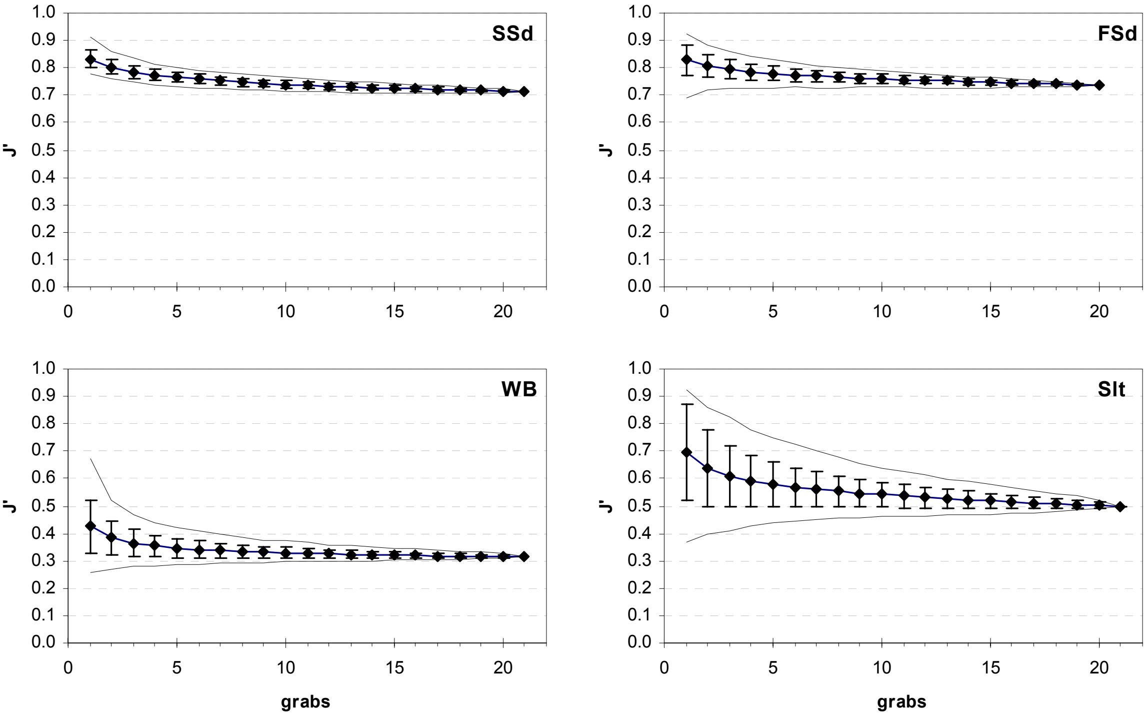

Fig. 4.2.10: Evenness as measured by Pielou's J' in relation to sample size.
Outer lines delineate the empirical 95% confidence interval.

Mean values of J' decrease by approximately 0.1 between single grabs and 20 grabs except at Slt where 20 grabs yield a value that is 0.2 lower than the mean value for single grabs.

The rank order of evenness estimates between the stations is not affected by the sample size as differences between the stations are large enough. The values from SSd are smaller than those from FSd at large sample sizes, but not significantly so. While the confidence intervals from Slt overlaps those of all other stations for small sample sizes, the C.I.s are clearly distinct for five grabs or more.

4.2.4.3 Sample size influence on heterogeneity diversity

The Shannon-Wiener diversity index H' rises with sample size for smaller samples, but reaches a plateau. At FSd this is reached at approximately seven grabs, five grabs seem sufficient for Slt and SSd and only two grabs combined are needed at WB to reach a stable value (Fig. 4.2.11). The variability of H' declines with sample size, it is largest at Slt, somewhat smaller and approximately equal at FSd and WB and smallest at SSd.

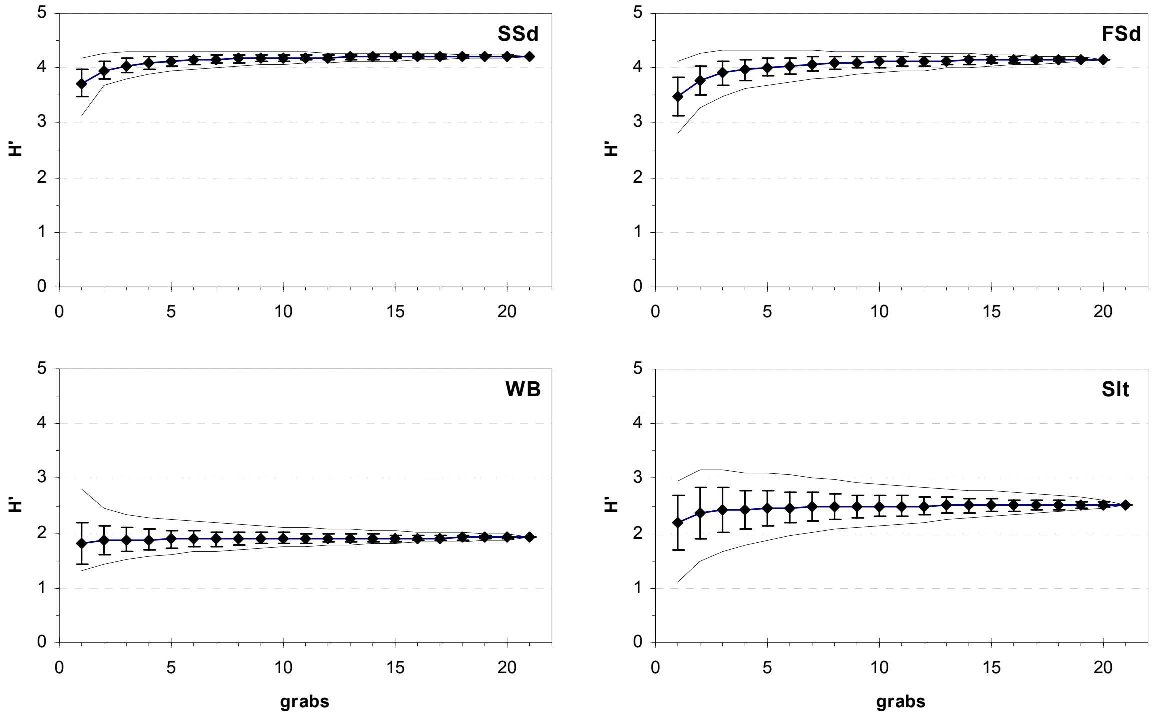

Fig. 4.2.11: Diversity as measured by Shannon-Wiener H' in relation to sample size. Outer lines delineate the empirical 95% confidence interval.

The rank order of mean evenness estimates between the stations is not strongly affected by the sample size as differences between most stations are large enough. The values from SSd are larger than those from FSd at small sample sizes, but with a large overlap of the C.I.s, while for larger sample sizes the difference of the mean value disappears. The confidence interval from Slt overlaps those of FSd and WB for small sample sizes. The C.I.s of Slt and FSd are clearly distinct for three grabs or more while more than ten grabs are needed to avoid an overlap of the C.I.s from Slt and WB.

4.2.5 Multivariate community similarity

Despite the spatial variability within each station, the mean similarity within any one station is in all cases higher than the mean similarity between the stations. There is an overlap in the range with some similarities *between* stations as large as the smallest similarities *within* the stations (Tab. 4.2.10), but nevertheless all stations are clearly distinct from each other (Fig. 4.2.12; ANOSIM global and pairwise tests p < 0.001).

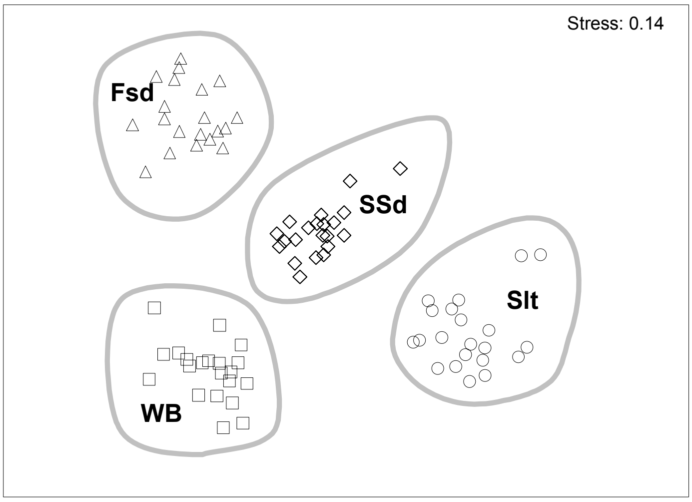

Fig. 4.2.12: MDS plot combining all grabs of the spatial sampling around the four stations. Bray-Curtis-similarity of 4th root transformed densities, each symbol represents one grab. Groups separated by cluster analysis (group average) are enclosed by lines.

Comparing the stations, SSd and WB are the most similar stations, with an average similarity of 33.5% (Tab. 4.2.10) while the other stations are less similar. SSd has an intermediate position being relatively similar to the three remaining stations. The largest difference is found between Slt and FSd (Tab. 4.2.10).

Tab. 4.2.10: Mean similarity within and between the stations (+ 95%-range); Bray-Curtis similarity of 4^{th} root transformed abundance data from single grabs.

	within	**SSd**	**WB**	**FSd**
SSd	63.6 (46.4 - 77.7)			
WB	56.2 (37.5 - 71.1)	33.5 (9.8 - 55.3)		
FSd	59.0 (42.8 - 72.7)	28.1 (10.8 - 52.3)	24.0 (4.0 - 40.5)	
Slt	57.6 (33.0 - 78.0)	30.4 (10.4 - 54.3)	18.0 (6.1 - 37.3)	11.4 (0.0 - 29.7)

Multivariate variability

The multivariate variability is reflected in the similarity between the grabs. Besides the average similarity of the samples within each station, the distribution of the similarity values needs to be considered to adequately describe the variability of the community. The distribution of the Bray-Curtis-similarities of all four stations can be approximated by a normal distribution (Fig. 4.2.13).

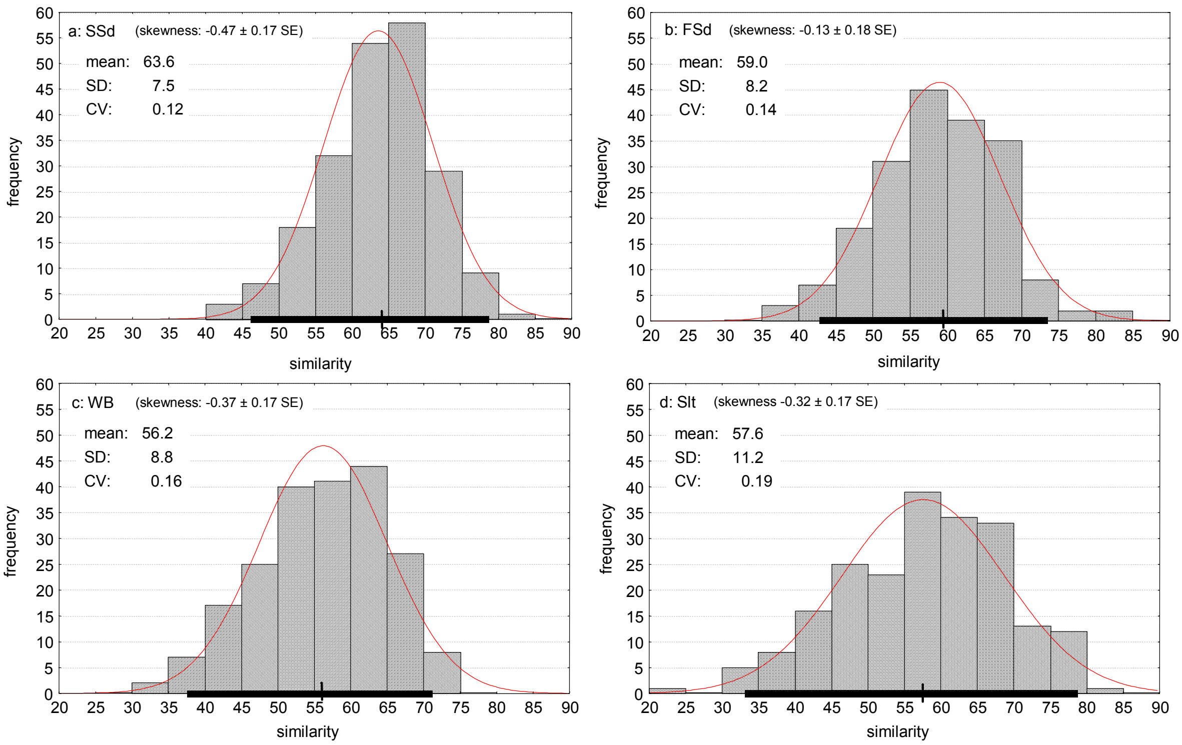

Fig. 4.2.13: Frequency distribution of similarity values at all stations. Bray-Curtis similarity of 4^{th} root transformed data. Thin line delineates the expected normal distribution; the black bar on the ordinate marks the empirical 95% interval. SD: standard deviation; CV: coefficient of variation.

All distributions are slightly skewed to the left, but only those from SSd and WB deviate significantly from normality (Shapiro-Wilk W-test $p < 0.05$). Nevertheless, 96 - 97% of the similarities are contained within the interval of ± 2 SD around the mean. Therefore, it is reasonable to use the mean and standard deviation to compare the similarities between the stations. The CV represents a convenient measure to compare the variability of the similarities between the areas.

The highest mean similarity is found between the samples from SSd, which also exhibits the lowest variability with a CV of only 0.12. SSd thus classifies as the spatially most homogeneous community. The samples from FSd are less similar and also more variable with a CV of 0.14. Slt or WB both show a lower mean similarity. Although the mean similarity at WB (56.7) is lower than that at Slt with 57.6, the variability of the similarities is lower at WB (CV 0.16) than at Slt (CV 0.19) indicating a more homogeneous community at WB.

4.2.5.2 Sample size influence on multivariate similarity

With an increasing number of pooled grabs, the mean similarity between the samples generally increases (Fig. 4.2.14). The exact slope and curve of the increase depends on the respective community.

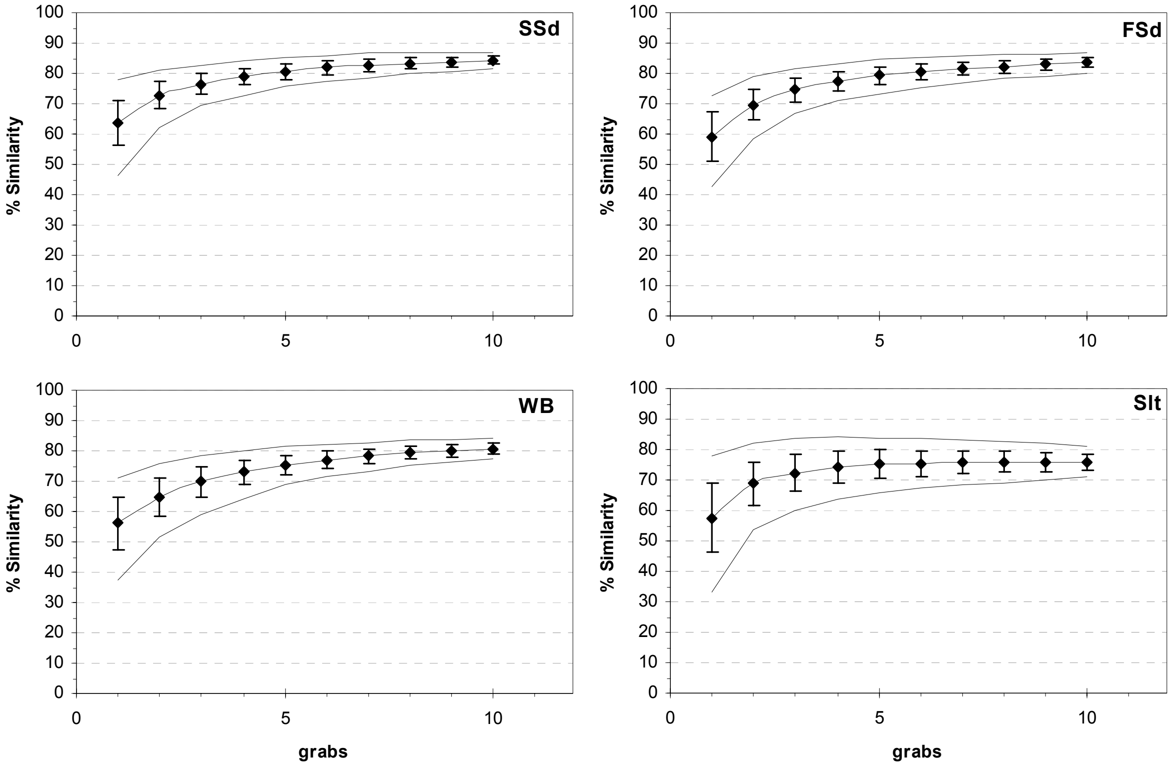

Fig. 4.2.14: Mean Bray-Curtis similarity between samples (± SD) in relation to sample size. Simple lines delineate the empirical 95% confidence interval.

At SSd a mean similarity of 80% is reached with five grabs. Although starting at a lower value for single grabs, a similarity of 80% is reached at FSd with five grabs too. The further increase of the mean similarity at these stations is only minor though a plateau is not even reached with ten grabs. At WB the increase is similar to that at FSd but at a slightly lower level, reaching 80% similarity with eight to nine grabs. At these three stations, the variability of the similarities is steadily decreasing with increasing sample size, while this decrease is weaker at Slt. At Slt the average similarity of single grabs is not lower than at WB, but the variability is much higher. The rise in similarity is much shallower, reaching a plateau at five to six grabs with 76%, never reaching 80%.

The 95%-range is very similar at most stations and evenly distributed around the mean. Only at Slt, the range is larger than at the other stations, with also a slower decline in range size with sample size.

4.2.6 Temporal changes in spatial variability

Several years could not be included in the calculation as no replicate samples were available. The spatial community variability is reflected in the similarity of the single grab samples, with a low mean similarity indicating a high spatial variability.

The sample size influence on the inter-sample similarity puts some restrictions on the comparability for the present time series. The smaller area sampled by the Reineck Box corers (RBC) results in a systematically lower similarity if a combination of van-Veen-grabs (vV) and RBC's is compared to samples with vV's only. The mean similarity was therefore calculated separately for these periods and does not allow a direct comparison *between* these periods, but only *within* each set. At SSd the data from 1978/79 differ from the rest as in 1978 a 0.2 m² vV-grab was used and in 1979 each two grabs were pooled. Nevertheless several points can be made:

The spatial variability detected in 1998 is above average at SSd and Fsd, somewhat less pronounced also at WB, while it is about average at Slt (1998 marked by circle in Fig. 4.2.15). Absolute similarity values from 1998 differ from the mean similarity in Fig. 4.2.14 because of the reduced species list used in the temporal analysis (see methods).

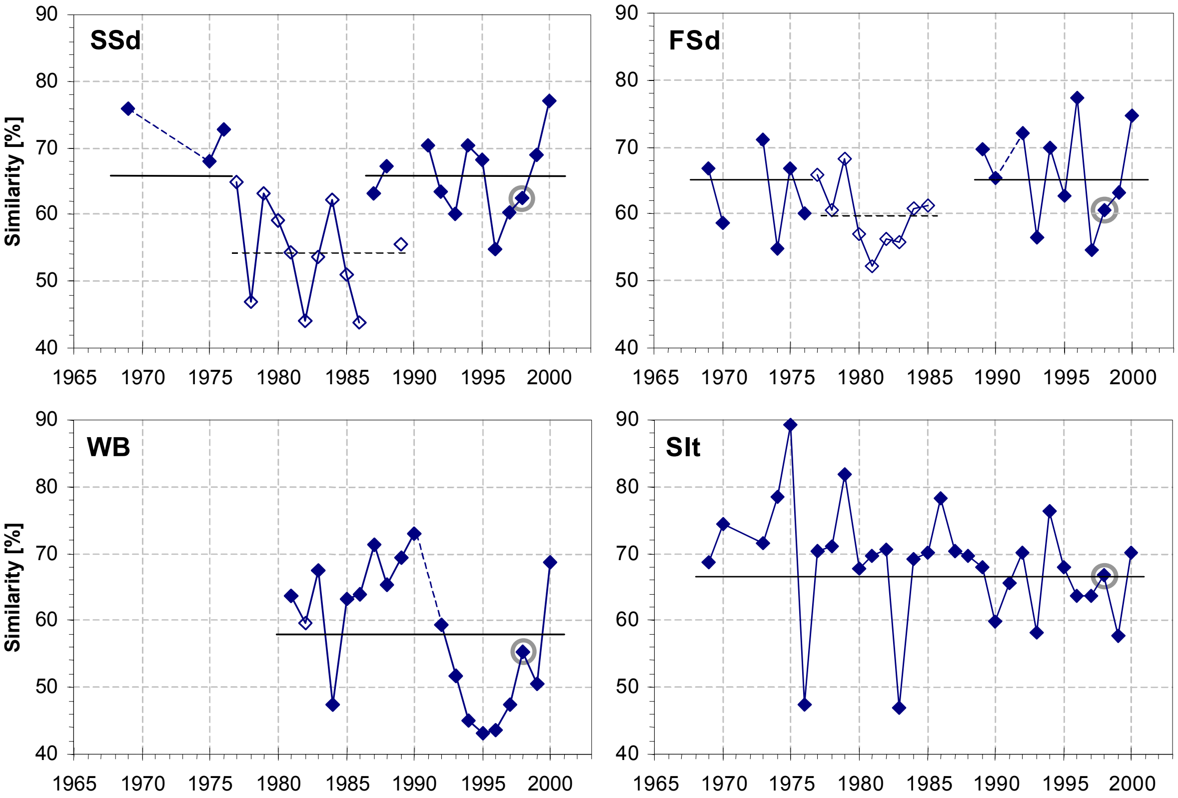

Fig. 4.2.15: Mean similarity between grabs over time. Broken lines indicate missing years. Open symbols stand for combinations of 2 vV plus 6 RBC, filled symbols for samples of 5 vV (horizontal lines mark the mean similarity per gear type; see text); The year 1998 is marked by a grey circle.

At SSd, the lowest similarity is reached in 1982, '86, '93 and '96. Following 1996, it strongly increases and reaches its highest value in 2000. The beginning of the series in '69 shows the second highest similarity and '76/'77, '79/80 as well as '84 are above average.

At FSd, the lowest similarity was observed in 1974, '81, '93 and '97, while '73, '79, '96 and 2000 are amongst the highest of all values. During the period of '97-2000, similarity increases from below average to very high values at FSd, a trend that is also visible at SSd and WB.

At WB the similarity increases from 1981 to '90 and is higher than average during the whole period with the exception of '84 when one of the lowest values is attained. A strong decrease starts in 1992/'93 continuing until the minimum similarity is reached in '95. All values from '93 until '99 are below average until in 2000 the similarity is very high again.

At Slt, the similarity in 1979 and '86 is amongst the highest values together with '74/'75 and '94. The lowest values are attained in '76 and '83.

The values at all stations from '69 are based on the similarity between four samples of two pooled vV-grabs each. This is inherently higher than the similarity between single grabs. Taking this into account and comparing the position of this year between the stations, the actual spatial variability in 1969 would probably have been lower than average at SSd and about average at FSd and Slt.

4.3 Methodological changes

The sampling protocol has not always been constant over the period of the long-term investigation. A careful selection of the most appropriate and comparable data minimises methodological influences as far as possible, but some differences remain. Differences due to different personnel and literature should be minimised by the taxonomic revision. The two main methodological influences that still need to be considered are the grab type (and penetration) and the time of sampling.

4.3.1 Penetration depth & grab type

The height of the sediment in the grab as an indication of the penetration depth varies significantly between the different types of grabs employed (Fig. 4.3.1).

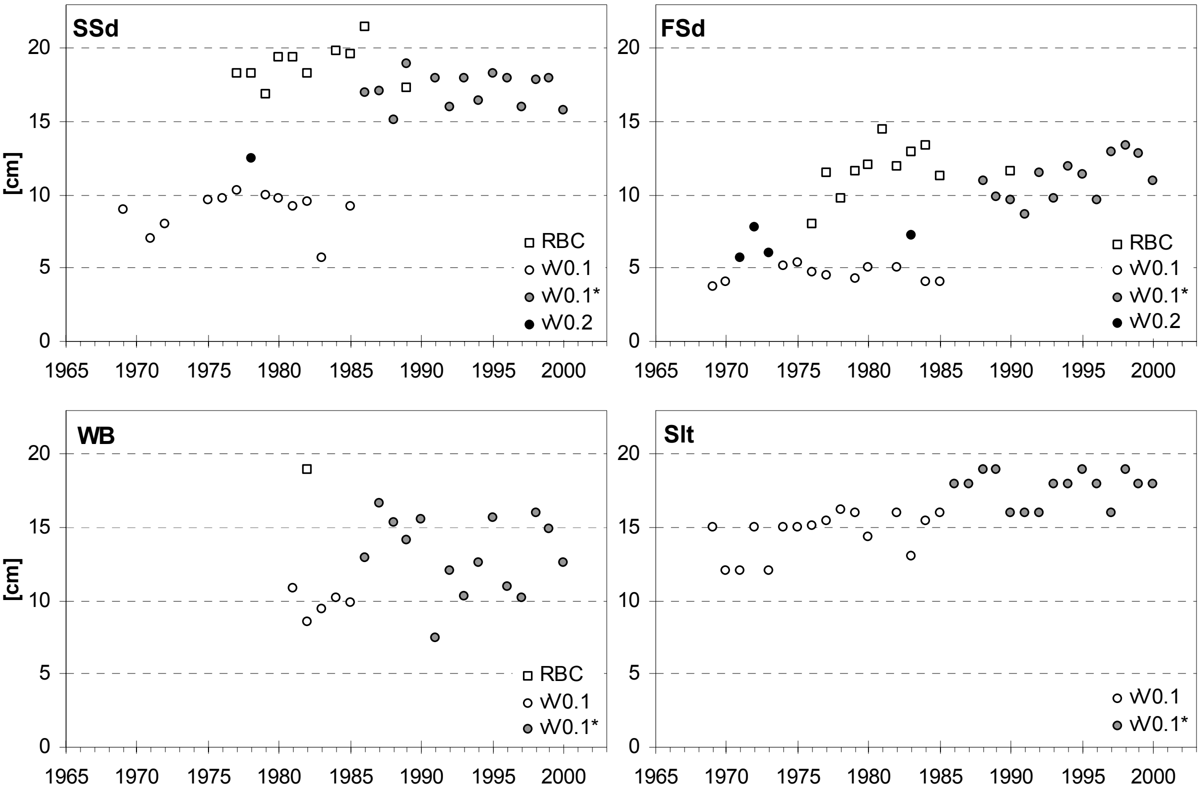

Fig. 4.3.1: Grab type and mean penetration depth per date as measured by depth of sediment contained in the grab. RBC: Reineck Box Corer 0.017m^2; vV0.1: van-Veen grab 0.1m^2; vV0.1*: modified vV-grab 0.1m^2; vV0.2: vV-grab 0.2m^2.

The penetration depth of the light 0.1 m^2 van-Veen grab (vV) used until 1985 is significantly lower than that of the new modified grab used since '86 (U-test: WB: $p < 0.01$; all other stations $p < 0.001$). At SSd the older vV reached only a mean penetration of 8.9 cm (± 1.3 SD) and at FSd a mere 4.6 cm (± 0.6 SD). Between '71 and '73 a 0.2 m^2 vV-grab was used at FSd. In '71 three replicates and in '72/'73 five replicates were taken, all of which were pooled to form a single sample. The 0.2 m^{-2} vV reached a 2-3 cm deeper penetration depth than the lighter 0.1 m^{-2} vV (Fig. 4.3.1).

To include deeper living organisms, a Reineck Box Corer (RBC) was used since '76 in addition to the light 0.1 m^{-2} vV. The RBC reached on average 18.9 cm (± 1.3 SD) at SSd and 11.7 cm (± 1.7 SD) at FSd. At Slt no RBC was employed, as the light vV was mostly filled to the top and reached a mean penetration depth of 14.7 cm already.

The new modified 0.1 m² van-Veen grab (vV*) employed since 1986 reached a penetration depth that was not significantly smaller than that of the RBC at FSd (mean ±SD: vV* = 11.0 ±1.5 cm; RBC = 11.7 ±1.7 cm; $p > 0.2$) and only 1.7 cm less at SSd (vV* = 17.2 ±1.2 cm; RBC = 18.9 ±1.3 cm; $p = 0.0027$).

4.3.2 Combination of different grabs

4.3.2.1 Univariate measures

The combination of two vV (0.1 m²) with six RBC (0.017 m²) from the extensive sampling in July 1976 shows some differences compared to results from five vVs (Tab. 4.3.1).

Tab. 4.3.1: Comparison of mean summary statistics (± SD) calculated from different combinations of sampling gear taken at FSd in July 1976 (weighted arithmetic means).
N: total number of organisms; N/m²: total organisms per m²; S: total number of species; H': Shannon-wiener diversity index; J': Pielou's evenness index.

	3 vV	**2 vV + 6 RBC**	**4 vV**	**5 vV**
N	388 (± 61)	438 (± 54)	516 (± 68)	644 (± 73)
N / m²	1294 (± 202)	1459 (± 181)	1291 (± 169)	1289 (± 146)
S	41.2 (± 4.1)	43.3 (± 3.6)	45.4 (± 4.0)	48.8 (± 3.9)
H'	4.12 (± 0.16)	4.15 (± 0.12)	4.18 (± 0.13)	4.22 (± 0.12)
J'	0.77 (± 0.02)	0.76 (± 0.02)	0.76 (± 0.02)	0.75 (± 0.02)

The number of species found (S) and the diversity (H') are lower, while evenness (J') is nearly the same. The mean values for S, H' and J' are in between those for three and four vVs, but the SD is slightly smaller. The overall density of organisms per m² (N/m²) is higher in the RBCs. This difference in the total number of organisms is mainly caused by differences in the density estimates of a few species between the two types of gear (Tab. 4.3.2). Densities of *Urothoë grimaldii* are more than four times higher in the RBC samples, those of *Goniada maculata* more than tree times higher and densities of *Tellina fabula* about twice as high.

The main differences in density are not only caused by species that live deeper in the sediment and can not be explained by the penetration depth of the grab alone. Mean penetration depth of the RBCs with 8.2 cm (±2.58 SD) is significantly deeper than that of the vVs with 6.2 cm (±0.98 SD)(U=82.5; p=0.0012) but seven out of 25 RBCs lost some material due to inappropriate closure.

Tab. 4.3.2: Mean density (± SD) of the dominant species calculated from different sampling gear taken at FSd in July 1976.
Main differences and significant *p*-values at α = 0.05 (U-test) are printed in bold.

	Mean density / m² (± SD)			
Species	1 vV (=0.1 m²)	6 RBC (=0.1 m²)	Difference	*p*
Magelona mirabilis	318.1 (±164.4)	309.6 (±105.0)	-8.5	0.483
Spiophanes bombyx	118.8 (±86.2)	184.8 (±55.6)	66.1	0.095
Tellina fabula	**115.0** (±60.4)	**218.4** (±44.7)	**103.4**	**0.001**
Chaetozone setosa	97.5 (±63.3)	112.8 (±43.2)	15.3	0.968
Echinocardium cordatum	60.6 (±56.9)	43.2 (±20.6)	-17.4	0.197
Urothoë poseidonis	**58.8** (±32.0)	**283.2** (±81.7)	**224.5**	**<0.001**
Ophiura spp. juv.	48.1 (±44.5)	16.8 (±18.1)	-31.3	**0.003**
Phyllodoce groenlandica	43.8 (±25.8)	40.8 (±16.9)	-3.0	0.682
Magelona minuta	40.6 (±42.3)	86.4 (±34.7)	45.8	**0.030**
Goniada maculata	**38.8** (±23.3)	**127.2** (±24.8)	**88.5**	**<0.001**
Scoloplos armiger	23.8 (±17.1)	31.2 (±18.9)	7.5	0.389
Lanice conchilega	28.1 (±45.9)	24.0 (±18.7)	-4.1	0.119
Euspira pulchella	28.8 (±15.0)	28.8 (±14.4)	0.1	0.517
Nephtys hombergii	16.3 (±14.1)	12.0 (±12.2)	-4.3	**0.032**
Chamelea gallina	11.9 (±11.7)	21.6 (±13.9)	9.7	0.843
Phoronis spp.	11.3 (±12.0)	31.2 (±20.1)	20.0	1.011
Ophiura albida	10.6 (±10.6)	4.8 (±16.6)	-5.8	**0.007**
Edwardsia spp.	5.6 (±8.9)	28.8 (±16.0)	23.2	0.361
Total	1287.5 (±379.5)	1789.8 (±168.7)	502.3	**<0.001**

Whether the large differences found for the densities are simply a result of sampling gear and sample size is doubtful. The different number of species may however be seen as a result of sample size and number of replicates.

The percentage of species (88.8%; see Tab. 4.3.3) found in the combinations of 2 vV/6 RBC relative to that found in five vV is the best possible estimate of the sampling influence and is used to correct for the sampling effort in the long-term series. The same applies for other gear types that have been used on rare occasions (Tab. 4.3.3).

Tab. 4.3.3: Percentage of species caught with different sampling gear relative to five vVs; based on samples taken at FSd in July 1976.

Gear	Area [m²]	% of species
2vV / 6 RBC	0.3	88.8%
2 * 0.2vV + 6 RBC	0.5	88.3%
3 * 0.2vV	0.6	86.8%
24 * RBC	0.4	99.4%
5 vV	***0.5***	***100.0%***
5 * 0.2vV	1.0	100.6%

Species numbers from samples with more or less than five replicate 0.1 m² vVs are corrected according to the relation found for the respective station in chapter 4.2.4.1 (Fig. 4.2.9 b).

4.3.2.2 Inter-sample similarity

The similarity between samples consisting of two vV plus six RBC is about the same as that between samples of four vV's, it may even be slightly larger (Tab. 4.3.4).

Tab. 4.3.4: Similarity between pooled samples from different grab types (Bray-Curtis similarity, 4th root transformed abundances). Calculated from data from July 1976 at FSd.
SD: Standard deviation; C.I.: empirical confidence interval.

Sample combination vV0.1 / RBC	Mean similarity [%]	SD	95% C.I.
3 / 0	74.6	3.4	67.5 - 80.8
4 / 0	76.7	2.8	70.8 - 81.9
2 / 6	76.9	2.9	71.1 - 82.5
5 / 0	78.0	2.5	73.1 - 82.8

A formal significance test is not useful here, as with the relatively wide confidence interval even the similarities of samples from three vV's would not be significantly smaller than those from samples with five vV's. The systematic relation shown between sample size and similarity remains however valid. This comparison is only intended to identify the sample size of vV's that results in the same inter-sample similarity as between samples of two vV's plus six RBC's. This result is used for the reference point of the expected similarity without community changes in the analysis of the time series (chapter 5.4).

4.3.3 Sampling time

During most years samples have been taken in March or April. For a few years no appropriate samples were available from this period, mainly because of bad weather conditions or lacking ship availability (Fig. 4.3.2).

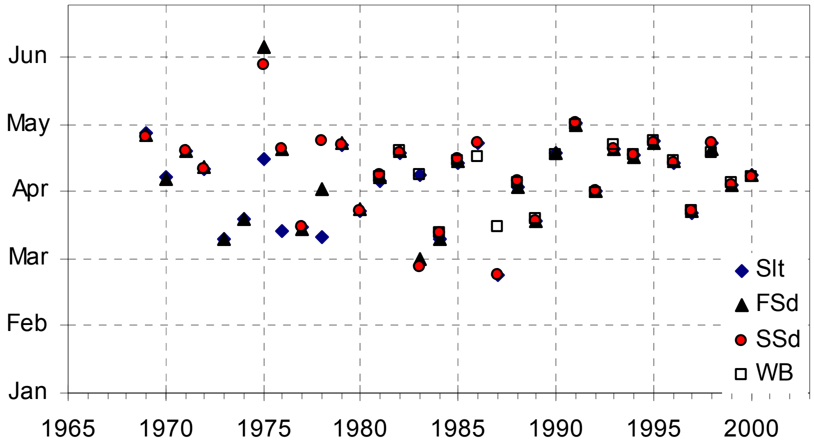

Fig. 4.3.2: Sampling date for the selected samples at all stations.

Samples from late May and early June had to be accepted in 1975 for SSd and FSd. In 1983 samples from the end of February had to be accepted for SSd and FSd and in 1987 for SSd again.

A sampling in late April may already produce larger numbers of organisms than in early March, therefore Fig. 4.3.2 serves as reference to explain or disprove the possibility of seasonal reasons for the observed differences in faunal data.

4.4 Benthos time series

4.4.1 Similarity between benthic communities

The investigation of spatial variability (chapter 4.2) showed a similarity of the benthic communities between stations and the presence of several species at more than one station. This might lead to the suspicion of a common development of the benthic communities of the German Bight. The degree of this similarity over the course of time and the differences between the stations will be examined by a joint analysis followed by separate analyses for each station.

A combined MDS and Cluster analysis of all four stations over the whole time period shows clearly that the stations represent different communities. For each station all samples over the whole period form one cloud separated from the other stations (Fig. 4.4.1). There is no overlap of the groups on the MDS-plot or in the cluster analysis at any time, as confirmed by ANOSIM results (Global and all pair-wise tests p<0.01%).

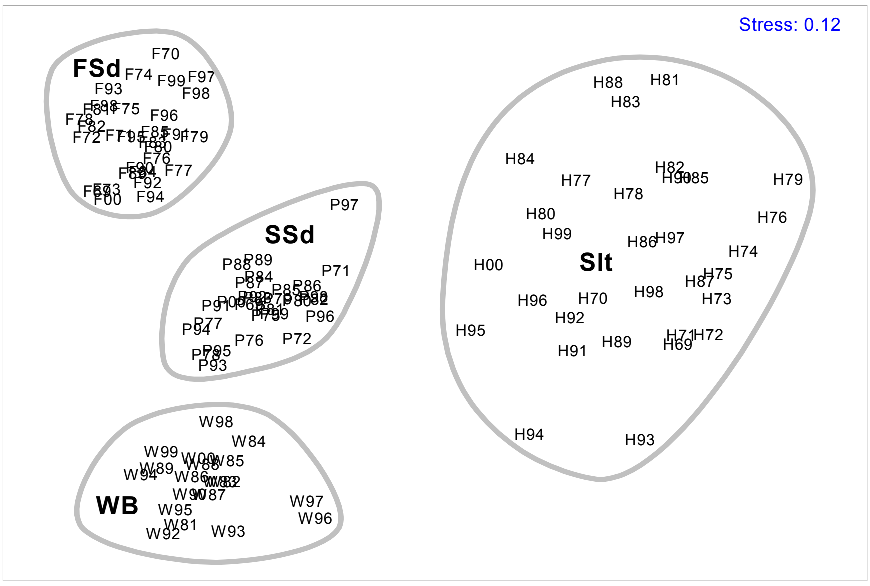

Fig. 4.4.1: MDS plot combining all four stations over the whole sampling period. Bray-Curtis-similarity of 4th root transformed densities [m^{-2}], pooled samples per year. Groups separated by Cluster analysis are enclosed by lines. Each sample is represented by a character denoting the station and two digits for the year.

The mean similarity of the individual communities between the years within each station is very similar for the stations SSd, FSd and WB with around 62%; only Slt has a lower mean similarity of only 49% (Tab. 4.4.1).

Tab. 4.4.1: Mean community similarity between years *within* each station and *between* the stations.
Bray-Curtis similarity of fourth root abundance data m^{-2} (+range).

	Within	SSd	WB	FSd
SSd	62.7 (45.0 - 78.3)			
WB	62.0 (43.4 - 81.2)	45.1 (28.7 - 61.1)		
FSd	62.3 (47.5 - 77.4)	43.9 (30.1 - 61.2)	33.2 (22.0 - 47.0)	
Slt	48.5 (26.2 - 73.6)	31.0 (11.2 - 53.9)	24.1 (11.0 - 45.7)	21.9 (6.7 - 38.9)

The temporal variability at SSd, WB and FSd is very similar. WB has the highest temporal variability (lowest mean similarity) amongst these three with also a larger range in similarities. The lower mean community similarity between the years at Slt with its very large range indicates a higher temporal variability at Slt than at any other station.

The maximum similarity between SSd and WB or between SSd and FSd almost reaches the average similarity between the years within these stations. The maximum similarity between Slt and SSd is even higher than the average similarity between the years at Slt. This is mainly caused by the high variability at Slt, but also indicates a large similarity between Slt and SSd.

The ranking of inter-station similarities is very similar to that found in the investigation of spatial variability (samples from 1998; Tab. 4.2.10) with some exceptions. Over the long term the community similarity of FSd to SSd and WB is larger than between Slt and any of the other stations, while in 1998 the similarity between SSd and Slt was higher than between FSd and WB or SSd (Absolute values in Tab 4.2.10 are not directly comparable to Tab. 4.4.1 because the similarities shown here are based on pooled samples [m^{-2}] while those in chapter 4.2.5 are similarities between single grabs).

4.4.2 Similarity of temporal development

A comparison of the temporal similarity matrices of the separate stations shows a similar development of the respective communities over time. This indicates similar periods of higher similarity and similar years of change, but does not imply a parallel population development for species present at both stations.

There is significant correlation between the development of the community at SSd and all the other stations (Tab. 4.4.2).

Tab. 4.4.2: Spearman's rank correlation between similarity matrices from different stations; *R* (+ *p-values)* from permutation test; BC-similarity, 4th root transformed densities m^{-2}.

R (p)	**SSd**	**WB**	**FSd**
WB	0.58 *(0.001)*		
FSd	0.31 *(0.002)*	0.24 (*0.069*)	
Slt	0.33 *(0.001)*	0.19 (*0.046*)	0.11 (*0.077*)

The highest correlation of 0.58 exists between SSd and WB, the correlation between SSd and Slt (0.33) and SSd and FSd (0.31) is weaker but still highly significant ($p \leq 0.002$). Correlations between the other stations are weak (WB-Slt: Rho = 0.19, $p < 0.05$) or not significant at all (WB-FSd and Slt-FSd)

4.4.3 Community development at single stations

Each station represents a different type of benthic community. Therefore the community development is analysed separately for each station.

4.4.3.1 SSd

Situated between the three other stations in geographical location (Fig. 4.1.1) as well as in community similarity (Fig. 5.4.3), this station reflects some aspects that can also be found at the other stations. The revised species list excluding inconsistent identifications contains 136 taxa (mostly species, some genera or higher taxa), consisting of 38% polychaetes, 24% crustaceans, 26% molluscs, 6% echinoderms and 7% belonging to various other phyla (details in the species list in annex A.1).

4.4.3.1.1 Sum parameters

Most sum parameters show a highly variable course of time with some remarkable extreme situations, but without major persistent changes.

To correct for differences sampling effort (chapter 5.4.1), species numbers have been adjusted to the expected number of species per 0.5 m², which corresponds to the most common sample size of five 0.1 m² vV's (correction factors in chapter 5.3.2). The species number *per grab* cannot be plotted for pooled samples from earlier years (Annex A.2). Apart from the early years from 1969 to 1972, species numbers at SSd fluctuated around 50 species per 0.5 m² (Fig. 4.4.2). Fluctuations between 40 and 60 species occur every three to four years. In 1996 the species number drops below 40 with a recovery starting in 1998.

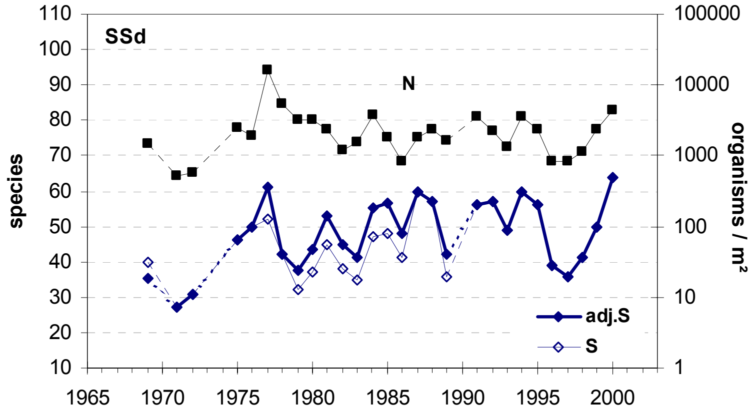

Fig. 4.4.2: Development of the number of species (left axis) and the total number of organisms (right axis) between 1969 and 2000 at station SSd; S: raw number of species found; adj.S: number of species adjusted for sampling effort [0.5 m^{-2}] (see text); N: total number of organisms [m^{-2}]. Dotted lines indicate missing years.

The fluctuations of the species number run very much in parallel to the development of the total density of organisms except for the decrease in species numbers in 1979/80 which is not reflected in the total number of organisms, which is strongly influenced by the density of the dominant *Phoronis* spp. and other opportunistic species (see chapter 5.4.3.1.5; Fig. 4.4.5).

The extremely high densities of opportunistic species from '77 to '80 result in the lowest diversity (H') and evenness (J') during these years, the most prominent feature in Fig. 4.4.3.

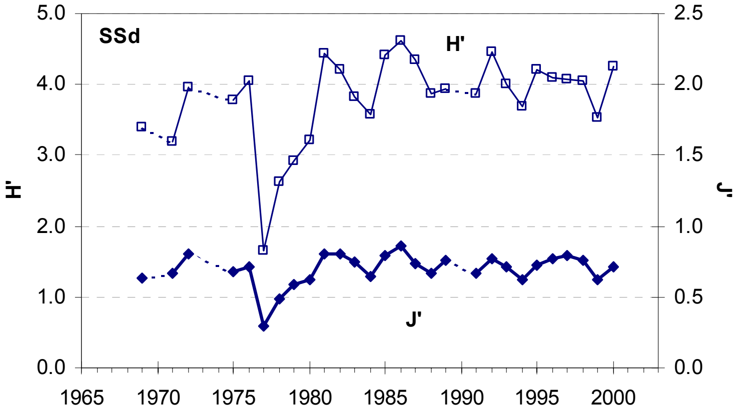

Fig. 4.4.3: Development of diversity [H'] (left axis) and evenness [J'] (right axis) between 1969 and 2000 at station SSd. Broken lines indicate missing years.

From '80 onwards H' fluctuates around 4.0, while several values during the 70ies were much lower. Values of H' closely follow the development of J'. Besides the period from 1977 to '80, low values of H' (and J') are also found in 1969/'71, '84, '94 and '99. Values for H' in '69 and '71 are relatively lower than those of J', because in these years the species number is also lower than usual. Maximum values of diversity couple to high evenness are found in '81, '86 and '92.

4.4.3.1.2 Community development

A multivariate analysis of the complete time series of the community at SSd using MDS indicates on the first look one big cloud of points with three clear outliers: 1971/72 and '97 (Fig. 4.4.4 a).

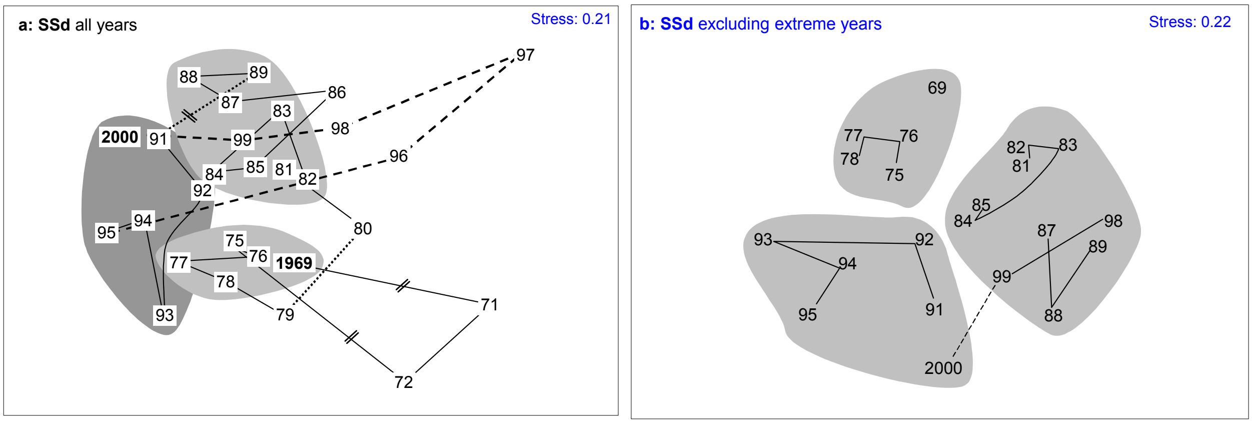

Fig. 4.4.4: Community development at SSd between 1969 and 2000. MDS-plot based on Bray-Curtis similarity of 4th root transformed densities [m^{-2}]. Consecutive years are connected by lines. Broken lines indicate major shifts in the community. Shaded areas indicate groups supported by cluster analysis (group average); a: all years; b: excluding extreme years.

Closer to the rest, but tending into the same direction, are the years '79/'80, '86, '96 and '98. No adequate samples are available from '70 and from '73/'74.

Excluding these extreme years, the remaining years are divided into three major groups, representing roughly the 70ies, 80ies (including '99) and the 90ies (Fig. 4.4.4 b).

Following the course of time, after the excursion of '71/'72, the second half of the 70ies constitutes a coherent group. 1979 moves in a similar direction as '71 and '72, but not as far as these (Fig. 4.4.4 a).

In the beginning of the 80ies a shift occurs to a new coherent group comprising most of the 80ies. During the 80ies, '86 takes a prominent position at the border of this group.

Another shift follows towards the early 90ies, indicating a higher similarity of the mid-90ies to the mid-70ies again. The biggest break from the left edge of the group of the 90ies to the outer right margin of the plot occurs in '96 and continues in '97. This trend is reversed in '98 and '99, approaching a mid-80ies situation. In the year 2000, the situation has reached the group of the early 90ies again.

Although the designated groups are not strictly the nominal decades, the agreement is quite good. The terms "70ies", "80ies" and "90ies" are used for the rest of the chapter strictly to refer to these groups identified by the community analysis and *not* to the ordinary decades.

4.4.3.1.3 Changes in community composition

The dissimilarity between the designated groups is based on a large number of species, each contributing only a small part.

Half of the mean dissimilarity between the 70ies and the 80ies is based on 28 species, with the largest contribution of 4.4 % by *Phoronis* spp. decreasing from an average of 3157 to 259 ind./m² (Tab. 4.4.3, next page). In addition to this, the most prominent changes are the decreasing densities of the polychaetes *Scalibregma inflatum*, *Owenia fusiformis*, *Pholoë minuta*, *Lanice conchilega*, *Goniada maculata* and *Glycinde nordmanni*, of the brittle star *Amphiura filiformis*, the bivalves *Mysella bidentata*, *Thyasira flexuosa,* of the amphipod *Ampelisca brevicornis* and of the anthozoans *Edwardsia* spp. and *Cerianthus lloydi*. In opposition to this, the densities of the polychaetes *Spiophanes bombyx*, the ghost shrimp *Callianassa subterranea*, the bivalves *Abra nitida* and *A. alba* as well as of juvenile Ophiuridae increase (Tab. 4.4.3).

The dissimilarity between the 80ies and the 90ies is based to 50% on 33 species (results of SIMPER-routine) with the largest contribution of 2.8 % from *Amphiura filiformis* increasing again to an average density of 95 ind./m² after being rare during the 80ies.

While the community composition of the 90ies approaches the situation during the 70ies in many aspects, some differences remain. The extremely high densities of *Phoronis* spp. are not reached again, while other species like *Scalibregma inflatum*, *L. conchilega*, *C. subterranea*, *Abra* spp. and *M. bidentata* reach higher densities than found during the 70ies. Other species like *O. fusiformis, S. armiger*, *G. maculata*, *G. nordmanni*, *Pectinaria koreni*, *C. lloydii*, *Edwardsia* spp., *Euspira pulchella* and *T. flexuosa* are not as abundant as during the 70ies.

Although not present in high densities, the polychaetes *Podarkeopsis helgolandica* and *Sthenelais limicola* are a frequent part of the community in the 90ies again after being rare during the 80ies. The brittle star *Acrocnida brachiata* appears frequently during the 90ies in low densities (2-6 m^{-2}), but is not found previously.

Each of the designated periods encompasses one or more years that differ markedly from the rest. All of these years ('71/'72, '79, '86 and '96-'98) follow cold winters and are characterised by a very low number of species and in most cases also a low total number of organisms (Fig. 4.4.2) .

Tab. 4.4.3: Dominant species at SSd and mean density and presence during the groups of years including the main species responsible for differences between them (SIMPER). Mean: ind./m²; SD: standart deviation; Pres.: % of years when the species was found.

	Total density		Pres.	Mean of period [m^{-2}]			Presence [%]		
Species	Mean	SD	[%]	70ies	80ies	90ies	70ies	80ies	90ies
Phoronis spp.	887	2453	100%	3157	259	480	100	100	100
Ophiura albida	176	99	100%	189	226	189	100	100	100
Ophiura juv.	36	50	68%	16	34	66	17	90	100
Amphiura filiformis	35	70	54%	46	3	95	100	40	83
Echinocardium cordatum	23	12	100%	31	19	21	100	100	100
Nucula nitidosa	151	133	100%	140	196	164	100	100	100
Mysella bidentata	116	123	100%	161	40	228	100	100	100
Montacuta ferruginosa	32	23	96%	35	33	38	100	100	100
Thyasira flexuosa	110	111	96%	210	109	114	100	100	100
Abra nitida	109	216	71%	39	161	182	67	90	67
Abra alba	54	72	96%	26	58	82	83	100	100
Tellina fabula	13	57	36%	2	4	45	17	60	33
Euspira pulchella	11	16	79%	24	13	7	83	100	100
Spiophanes bombyx	139	317	86%	40	174	40	67	100	100
Nephtys hombergii	104	47	100%	95	109	131	100	100	100
Owenia fusiformis	93	106	96%	186	54	95	100	100	100
Scalibregma inflatum	87	208	71%	73	21	221	67	60	100
Pholoe minuta	48	38	96%	64	38	62	100	100	100
Scoloplos armiger	45	79	86%	78	71	10	100	100	50
Goniada maculata	38	41	96%	62	37	11	100	90	100
Glycinde nordmanni	6	14	39%	23	1	3	67	30	50
Lanice conchilega	26	31	79%	10	33	30	50	100	83
Podarkeopsis helgolandica	5	9	29%	7	0	13	50	0	83
Sthenelais limicola	3	4	57%	5	1	6	100	20	100
Pectinaria koreni	14	19	89%	17	15	7	100	100	83
Eudorella spp.	51	60	86%	50	66	58	100	80	100
Callianassa subterranea	12	16	68%	1	12	34	33	100	100
Ampelisca brevicornis	10	16	82%	11	4	12	67	70	100
Edwardsia spp.	27	62	86%	76	16	10	100	70	100
Cerianthus lloydi	3	11	25%	12	2	0	67	30	0
Nemertini	27	25	100%	37	26	29	100	100	100

Although the number of species is already low in 1969, it further declines to '71 and then gradually increases again to '72. The decline in density affects most species, especially *A. filiformis* which is absent in both years. An exception is *Owenia fusiformis* which reaches 222 ind./m² in '71 and disappears again in '72.

In 1979 the species number is low but the total density of organism is higher than average (Fig. 4.4.2). Many species decrease in density relative to '78 like *A. filiformis*, *Abra nitida*, *Euspira pulchella*, *Scalibregma inflatum* and even *N. hombergii*. Others increase in density like *Nucula nitidosa*, *Eudorella* spp. and *Spiophanes bombyx*. For many species this trend is reversed in 1980 with a strong increase in *Ophiura albida*, *A. alba*, *Spiophanes bombyx* and *N. hombergii* while others, especially *Phoronis* spp., decrease. Together with the absence of *A. filiformis* this initiates a development towards the mean situation of the 80ies.

In 1986 the densities of nearly all species decrease relative to '85, except for those of *Scalibregma inflatum*, *Owenia fusiformis*, *Lanice conchilega* and Nemertini.

1996 is marked by the reduction of *A. filiformis* from 290 ind./m² in '95 to complete absence. Parallel to this, many species decline in density including *Phoronis* spp. or *Mysella bidentata* and others like *T. flexuosa* or *E. pulchella* are completely absent.

Mean densities of the species for the designated periods give a rough idea of the community composition during the designated periods. They imply however a more or less constant density during the respective period with (random) fluctuations around this mean. In reality each of these periods is often characterised by a development within the period. Therefore a more accurate description of the community development has to return to the time series of the contributing species.

4.4.3.1.4 Selected species

A couple of species has been selected from the species listed above, that represent patterns in their temporal development, which are roughly followed by several other species. They stand as examples to explain the development of the community.

In many years *Phoronis* spp. plays the numerically dominant role at SSd. The development of the total density of organisms reflects the density changes of *Phoronis* spp. that account for 30 to 80% of all organisms during years of high abundance ('69, '75, '77-'79, '84, '94) (Fig. 4.4.5). During these years it may reach densities of around 1000 ind./m² up to a maximum of over 13000 ind./m² attained in '77 (Fig. 4.4.5).

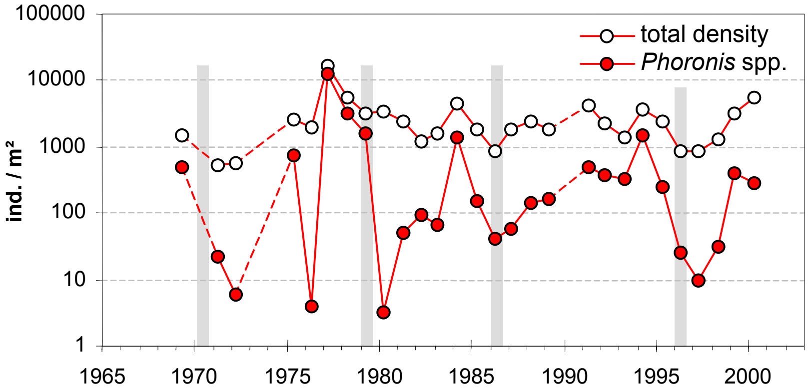

Fig. 4.4.5: Total density of organisms and density of *Phoronis* spp. between 1969 and 2000 at station SSd. Broken lines indicate missing years. Vertical bars indicate cold winters.

Several opportunistic polychaetes reaches peak densities only in a few years like *Spiophanes bombyx* ('80 and '87/'88), *Owenia fusiformis* ('71) and *Scalibregma inflatum* ('91) (Fig. in Annex: A.7.1.1).

Amphiura filiformis declines from its already low densities in '69 to total absence in '71/'72. It starts to increase in density in '76 and reaches a maximum density of 130 ind./m² in '78.

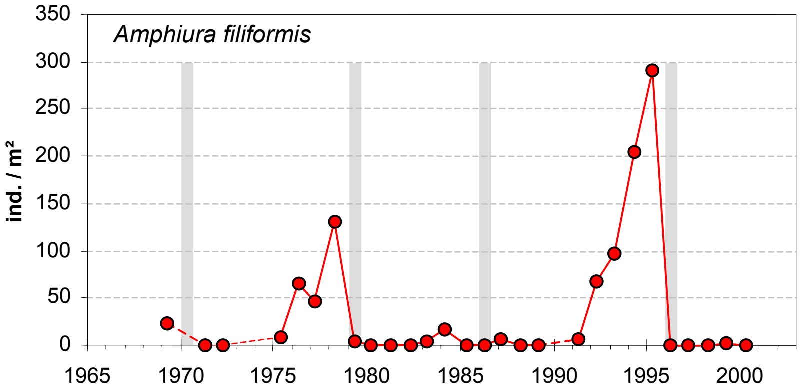

Fig. 4.4.6: Development of the density of *Amphiura filiformis* at SSd; density as individuals/m². Broken lines indicate missing years. Vertical bars indicate cold winters.

From '79 until '83 it is either absent or only found as single individual, then it is present with 17 ind./m² in '84 and disappears again in '85. Another six years after the cold winter of '86 it starts to increase again in '92 until it reaches a peak density of 290 ind./m² in '95. In '96 it disappears again and has not recovered since.

This general pattern of an increase towards the late 70ies, to '84 and towards '95 coupled with strong decreases after the cold winters and generally lower densities during the 80ies is also followed by *Mysella bidentata*, although it appears in higher densities than *A. filiformis* and recovers earlier after the cold winters (Fig. 4.4.7).

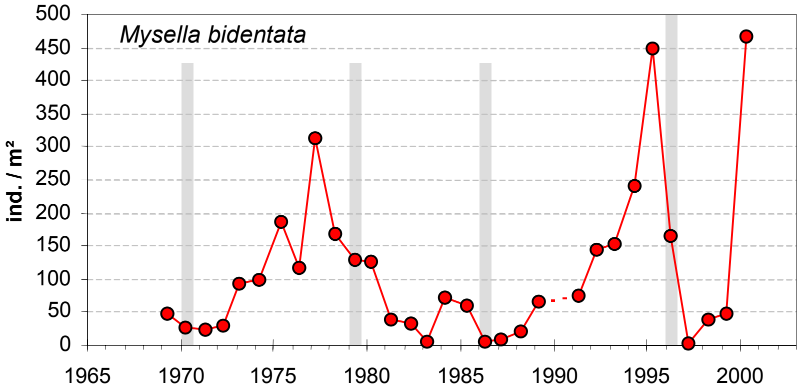

Fig. 4.4.7: Development of the density of *Mysella bidentata* at SSd; density as individuals/m². Broken lines indicate missing years. Vertical bars indicate cold winters.

A similar pattern is also discernible for the polychaetes *Pholoë minuta*, *Podarkeopsis helgolandica* and *Glycinde nordmanni* and for the echinoid *Echinocardium cordatum* although the latter's density is very variable (Fig. A.7.1.2).

Contrary to this, *Abra* spp., which also exhibit low densities after the severe winters, are only present in high numbers during years when *A. filiformis* is rare or absent (Fig. 4.4.8)

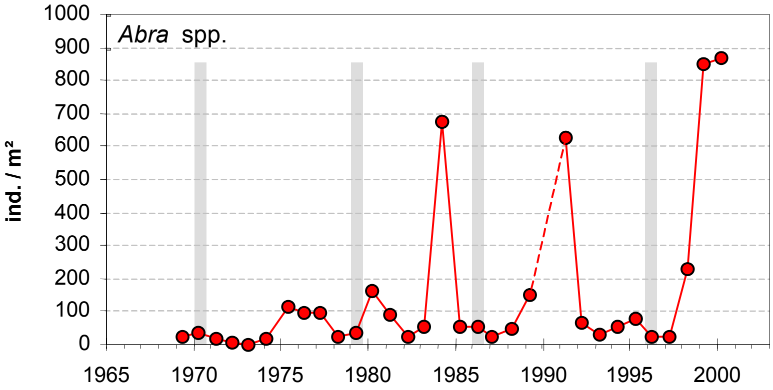

Fig. 4.4.8: Development of the density of *Abra spp. (A. alba* & *A. nitida)* at SSd; density as individuals/m². Broken lines indicate missing years. Vertical bars indicate cold winters.

Another pattern is an increasing tendency during the late 70ies combined with a decrease during the 80ies and generally lower densities during the 90ies as exemplified by *Goniada maculata*, reaching its peak density of over 180 ind./m² in '80 (Fig. 4.4.9).

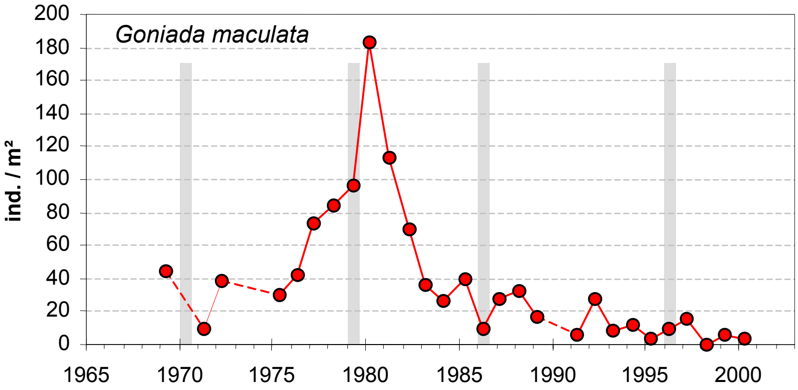

Fig. 4.4.9: Development of the density of *Goniada maculata* at SSd; density as individuals/m². Broken lines indicate missing years. Vertical bars indicate cold winters.

Although subject to larger variability, this pattern is also discernible for *Scoloplos armiger*, *Pectinaria koreni*, *Edwardsia* spp. and *Ophiura albida* (Fig. A.7.1.3). These species reach relatively low densities during years of higher densities of *A. filiformis* ('78, '93-'95).

Thyasira flexuosa increases markedly already in '72, reaches a maximum density of nearly 400 ind./m² in '76/'77 and declines strongly in '78 (Fig. 4.4.10).

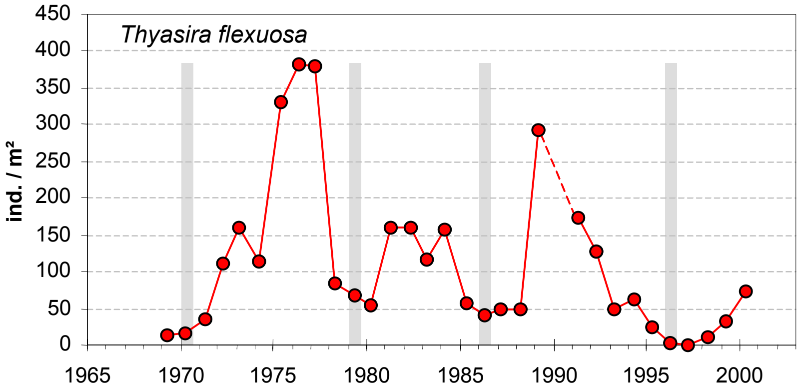

Fig. 4.4.10: Development of the density of *Thyasira flexuosa* at SSd; density as individuals/m². Broken lines indicate missing years. Vertical bars indicate cold winters.

T. flexuosa is always present in densities of 50 to 150 ind./m² during the 80ies, reaches a second peak in '89 and declines towards '95. This development stands in opposition to the increasing density of *A. filiformis* in '78 and in '92-'95.

N. nitidosa and *M. ferruginosa* vary very much in parallel at SSd (see chapter 5.4.5) and reach also higher densities during the late 70ies, but then only gradually decline towards the early 90ies and finally increase towards their overall highest density in 2000 (408 and 96 ind./m² respectively) (Fig. 4.4.11 & Fig. 4.4.12).

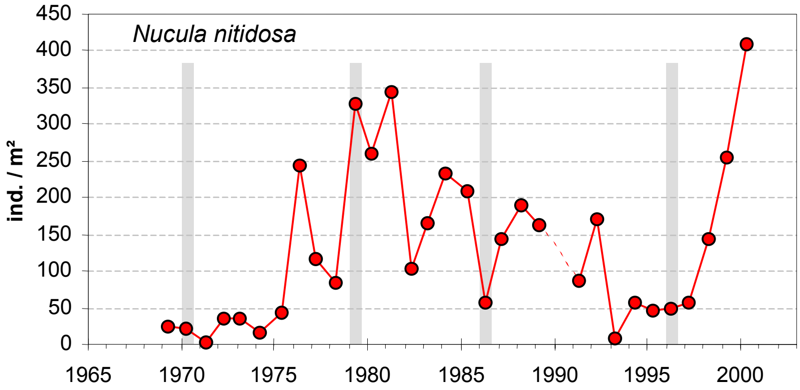

Fig. 4.4.11: Development of the density of *Nucula nitidosa* at SSd; density as individuals/m². Broken lines indicate missing years. Vertical bars indicate cold winters.

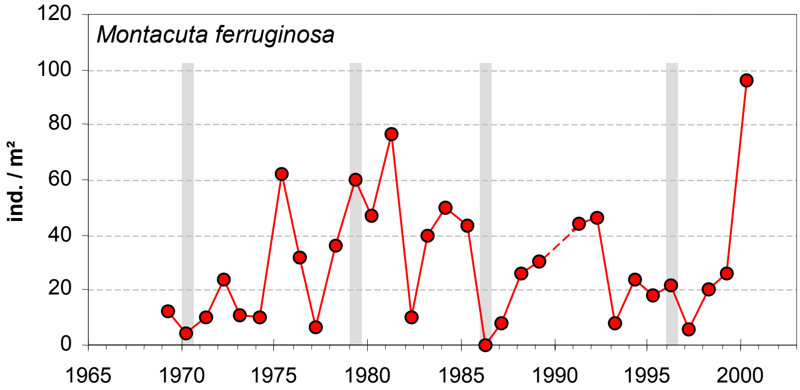

Fig. 4.4.12: Development of the density of *Montacuta ferruginosa* at SSd; density as individuals/m². Broken lines indicate missing years. Vertical bars indicate cold winters.

This pattern is also followed by *Eudorella* spp. and *Tellina fabula*, although the latter is only present in low numbers at SSd (Fig. A.7.1.4).

In opposition to this, *Lanice conchilega* and *Callianassa subterranea* are rare during the 70ies, then increase during the 80ies and reach their highest densities during the 90ies (Fig. A.7.1.4).

Other species mentioned in the description of community differences often exhibit very large inter-annual variability interfering with the distinction of any longer-term pattern. Some of the more common species are shown in the annex (Fig. A.7.1.5-6).

4.4.3.2 WB

The deepest and furthest offshore of the investigated stations shows a couple of very similar developments as at SSd while some species show opposite trends at both stations. The revised species list contains 130 taxa (mostly species, some genera or higher taxa), consisting of 37% polychaetes, 25% crustaceans, 22% molluscs, 9% echinoderms and 7% belonging to various other phyla (details in annex A.1).

4.4.3.2.1 Sum parameters

The overall species density [0.5 ind./m²] is at WB higher than at the other stations. Maximum species numbers are recorded in the late 80ies and in '92 (Fig. 4.4.13).

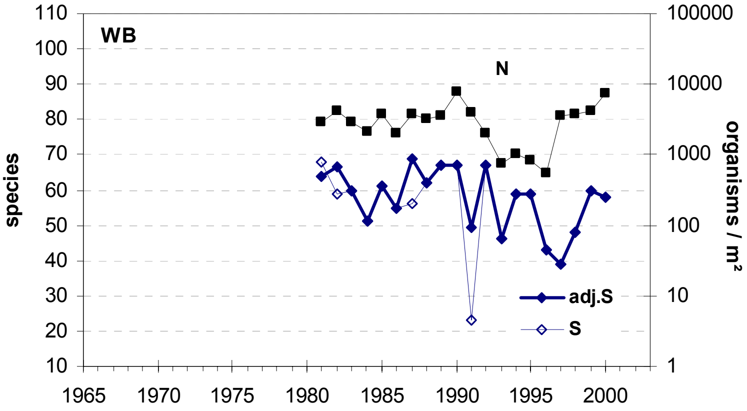

Fig. 4.4.13: Development of the number of species (left axis) and the total number of organisms (right axis) between 1969 and 2000 at station WB; S: raw number of species found; adj.S: number of species adjusted for sampling effort [0.5 m^{-2}] (using percentages from chapter 5.3.2); N: total number of organisms [m^{-2}].

Apart from the low number in '91 when only one vV with a rather low penetration depth was available, major drops in species richness of between 10 and 20 species occur in '83, '93, with the deepest drop in '96/'97. A recovery starts in '98 and about average species densities of 60 species are reached again in '99.

Total organism density fluctuates between 2000 and 4000 ind./m² during the 80ies with minimum values in '84 and '86. A single peak of nearly 8000 ind./m² in '90 is followed by a continuous decrease to only 760 ind./m² in '93. This low level is kept until '96. A marked increase in '97 brings the total density back to around 4000 ind./m² until another strong increase in 2000 leads to the second peak density of nearly 8000 ind./m².

The values for evenness (J') and diversity (H') vary again very much in parallel. H' fluctuates between 3.0 and 4.0 during the 80ies with lowest values attained in '84, '88 and '90 (Fig. 4.4.14). The extremely low value in '91 (plotted in brackets) is based on a single grab sample with low penetration depth and is therefore unlikely to be representative.

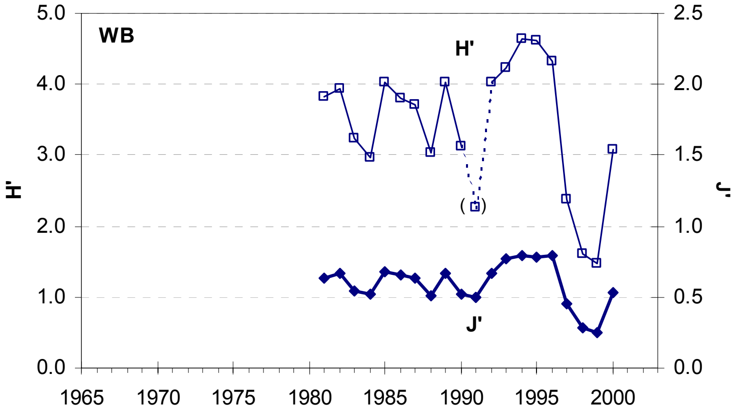

Fig. 4.4.14: Development of diversity [H'] (left axis) and evenness [J'] (right axis) between 1969 and 2000 at station WB. Dotted lines indicate missing years. The value from '91 (in brackets) is based on a single grab.

During the period from '92 to '96 the highest diversity values are reached up to a maximum of 4.6 in '94 and '95. Evenness stays in '96 at the same high level of 0.8 like in the preceding three years while the species density declines resulting in small decline of H'. The major decrease of H' to 2.4 and 1.5 follows in '97 and '98/'99 respectively. A recovery of H' and J' to a level comparable to about the minimal values of the remaining period (H': 3.1; J': 0.5) appears in 2000.

4.4.3.2.2 Community development

The multivariate community analysis of the complete time series at WB indicates results in an MDS plot with one big cloud of points and several clear outliers (Fig. 4.4.15).

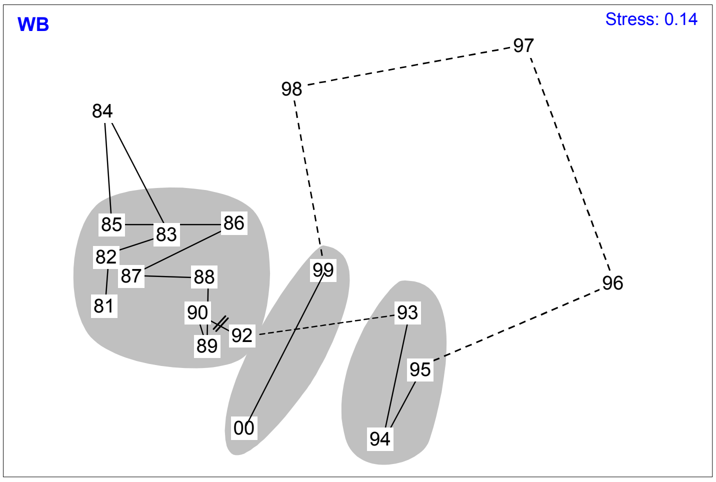

Fig. 4.4.15: Community development at WB between 1981 and 2000. MDS-plot based on Bray-Curtis similarity of 4th root transformed densities [m^{-2}]. Consecutive years are connected by lines. Broken lines indicate major shifts in the community. Shaded areas indicate groups separated by cluster analysis (group average). The sample from 1991 (one grab) is excluded.

The relatively low stress value indicates a good presentation of the similarity matrix, which is supported by the results from the cluster analysis indicated by the shaded areas on the MDS. Within the larger cloud, three subgroups are distinguished by the cluster analysis. All years from 1981 until '92 form the largest group ("80ies) followed by a smaller groups containing the years '93-'95 ("90ies") and a third group of '99/2000 ("99ies") in between the first two groups. 1984 is separated from the rest of the 80ies and '96 – '98 are isolated at larger distance.

4.4.3.2.3 Changes in community composition

Also at WB the difference between the designated groups is based on a large number of species, each contributing a small part. 50% of the dissimilarity between the 80ies and the mid-90ies is based on 32 species. The largest share of theses differences are due to the lower densities of *Mysella bidentata* decreasing from 532 ind./m² to 13 ind./m² and *Amphiura filiformis* decreasing from an average of 1413 ind./m² to 117 ind./m² (Tab. 4.4.4).

Tab. 4.4.4: Dominant species at WB and mean density and presence during the groups of years including the main species responsible for differences between them (SIMPER). Mean: ind./m²; SD: standart deviation; Pres.: % of years when the species was found.

	Total density		Pres.	Mean of period $[m^{-2}]$			Presence [%]		
Species Name	Mean	SD	[%]	80ies	90ies	99ies	80ies	90ies	99ies
Amphiura filiformis	1234	1072	100	1413	117	2728	100	100	100
Amphiuridae juv.	269	670	30	79	0	1146	30	0	50
Ophiuridae juv.	89	177	75	69	38	103	70	100	100
Ophiura albida	24	28	85	32	9	2	90	100	50
Echinocardium cordatum	20	21	95	21	19	13	90	100	100
Mysella bidentata	321	413	95	532	13	354	100	67	100
Corbula gibba	80	103	100	78	118	180	100	100	100
Hyala vitrea	61	92	75	83	30	16	80	100	100
Cylichna cylindracea	57	44	90	65	24	100	100	100	100
Nucula nitidosa	56	53	100	68	26	41	100	100	100
Nucula spp. juv.	55	117	90	56	7	256	100	100	100
Euspira pulchella	15	27	75	3	15	14	60	100	100
Abra spp.	12	15	80	8	12	10	70	100	100
Montacuta ferruginosa	12	17	80	9	7	8	80	67	100
Chamelea gallina	12	16	85	15	15	11	80	100	100
Vitreolina philippi	12	17	75	16	1	24	90	33	100
Pholoe minuta	244	263	100	351	57	262	100	100	100
Levinsenia gracilis	34	48	75	65	7	0	90	100	0
Nephtys spp. juv.	33	27	90	48	11	24	100	100	100
Oweniidae	31	45	75	52	3	5	90	33	100
Pectinaria auricoma	25	43	75	43	1	7	100	33	50
Chaetozone setosa	23	30	70	40	0	4	90	0	100
Diplocirrus glaucus	19	20	90	30	3	20	100	67	100
Lumbrineris spp.	18	15	100	29	9	7	100	100	100
Glycera spp.	15	18	80	26	4	3	90	100	100
Nephtys hombergii	13	10	100	12	11	15	100	100	100
Goniada maculata	9	6	95	10	5	2	90	100	100
Diastylis spp.	61	96	85	112	3	20	100	67	100
Harpinia crenulata	35	63	60	43	59	0	60	100	0
Harpinia antennaria	33	36	95	22	79	25	100	100	100
Eudorella truncatula	24	32	90	31	13	36	90	100	100
Callianassa subterranea	12	9	95	15	11	12	100	100	100
Eudorella emarginata	9	12	75	15	4	1	90	67	50
Nemertini	24	25	95	35	12	17	90	100	100
Phoronis spp.	24	33	65	28	11	71	50	100	100

Most of the dominant species like *Pholoë minuta*, Oweniidae, *Pectinaria auricoma*, *Diastylis* spp, *Eudorella* spp. and Nemertini are also present in lower densities in the mid-90ies except for *Harpinia crenulata* and *H. antennaria* reaching much higher densities than in previous years. Densities of other species like *Nephtys hombergii*, *Echinocardium cordatum* or *Callianassa subterranea* remain constant.

1984 differs from the rest of the 80ies because of lower densities of *Mysella bidentata*, *Pholoe minuta* and a large number of other species and consequently also a lower number of species present. The density of *Amphiura filiformis* is with 1102 ind./m² not much smaller than average, and there is a relatively high number of juvenile Amphiurids (276 ind./m²) present.

The large changes in the community in 1996 are mainly due to further decreasing densities of *A. filiformis* (to 10 ind./m²) and of many more species leading to a decrease in total species number from 59 to 42 species. This decrease is however coupled to an increase in a few species e.g. juvenile *Nephtys* spp., *Abra* spp. and *Nucula nitidosa*. The following year 1997is characterised by a massive settlement of juvenile Amphiurids (2014 ind./m²) and Ophiurids (752 ind./m²), while the overall number of species further declines to 40 species, the lowest value obtained over the period of observation.

Many of the changes that occurred after 1992 are reversed in the last three years starting in '98 and leading to the last group formed by '99 and 2000. *A. filiformis* reaches high densities of over 2000 ind./m² again. Also the number of species reaches high values of 60 spp. again and the overall density of organisms increases strongly. This is mainly caused by rising densities of several mollusc species like *M. bidentata*, *C. gibba*, *Nucula* spp., *Cylichna cylindracea* and *Vitreolina phillipi* that reach in 2000 exceptionally high densities. But also *Diastylis* spp., *Eudorella truncatula* or *Phoronis* spp. reach high densities in these last two years. At the same time the density of *Harpinia* spp. is lower than during the mid-90ies again and *Ophiura albida, Levinsenia gracilis*, Oweniidae, or *Pectinaria auricoma* stay at low densities.

4.4.3.2.4 Selected species

A couple of species have been selected that represent patterns in their temporal development, which are roughly followed by several other species. They stand as examples to explain the development of the community.

Amphiura filiformis is the dominant species at WB during most years. From '81 until '91 it appears in densities usually above 1000 ind./m² up to more than 3000 ind./m² (Fig. 4.4.16).

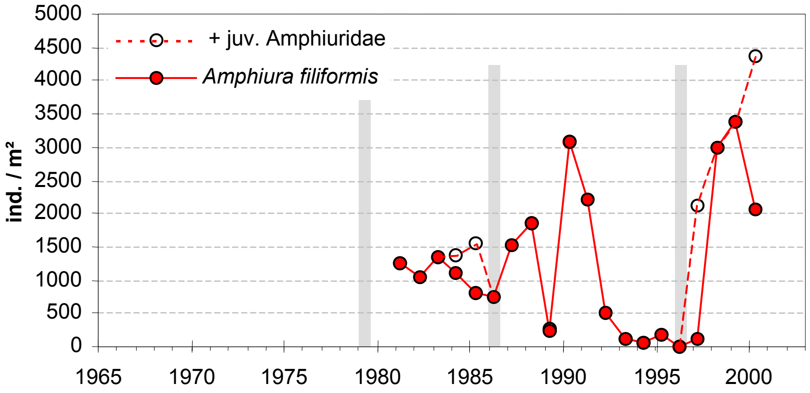

Fig. 4.4.16: Development of the density of *Amphiura filiformis* at WB; density as indivduals/m²; Vertical bars indicate cold winters; juvenile Amphiurids added *on top* of the abundance of *A. filiformis*.

In '89 the density drops dramatically from nearly 2000 ind./m² to only 240 ind./m². Another sharp drop from over 2000 ind./m² to only 518 ind./m² appears in '92. The decline continues to and a mere 116 ind./m² in '93. A recovery of high densities is initiated by a strong recruitment of juvenile Amphiurids in '97 and leads to a density of around 3000 ind./m² in '98/'99. The following decline in 2000 to just over 2000 ind./m² is accompanied by another recruitment of over 2000 ind./m² juvenile Amphiurids.

This general pattern of relatively high densities during the 80ies with a peak in '90 and a strong decline to low densities from '93 to about '97 and finally increasing densities towards 2000 is followed by *Mysella bidentata* (Fig. 4.4.17) and a number of other species like e.g. *Lumbrineris* spp. (mainly *L. latreilli*), *Diplocirrus glaucus*, *Pholoë minuta*, *Phoronis* spp., *Callianassa subterranea*, *Cylichna cylindracea* or *Vitreolina phillippi* (Annex Fig. A.7.2.1+2).

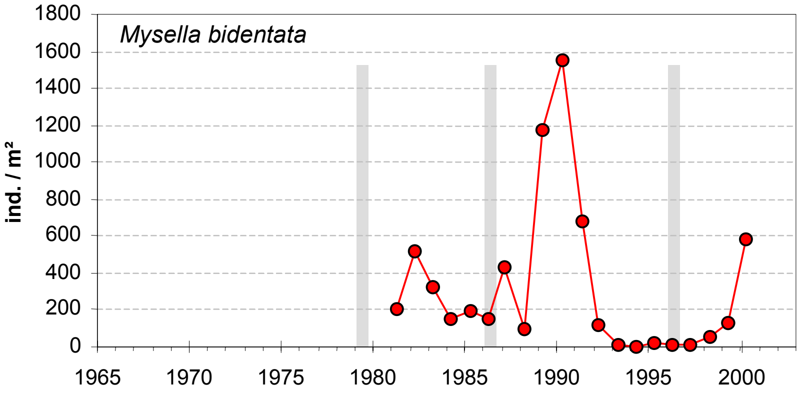

Fig. 4.4.17: Development of the density of *Mysella bidentata* at WB; density as indivduals/m². Vertical bars indicate cold winters.

This pattern is often (but not always) combined with strong decreases in '84, '86 and '93. *Mysella bidentata*, though at WB in much lower densities than *A. filiformis*, differs from the latter only in a remarkable density drop in '88 instead of '89 and a somewhat delayed recovery after '96, slowly rising until '99 and then stronger in 2000.

A different pattern of a peak density during the early 80ies with a declining trend during the 80ies and very low densities during the 90ies can be seen in *Glycera* spp. (mainly *G. alba* Fig. 4.4.18).

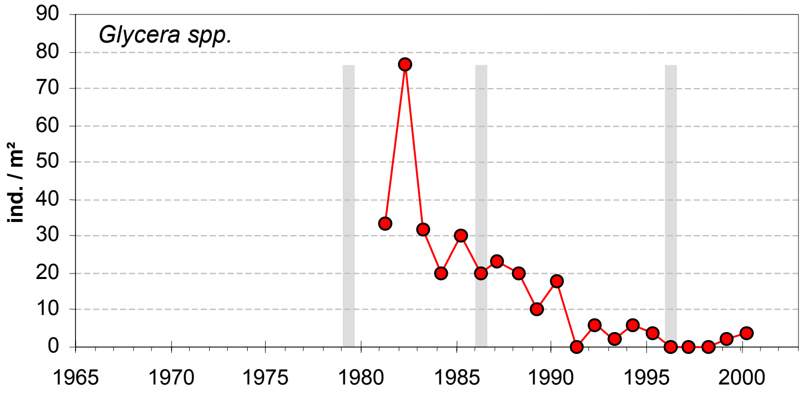

Fig. 4.4.18: Development of the density of *Glycera* spp. (mainly *G. alba*) at WB; density as individuals/m². Vertical bars indicate cold winters.

This general pattern is shared by other polychaetes like Oweniidae (mainly *O. fusiformis*), *Chaetozone setosa, Levinsenia gracilis* or *Pectinaria* spp. (mainly *P. auricoma),* by the

Cumaceans *Diastylis* spp. (mainly *D. bradyi*) and *Eudorella* spp. (mainly *E. truncatula*) and by Nemertini (Fig. A.7.2.3+4).

Echinocardium cordatum shows peak abundances of over 60 ind./m² in '90 and '98 and especially low densities in '84, '93, '96 and 2000, a pattern shared by *Montacuta ferruginosa* (Fig. 4.4.19 & Fig. 4.4.20).

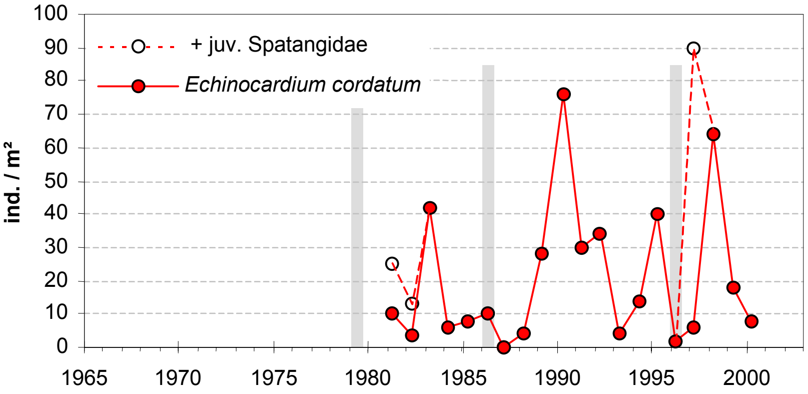

Fig. 4.4.19: Development of the density of *Echinocardium cordatum* at WB; density as individuals/m². Vertical bars indicate cold winters; juvenile Spatangidae added *on top* of the abundance of *E. cordatum*.

The development is though not always in parallel. Unlike *E. cordatum*, *M. ferruginosa* is absent in '91 and '95 and reaches its maximum density of nearly 60 ind./m² in '92 (Fig. 4.4.20).

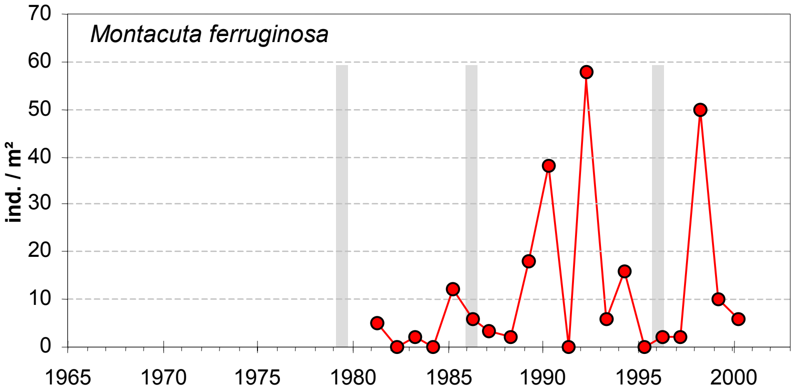

Fig. 4.4.20: Development of the density of *Montacuta ferruginosa* at WB; density as individuals/m². Vertical bars indicate cold winters.

A different pattern again is followed by *Harpinia* spp. (mainly *H. antennaria* and, especially in '81/'82, *H. crenulata* plus low densities of *H. pectinata* during the 90ies). It is present in densities above 200 ind./m² in '81/'82, then declines to below 20 ind./m² between '83 and '87, then increases again to another peak density of nearly 300 ind./m² in '94 and declines again to densities below 40 ind./m² during the late 90ies (Fig. 4.4.21).

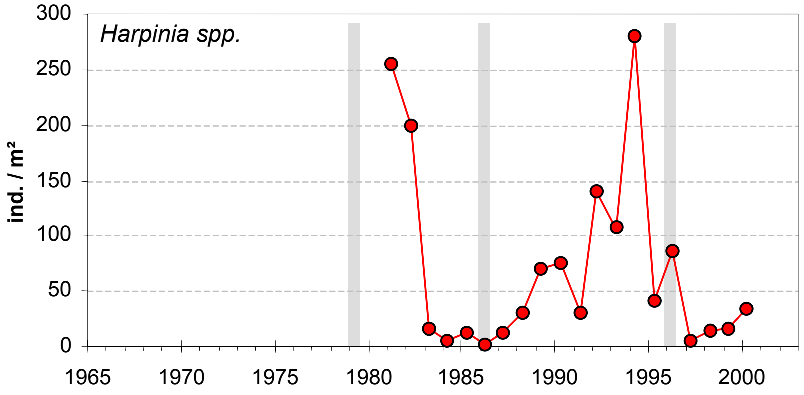

Fig. 4.4.21: Development of the density of *Harpinia* spp. at WB; density as individuals/m². Vertical bars indicate cold winters.

The density of *Nucula nitidosa* is always below 50 ind./m² except for '86 (66 ind./m²), '90/'91 (130/250 ind./m²) and '96 (88 ind./m²) (Fig. 4.4.22). Remarkable densities of juvenile *Nucula* spp. are found during the late 80ies (up to 150 ind./m²) and in 2000 (over 500 ind./m²).

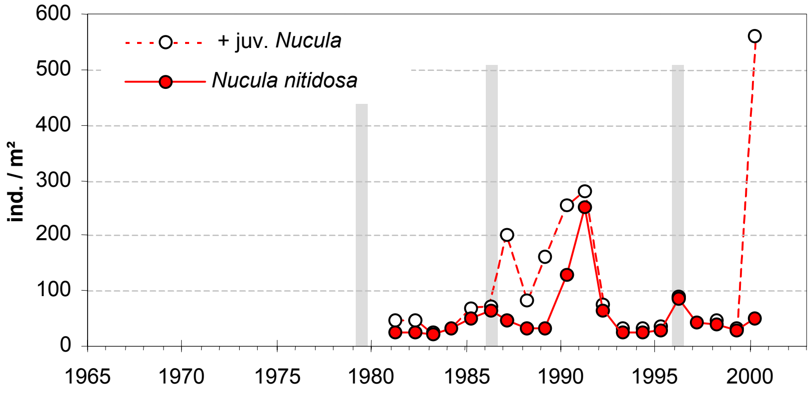

Fig. 4.4.22: Development of the density of *Nucula nitidosa* and additional juvenile *Nucula* spp. at WB; density as individuals/m². Vertical bars indicate cold winters.

Other species mentioned in the description of the community at WB often exhibit very large inter-annual variability interfering with the distinction of any longer-term pattern. Some of the more common species are shown in the annex (Fig. A.7.2.5).

4.4.3.3 Slt

As might be expected from its position in the innermost part of the German Bight in front of the river mouths of Elbe and Weser and the muddy sediments, the benthic community at Slt is the poorest and most variable of all investigated stations. The revised species list contains 89 taxa (mostly species, some genera or higher taxa), consisting of 39% polychaetes, 30% crustaceans, 18% molluscs, 7% echinoderms and 6% belonging to various other phyla (details in Annex A.1).

4.4.3.3.1 Sum parameters

During the early 70ies the total density is fairly constant at around 1000 ind./m² with the exception of '72 and '76 when only 150 ind./m² were found (Fig. 4.4.23).

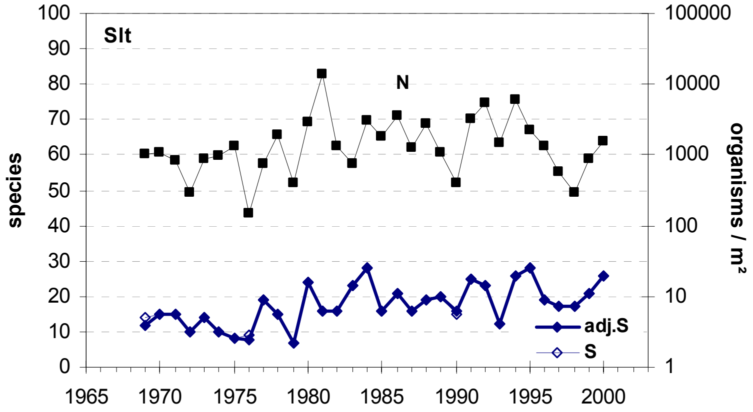

Fig. 4.4.23: Development of the number of species (left axis) and the total number of organisms (right axis) between 1969 and 2000 at station Slt; S: raw number of species found; adj.S: number of species adjusted for sampling effort [0.5 m^{-2}] (using percentages from chapter 5.3.2); N: total number of organisms [m^{-2}].

In '81 the overall maximum density is reached with 13900 ind./m². During the mid-80ies to mid-90ies, the total density of organisms fluctuates around 2000 ind./m² including a pronounced drop to only 392 ind./m² in '90 and peaks of nearly 6000 ind./m² in '92 and '94. Starting in '96, the total density decreases until '98 to only 290 ind./m² and then starts to increase again to 1574 ind./m² in 2000.

The total number of species (0.5 m^{-2}) does not follow the same pattern. Compared to the other stations, it is very low and variable. During the 70ies it never reaches 20 spp. and stays even below 15 species until '76. Lowest numbers are reached in '75/'76 (8 spp.) and '79 (7 spp.). The species density rises towards the 80ies and stays above 16 species from '80 onwards with the exception of 1993 (12 spp.). Peak values of 28 species are reached in '84 and '95. The strongest decreases are found in '79, '85, '93 and '96.

Diversity as measured by H' closely follows evenness (J') just with larger values (Fig. 4.4.24). Peak values of around 3.0 are reached in '77 and during the late 90ies.

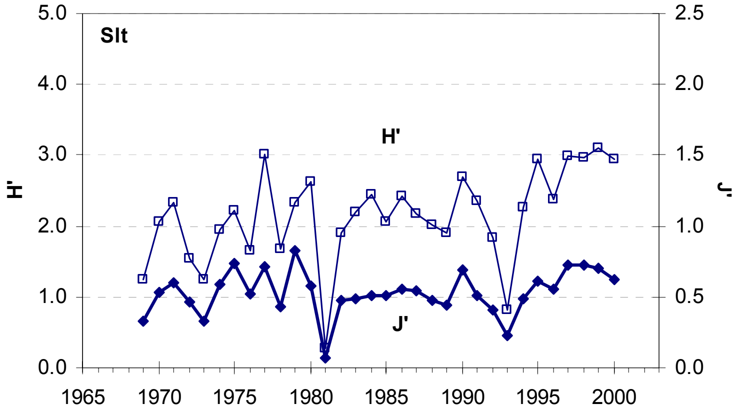

Fig. 4.4.24: Development of diversity [H'] (left axis) and evenness [J'] (right axis) between 1969 and 2000 at station Slt.

Evenness fluctuates between 0.3 and 0.8 during the 70ies. It drops to the lowest value of 0.07 in '80 due to an extreme dominance of *Diastylis* spp. and then stays at around 0.5 for most of the 80ies. In '93 another sharp drop to 0.25 is caused by a high dominance of *Nucula nitidosa*, followed by an increase to values around 0.7 during the late 90ies. Parallel to this the diversity rises from its second lowest value (0.9) and reaches in the late 90ies higher values than during most of the time series.

4.4.3.3.2 Community development

Although the time series from Slt is the most continuous series without missing years and with less changes of the sampling gear, the community analysis distinguishes no obvious groups (Fig. 4.4.25).

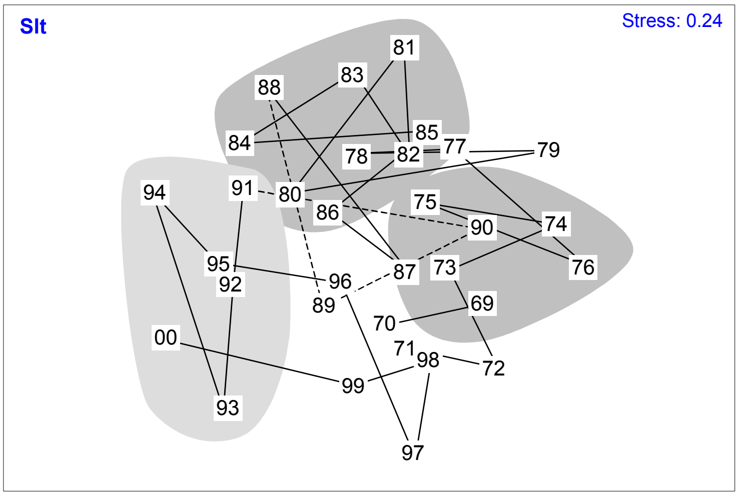

Fig. 4.4.25: Community development at Slt between 1969 and 2000. MDS-plot based on Bray-Curtis similarity of 4th root transformed densities $[m^{-2}]$. Consecutive years are connected by lines. Broken lines indicate major shifts in the community. Shaded areas indicate larger groups of higher similarities.

On the MDS-plot all years form one big cloud without a clear structuring or extreme years and with a high stress value of 0.24. Within this big cloud, some sub-clouds can be designated that comprise certain periods.

The first group comprises mainly the first half of the 70ies until '76. 1970 - '72 are positioned at the periphery of this group towards the centre of the total cloud.

The second group consists of '77 to '88 with '79 taking a prominent position closer to the early 70ies again. '86 is positioned at the edge of this group towards the centre of the plot and '87 close to the 70ies again.

The last group comprises the early 90ies from '91 until '95 and 2000.

1996 is in the centre of the plot, '97 and '98 moving out and towards the 70ies (especially '70-'72) and '99 approaching the early 90ies again. Unlike the other stations, the years '70, '71, '86 and '96 form the centre of the cloud together with '89. Only '79 is positioned at the periphery. '87 is most similar to '73 and '98.

This relatively complicated structure cannot be resolved in any meaningful way by a cluster analysis. The high stress value indicates that the relations between the samples cannot be represented very well within two dimensions. The reappearance of a similar pattern as at the other stations may however justify the definition of the groups.

4.4.3.3.3 Changes in community composition

The 70ies are characterised by a generally low number of species and low density of most species with the exception of *Nucula nitidosa* and *Ophiura ophiura* (Tab. 4.4.5). *N. nitidosa* has a lower mean density in the 80ies while most other species are more abundant, most notably *Diastylis* spp, *Abra* spp., *Nephtys hombergii* and *Pectinaria koreni*.

Tab. 4.4.5: Dominant species at Slt and mean density and presence during the groups of years including the main species responsible for differences between them (SIMPER). Mean: ind./m²; SD: standart deviation; Pres.: % of years when the species was found.

	Total density		Pres.	Mean of period [m^{-2}]			Presence [%]		
Species	Mean	SD	[%]	70ies	80ies	90ies	70ies	80ies	90ies
Nucula nitidosa	608	701	100	453	255	1570	100	100	100
Abra spp.	102	226	88	17	60	364	80	100	100
Mysella bidentata	31	79	63	7	7	130	60	56	100
Ensis directus	17	40	31	0	7	30	0	11	50
Tellina fabula	9	39	34	0	7	38	0	78	50
Spisula subtruncata	5	17	19	0	10	9	0	11	67
Montacuta ferruginosa	2	6	16	0	0	3	0	11	17
Macoma baltica	2	5	22	2	0	0	40	11	0
Diastylis spp.	767	2364	100	130	2310	266	100	100	100
Pseudocuma longicornis	10	42	31	0	30	7	0	56	67
Pariambus typicus	2	6	16	0	0	8	0	11	67
Ophiura ophiura	97	124	94	121	134	95	100	100	67
Ophiura spp. juv.	31	48	59	66	25	33	40	78	83
Ophiura albida	5	15	31	2	3	5	60	22	33
Amphiura spp. juv.	3	13	6	0	0	15	0	0	33
Nephtys hombergii	127	140	100	67	192	114	100	100	100
Owenia fusiformis	71	371	22	0	0	375	0	11	83
Scalibregma inflatum	36	149	16	0	94	50	0	22	17
Pholoe minuta	31	66	69	1	10	78	20	56	100
Pectinaria koreni	19	61	38	0	43	12	0	22	83
Phyllodoce spp.	7	16	75	2	6	17	80	67	67
Scoloplos armiger	6	11	44	0	10	1	0	78	33
Bylgides sarsi	4	7	41	0	7	0	0	56	0
Phoronis spp.	11	34	41	0	5	4	20	22	50
Echiurus echiurus	7	17	31	0	1	0	20	33	0

Towards the 90ies *N. nitidosa* increases again and becomes the most dominant species while *Diastylis* spp. decreases. Especially bivalves increase strongly in density, but also some polychaetes like e.g. *Owenia fusiformis*, *Pholoë minuta* or *Phyllodoce* spp. while other polychaetes like the most abundant ones from the 80ies e.g. *N. hombergii*, *S. inflatum* or *P. koreni* show a lower mean density in the 90ies.

4.4.3.3.4 Selected species

The characterisation of the changes between major periods by mean densities may only serve as a rough hint. For a more detailed description several exemplary species are selected.

Despite the large inter-annual fluctuations, some species exhibit rough long-term pattern. The Cumacean *Diastylis* spp. (mainly *D. rathkei*) is at Slt present in rather low densities during the early 70ies but rises to a dominant position with densities around 1000 ind./m² in most years from '78 until '88 (Fig. 4.4.26).

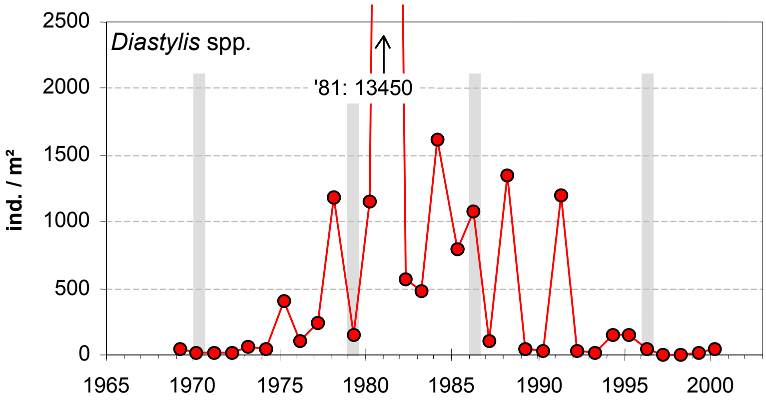

Fig. 4.4.26: Development of the density of *Diastylis* spp. at Slt; density as individuals/m². Vertical bars indicate cold winters.

The most extreme value is reached in '81 with 13450 ind./m². During the late 80ies the density declines and reaches maximum values of only slightly above 100 ind./m² during most of the 90ies.

Also *Nephtys hombergii* reaches its peak densities between '78 and '88 and *Scoloplos armiger* between '77 and '89. Peak abundances of *N. hombergii* are in most cases followed by low abundances of *S. armiger* in the following year (Fig. 4.4.27 & Fig. 4.4.28).

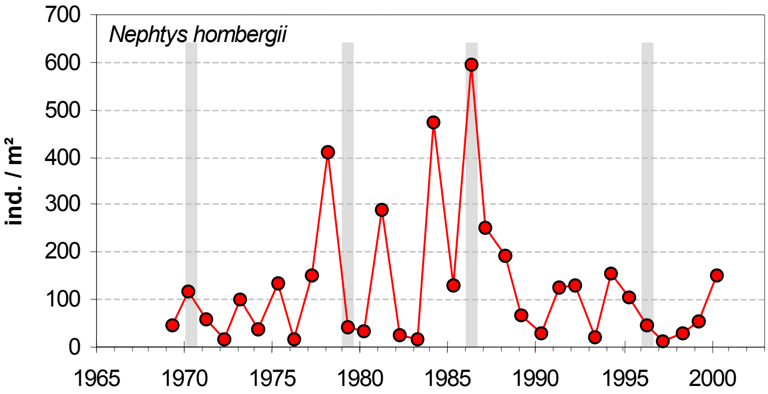

Fig. 4.4.27: Development of the density of *Nephtys hombergii* at Slt; density as individuals /m². Vertical bars indicate cold winters.

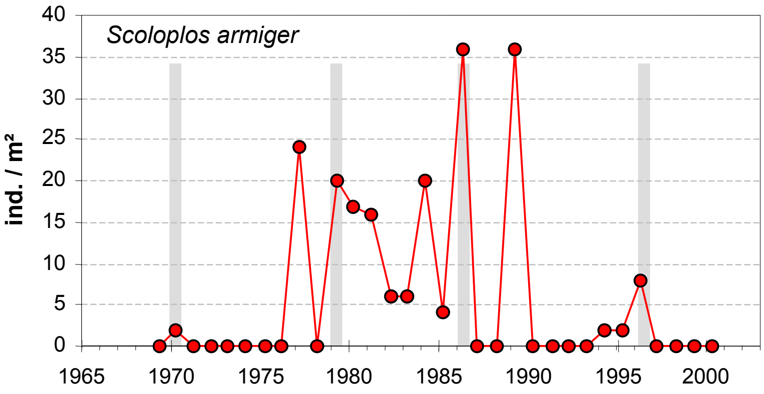

Fig. 4.4.28: Development of the density of *Scoloplos armiger* at Slt; density as individuals/m². Vertical bars indicate cold winters.

A similar tendency can be seen for *Bylgides sarsi* and Phyllodocids (mainly *P. groenlandica*) (Annex, Fig. A.7.3.1).

This is contrasted by the development of the bivalve *Nucula nitidosa* that appears in high densities of around 500 ind./m² until '75 and densities below 200 ind./m² between '76 and '84 (Fig. 4.4.29).

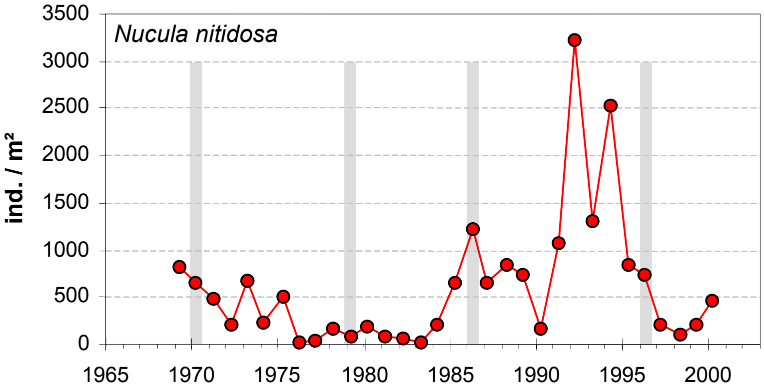

Fig. 4.4.29: Development of the density of *Nucula nitidosa* at Slt; density as individuals/m². Vertical bars indicate cold winters.

Between '85 and '96 the densities of *N. nitidosa* are mostly above 500 ind./m² up to more than 3000 ind./m² in '92, with the exception of '90 when only 162 ind./m² are found. In '97 the density of *N. nitidosa* declines again to only 113 ind./m² in '98 and then increases again towards the end of the series.

The increasing tendency during the late 80ies and early 90ies is also visible for *Abra* spp. (mainly *A. alba*) that reaches its highest densities during the early 90ies (Fig. 4.4.30).

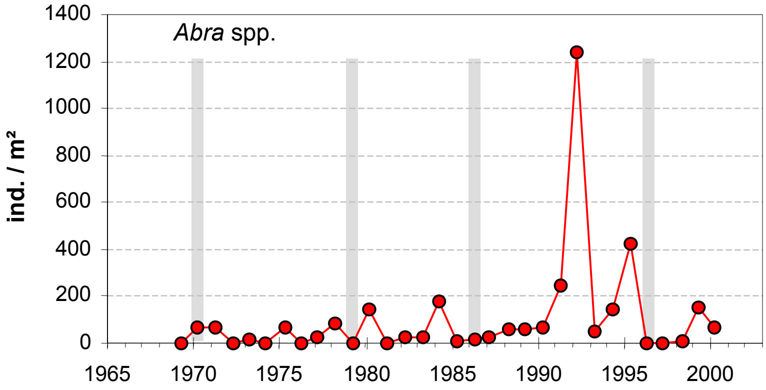

Fig. 4.4.30: Development of the density of *Abra* spp. at Slt; density as individuals/m². Vertical bars indicate cold winters.

This period of the late 80ies and early 90ies is also characterised by increasing densities of *Spisula subtruncata, Mysella bidentata, Acrocnida brachiata*, *Eudorella* spp., *Pariambus typicus* and *Pholoe minuta*, all of which decline strongly in '96/'97 (Fig. A.7.3.1+2)

Echiurus echiurus reaches high densities only in single years, amongst these '70/'71, '80, '86 and '96-'98. The density of *E. echiurus* already declines during the year following its appearance (Fig. 4.4.31).

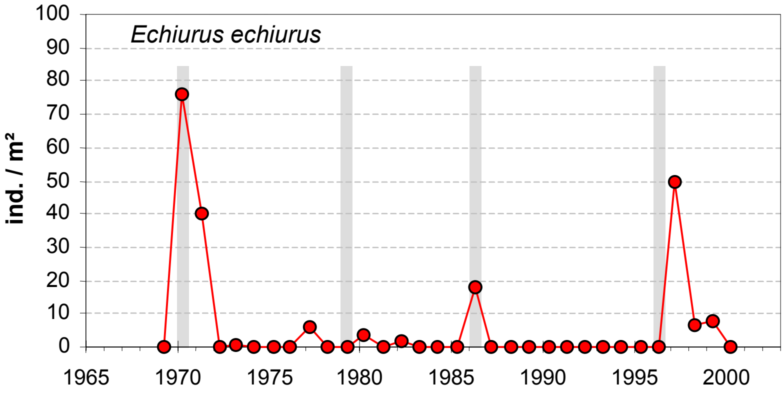

Fig. 4.4.31: Development of the density of *Echiurus echiurus* at Slt; density as individuals/m². Vertical bars indicate cold winters.

A couple of species exhibit a similar pattern as they appear in few years and reach high densities like the cumacean *Pseudocuma longicornis* ('84), the polychaetes *Scalibregma inflatum* ('80), *Pectinaria koreni* ('80) and *Owenia fusiformis* ('94) or *Phoronis* spp. ('99) while playing a minor role during the rest of the period of investigation (Fig. A.7.3.3).

Although it was recorded at Slt occasionally already in 1979 and '82 (autumn data not presented here) *Ensis directus* appears in the spring samples for the first time in '84.

Only single individuals are found until '95 when the density of *E. directus* increases to 170 ind./m². This high density declines again during the following years to only 7 ind./m² in 2000 (Fig. 4.4.32).

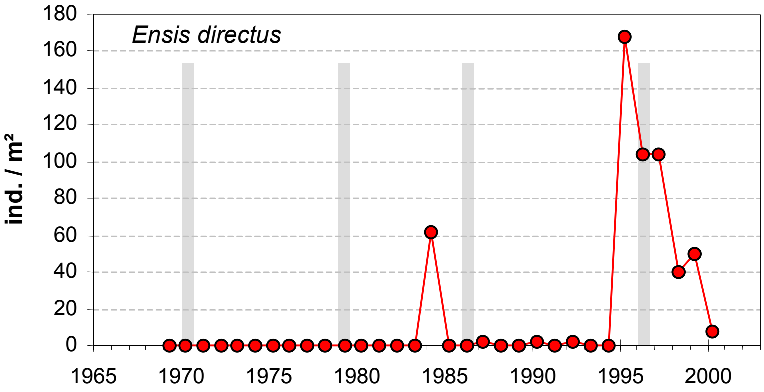

Fig. 4.4.32: Development of the density of *Ensis directus* at Slt; density as individuals/m². Vertical bars indicate cold winters.

Most other species are too rare or variable to distinguish a long term trend. Some of the more common species, such as *Phoronis* spp., *Ophiura ophiura*, *Montacuta ferruginosa* and *Nephtys hombergii* are shown in the annex (A.7.3.4).

4.3.3.4 FSd

Indicated already by the coarser sediment prevailing at the FSd station, the benthic community is adapted to higher current speeds and more variable conditions and is often dominated by opportunistic species. The revised species list contains 132 taxa, consisting of 39% polychaetes, 24% crustaceans, 24% molluscs, 5% echinoderms and 8% belonging to various other phyla (details in Annex A.1).

4.3.3.4.1 Sum parameters

At FSd the total density of organisms is relatively low during the early 70ies with less than 2000 ind./m² until '76 except for '73. From '77 onwards the total density fluctuates widely around a mean of about 3000 ind./m² (Fig. 4.3.33).

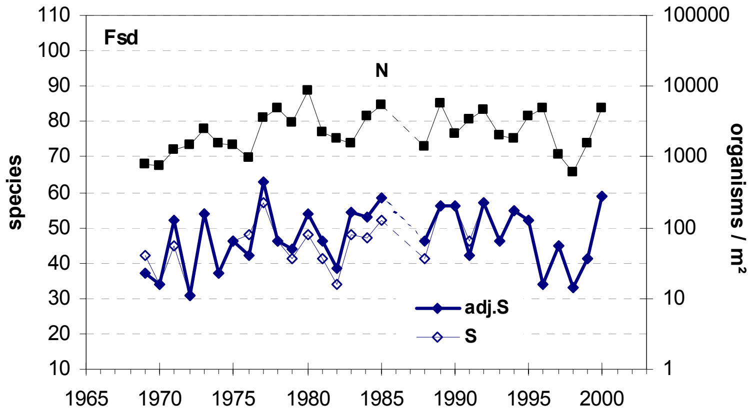

Fig. 4.3.33: Development of the number of species (left axis) and the total number of organisms (right axis) between 1969 and 2000 at station FSd; S: raw number of species found; adj.S: number of species adjusted for sampling effort [0.5 m^{-2}] (using percentages from chapter 5.3.2); N: total number of organisms [m^{-2}]. Dotted lines indicate missing years.

From the late 70ies onwards, peak densities of 5000 to 6000 ind./m² are reached every two to four years. The highest total density is reached in 1980 when nearly 9000 organisms are found per m². Minimum total densities of the 80ies and 90ies with less than 1000 ind./m² are reached in '97 and '98.

The total species density reaches its lowest values down to 30 species (0.5 m^{-2}) during the early 70ies, then fluctuates between 40 and 60 from '75 to '95. It decreases in '96 and '98 to 33 and 32 species respectively and finally reaches its maximum measured value of 59 species in 2000. Fluctuations of species density are often in parallel to the development of the total density of organisms but not always. Peak species densities are reached at high organism densities in '85, '89, '92 and 2000. Other years like '77, '90 and '94 show high species densities at rather low organism densities whereas in '96 the total number of organisms is quite high while the number of species is very low.

Diversity and evenness fluctuate widely but without a long-term trend. Diversity as measured by H' varies at a higher level but very much in parallel to the evenness (J') (Fig. 4.3.34).

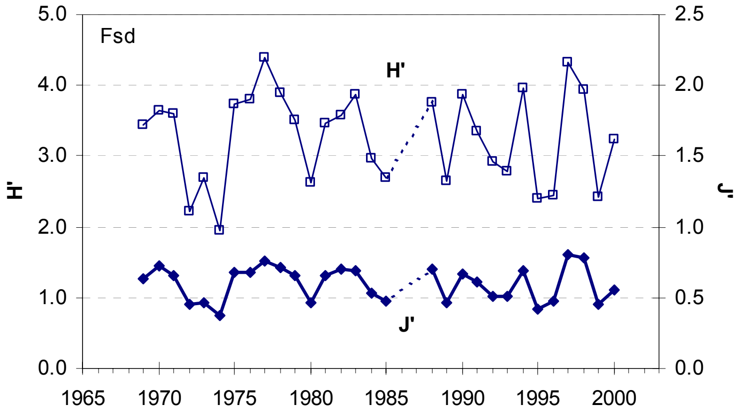

Fig. 4.3.34: Development of diversity [H'] (left axis) and evenness [J'] (right axis) between 1969 and 2000 at FSd. Dotted lines indicate missing years.

Maximum values for H' above 4.5 are reached in '77 and '97 and minimum values below 3.0 are attained in the years of low evenness. Species density seems to play only a subordinate role for the value of H'.

Variations of J' reflect the changes in dominance structure. Values below 0.5 are reached in years when single species dominate the community like '72-'74 (*Magelona*, *Phoronis*), '80 (*Spiophanes*, *Magelona* and opportunistic polychaetes), '85 and '95/'96 (*Phoronis*) and '99 (*Magelona*) (see chapter 4.3.3.4.4). During most of the other years evenness values lie between 0.7 and 0.8 (Fig. 4.3.34).

4.3.3.4.2 Community development

The MDS-plot for the community development at FSd shows that a clear grouping of years is hard to distinguish. Early years from 1969 until '73 are grouped together ("70ies") with a change occurring in '74 (Fig. 4.3.35).

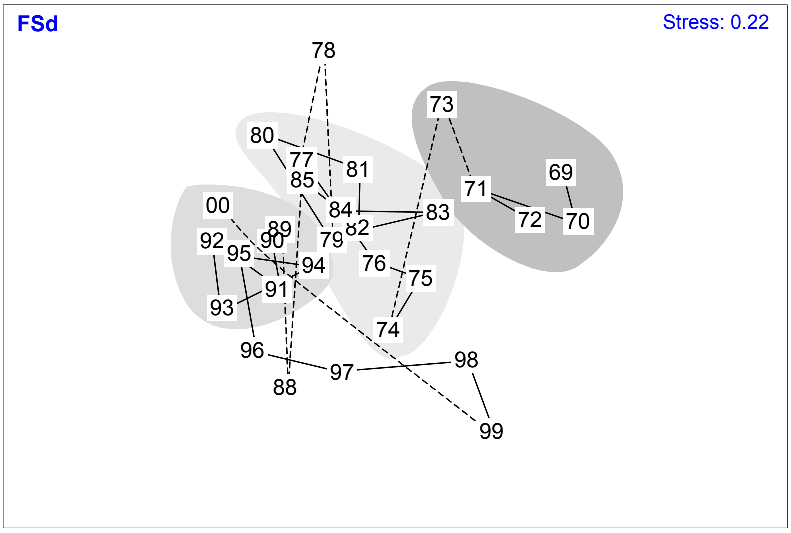

Fig. 4.3.35: Community development at FSd between 1969 and 2000. MDS-plot based on Bray-Curtis similarity of 4th root transformed densities [m^{-2}]. Consecutive years are connected by lines. Broken lines indicate major shifts in the community. Shaded areas indicate larger groups of higher similarities.

The following two years a transition towards the "80ies" situation appears, that lasts until '85. '83 is somewhat similar to the early 70ies and '97/'98 but still belongs to the 80ies group.

1986 and '87 are missing and '88 marks a strong change initiating a transition towards the early 90ies. The "90ies" group comprise the period from '89 until '95 and 2000.

During the 80ies, two years show an extreme position: '78 and '88.

After the cold winter of '95/'96, the community becomes more similar to the '88 situation and then to the mid-70ies group, while 2000 lies amidst the early 90ies again.

'99 takes a prominent position as it cannot be appropriately located on the MDS, its most similar years are '98, '75 and '91, and it represents a transition back towards the early 90ies situation already.

The cluster analysis mingles the 80ies and 90ies but supports the separation of the early 70ies. It does also separate all of the extremes identified on the MDS and groups '79 and '96 together, as in fact '79 is the most similar year to '96 at Slt (BC=72.1).

4.3.3.4.3 Changes in community composition

The early 70ies are characterised by low mean densities of most species. Most prominent increases towards the 80ies are those of *Magelona mirabilis* and *M. minuta*, of *Tellina fabula*, *Spiophanes bombyx*, *Scoloplos armiger* and many other polychaetes (Tab. 4.3.6).

Tab. 4.3.6: Dominant species at FSd and mean density and presence during the groups of years including the main species responsible for differences between them (SIMPER). Mean: ind./m²; SD: standart deviation; Pres.: % of years when the species was found.

	Total density		Pres.	Mean of period [m^{-2}]			Presence [%]		
Species	Mean	SD	[%]	70ies	80ies	90ies	70ies	80ies	90ies
Magelona mirabilis	850	748	100	382	947	1040	100	100	100
Spiophanes bombyx	228	766	97	140	449	64	100	92	100
Scoloplos armiger	92	128	100	35	141	58	100	100	100
Magelona minuta	70	140	57	0	96	130	0	83	71
Nephtys hombergii	67	76	100	22	99	68	100	100	100
Chaetozone setosa	40	40	100	22	63	25	100	100	100
Owenia fusiformis	32	61	83	48	25	58	100	83	100
Goniada maculata	26	29	100	20	40	15	100	100	100
Spio filicornis	25	80	90	8	54	7	100	100	100
Capitellidae	20	42	80	7	27	15	60	92	86
Eteone longa	16	30	80	5	28	7	40	92	100
Phyllodocidae	10	23	83	5	18	2	100	92	71
Scolelepis bonieri	10	16	77	0	13	13	20	83	86
Lanice conchilega	9	14	63	3	6	15	60	58	71
Pholoe minuta	8	14	73	2	6	18	80	75	71
Glycinde nordmanni	8	20	67	26	6	3	100	75	71
Sthenelais limicola	6	7	70	8	3	12	100	58	100
Tellina fabula	193	155	100	26	291	141	100	100	100
Montacuta ferruginosa	26	28	93	2	39	23	60	100	100
Chamelea gallina	13	22	90	4	25	6	100	100	86
Euspira pulchella	12	13	80	16	15	13	100	83	100
Mysella bidentata	11	14	73	2	16	9	40	83	86
Spisula subtruncata	7	15	50	0	2	21	20	42	57
Phaxas pellucidus	5	8	57	5	5	2	100	42	43
Phoronis spp.	518	765	90	294	251	1123	80	83	100
Edwardsia spp.	69	146	93	30	116	46	100	92	100
Nemertini	53	55	97	44	53	67	100	92	100
Urothoe poseidonis	76	91	97	10	89	52	80	100	100
Bathyporeia elegans	41	50	83	26	62	19	80	100	71
Bathyporeia guilliamsoniana	27	38	87	13	13	30	60	83	100
Perioculodes longimanus	23	22	90	3	29	33	80	100	100
Ampelisca brevicornis	11	12	93	13	16	3	100	92	86
Synchelidium haplocheles	9	14	63	0	11	17	20	67	100
Batyporeia spp.	8	18	30	0	0	22	0	0	86
Ophiura albida	43	63	100	95	56	13	100	100	100
Ophiura spp. juv.	25	42	63	0	16	43	0	50	100
Echinocardium cordatum	16	20	100	4	20	18	100	100	100

The mean densities of *Edwardsia* spp. and most amphipods also increase while those of *Ophiura albida* and *Glycinde nordmanni* decrease.

During the 90ies, the mean density of many polychaetes is lower again with the exception of *Magelona* spp. that remain at about the same level and *Owenia fusiformis* that even increases in density. The density of most bivalves decreases except for *Spisula subtruncata*, which reaches a higher mean density during the 90ies. Most prominent is the strong increase of the mean density of *Phoronis* spp.. The mean density of most amphipods is in the 90ies very similar to the 80ies with the exception of *Bathyporeia* spp. that reach a higher mean density. *Edwardsia* spp. return to the same mean density as during the 70ies while *O. albida* further declines to an even lower mean density.

4.3.3.4.4 Selected species

The dominant species at FSd are small opportunistic worms, in most cases *Magelona mirabilis* (Fig. 4.3.36). The density of *M. mirabilis* reaches its maximum of over 3000 ind./m² in '85, further peaks occur in '80, '92 and 2000 with over 2000 ind./m².

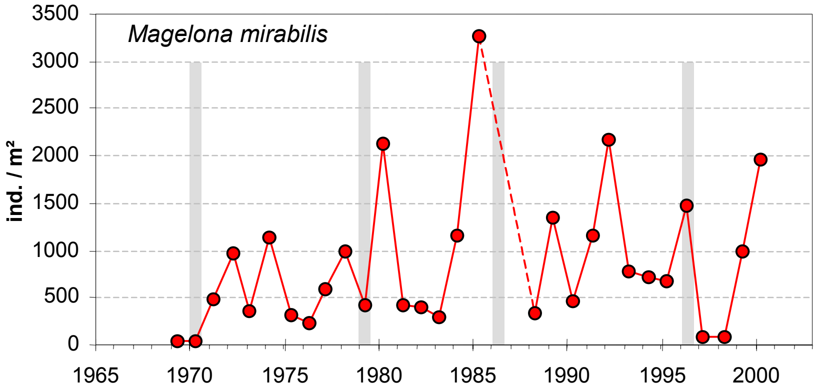

Fig. 4.3.36: Development of the density of *Magelona mirabilis* at FSd; density as individuals/m². Broken lines indicate missing years. Vertical bars indicate cold winters.

During most of the remaining years *M. mirabilis* is present in densities fluctuating between 300 and 1200 ind./m² while extremely low densities below 100 ind./m² occur in 1971/'72 and '97/'98.

In few years some other opportunistic species reach very high densities like e.g. *Spiophanes bombyx, Spio filicornis*, *Owenia filiformis* or *Phoronis* spp. (Fig. A.7.4.1).

Large inter-annual fluctuations of the densities of these species make a clear distinction of consistent periods rather difficult. Nevertheless some rough pattern are visible for a couple of species, allowing a description of some longer-term aspects of the development of the community.

A number of bivalve species exhibits a general pattern of peak densities during the late 70ies and early 80ies as exemplified by *Tellina fabula*, after the polychaetes one of the most dominant species at the FSd station. It occurs in rather low densities well below

100 ind./m² until '74. It then rises strongly and reaches peaks of nearly 600 ind./m² during the period from '75 to '85, with the exception of '79 when it declines to 150 ind./m² (Fig. 4.3.37).

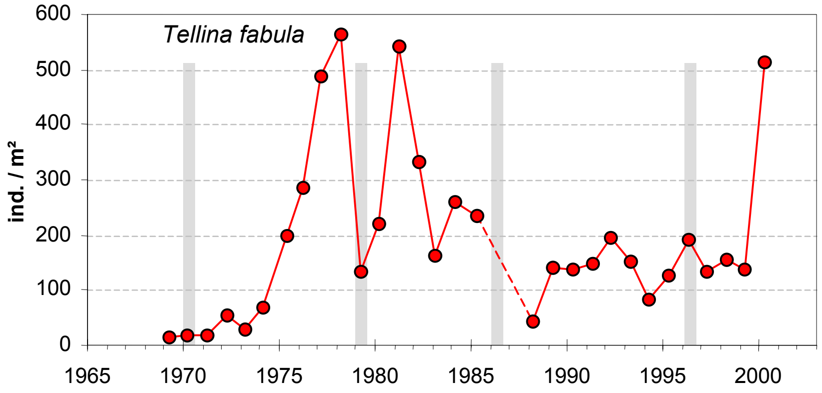

Fig. 4.3.37: Development of the density of *Tellina fabula* at FSd; density as individuals/m². Broken lines indicate missing years. Vertical bars indicate cold winters.

After a decrease to less than 50 ind./m² in '88 the density of *T. fabula* stays between 100 and 200 ind./m² until '99. In 2000 it reaches again a peak density of more than 500 ind./m². A similar trend can be seen in *Chamelea gallina, Mysella bidentata* and *Montacuta ferruginosa.* Like *T. fabula, M. bidentata* and *Phaxas pellucidus* reach another peak density in 2000 (Annex, Fig. A.7.4.2).

Several polychaetes exhibit a similar pattern to the molluscs described above, although for some the period of peak densities is slightly later. As an example *Chaetozone setosa* reaches peak densities between '77 and '85 (Fig. 4.3.38). During the remaining years its densities are mostly below 50 ind./m² with the exception of another peak density in '91.

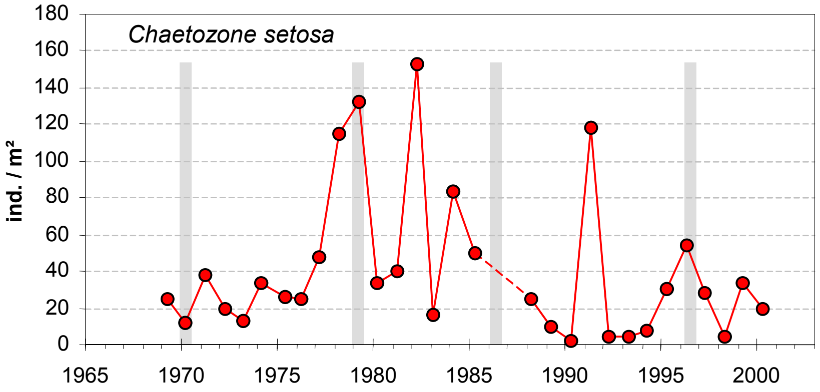

Fig. 4.3.38: Development of the density of *Chaetozone setosa* at FSd; density as individuals/m² Broken lines indicate missing years. Vertical bars indicate cold winters.

This higher frequency of high densities during late 70ies and 80ies can also be seen for Goniadidae (mainly *Goniada maculata* and *Glycinde nordmanni*), Phyllodocidae (here mainly *Eteone longa* and *Phyllodoce groenlandica*), *Nephtys hombergii* and *Scoloplos* *armiger* (Fig. A.7.4.3). As already noticed at Slt, peak densities of *N. hombergii* are followed by low densities of *S. armiger* in the next year at FSd as well.

Although highly variable in density, amphipods represent an important part of the benthic community at FSd, and several species are present throughout the period of investigation. *Urothoë poseidonis* is present in low densities in the early 70ies. It reaches a peak density of over 300 ind./m² in '75 and high densities of around 150 ind./m² during the end of the 70ies.

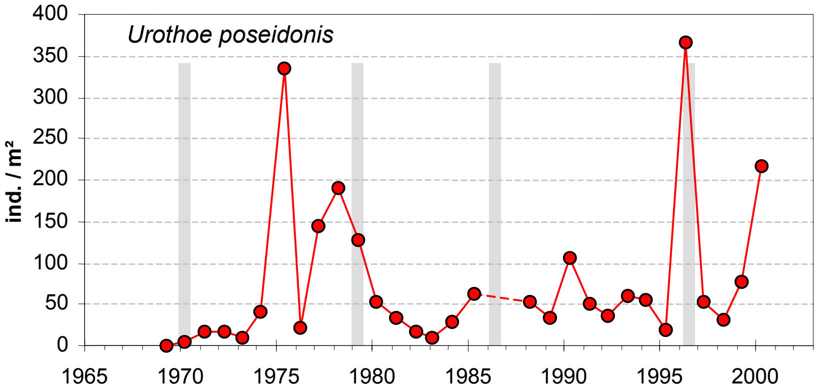

Fig. 4.3.39: Development of the density of *Urothoe poseidonis* at FSd; density as individuals/m² Broken lines indicate missing years. Vertical bars indicate cold winters.

Throughout the 80ies and up to '95 its density fluctuates around 50 ind./m², then reaches a second peak of over 350 ind./m² in '96 and finally rises again to over 200 ind./m² in 2000. The lower density during the 80ies is also visible for *Bathyporeia* spp., *Synchelidium haplocheles* and *Perioculodes longimanus,* reaching peak densities in '77 (Fig. A.7.4.4).

A slightly different pattern is apparent for *Ampelisca brevicornis*. It reaches its peak density of 60 ind./m² in '80, one year after the cold winter, then decreases to very low densities during the early 90ies and increases again in '97, one year after the cold winter of '96 (Fig. 4.3.40).

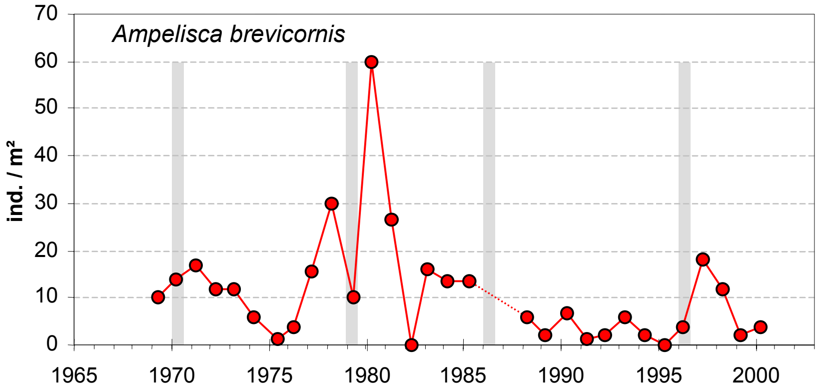

Fig. 4.3.40: Development of the density of *Ampelisca brevicornis* at FSd; density as individuals/m². Broken lines indicate missing years. Vertical bars indicate cold winters.

Ophiura albida often occurs in high densities of 50 to 150 ind./m² during the 70ies with a peak density of over 250 ind./m² in '78. During the 80ies and 90ies it is always present, but in densities below 30 ind./m² except for '92 when 60 ind./m² are reached (Fig. 4.3.41).

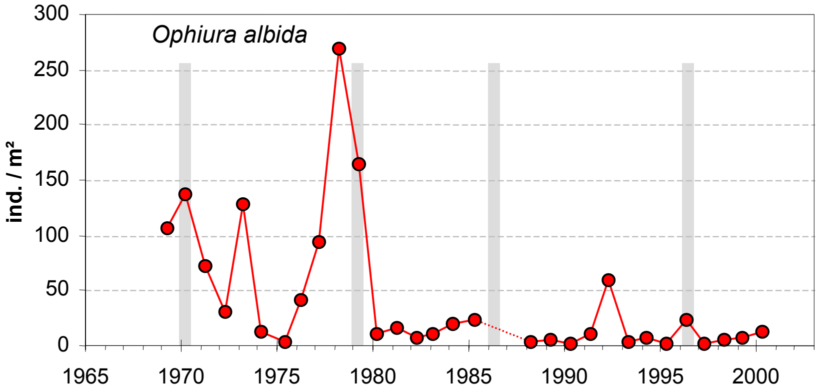

Fig. 4.3.41: Development of the density of *Ophiura albida* at FSd; density as individuals/m². Broken lines indicate missing years. Vertical bars indicate cold winters.

This peak abundance in '78 is shared by *Echinocardium cordatum* (110 ind./m²), *Scolelepis bonnieri* (85 ind./m²) and *Edwardsia* spp. (800 ind./m²), all of which never again reach comparable densities (Fig. A.7.4.5). Unlike *O. albida*, these three species have lower densities during the 70ies than during the 80ies and 90ies with stronger fluctuation during the 90ies.

Most other species are too rare or variable to distinguish a long term trend. Some of the more common species are shown in the annex (A.7.4.6).

4.4.4 Temporal autocorrelation

Inter-annual changes of the communities are not random fluctuations around some mean state but exhibit significant temporal autocorrelation for a time lag of two to three years (Fig. 4.4.4.1). The still positive correlation up to the seventh year is not significant at the 5% level.

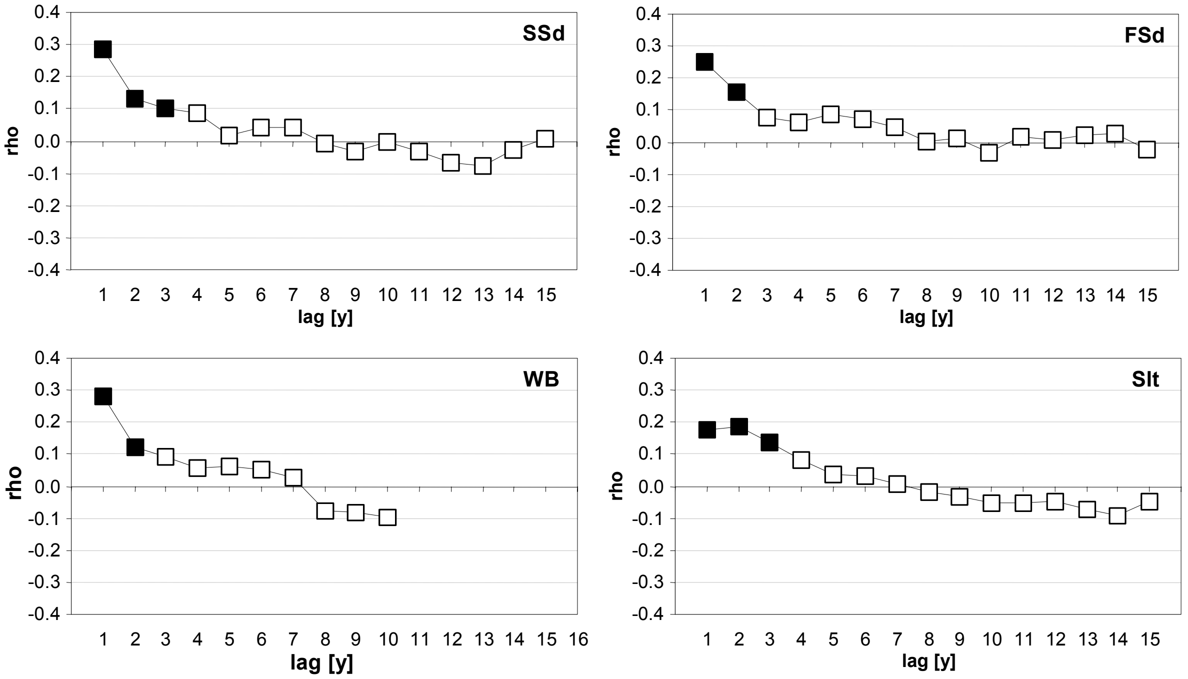

Fig. 4.4.4.1: Temporal Mantel-Correlograms using Spearman's rank correlation (rho). Filled squares indicate significant correlations; Values for larger lags based on less than 10 comparisons are omitted (e.g. lag > 10 y at WB).

The mean similarity between years is the lower, the further two samples are separated in time, up to a time lag of ten (FSd) to 14 years (Slt). The short time series at WB does not allow conclusions about longer time lags than ten years.

No significant negative correlation was found at any of the stations, which could indicate a periodic fluctuation. Although an increase of the correlation is visible for lags of 14 and/or 15 years at SSd and Slt (Fig. 4.4.4.1), this is only a minor variation which is put into perspective if the similarities for larger lags are included that continue to decrease (Annex, Fig. A.4.5). These comparisons over larger time lags are however based on very few values and therefore not reliable.

4.5 *Abiotic environmental time series*

4.5.1 Climate: The North Atlantic Oscillation Index (NAOI)

The North Atlantic Oscillation (NAO) is the dominant signal of interannual variation in the atmospheric circulation over the North Atlantic (Hurrell 1995). The winter NAO-index (Dec. – Mar.) summarises the large scale weather pattern over the north-east Atlantic region during winter. It is based on the difference of sea level pressure (SLP) between Lisbon, Portugal and Reykjavik, Iceland. The SLP anomalies were normalized by division of each seasonal mean pressure by the long-term mean (1864-1983) standard deviation. During winters with a high NAO-index westerly winds in Europe are more than 8 m/s stronger than during winters with a low NAOI. Consequently the moderating influence of the ocean results in unusually warm winter temperatures in Europe (Hurrell 1995). The long term development was given by Hurrel (1995) (Fig. 4.5.1).

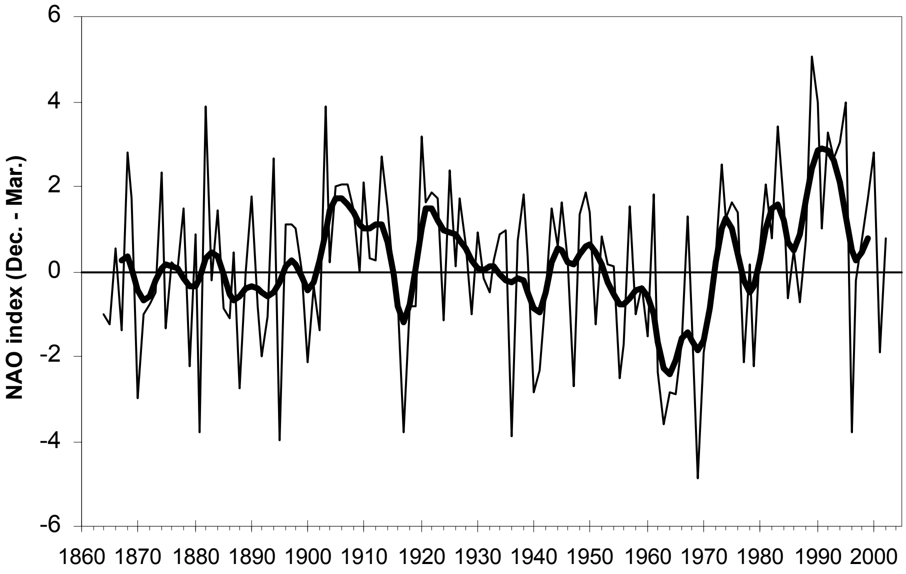

Fig. 4.5.1: Long term development of the winter NAO-index (Dec. – Mar.) 1864 - 2002; The heavy solid line represents the NAOI smoothed with a low-pass filter with seven weights (1,3,5,6,5,3,1) to remove fluctuations with periods less than 4 years; [data from J. Hurrel (extended from Hurrell 1995)].

Compared to the long-term development of the NAOI, the start of the benthos time series in 1969 was at the end of a prolonged phase of a predominantly negative NAOI. For most of the period of the benthos time series, the NAOI was above its long term mean.

During the period of the present investigation, an increasing tendency can be seen towards the early 90ies (Fig. 4.5.2).

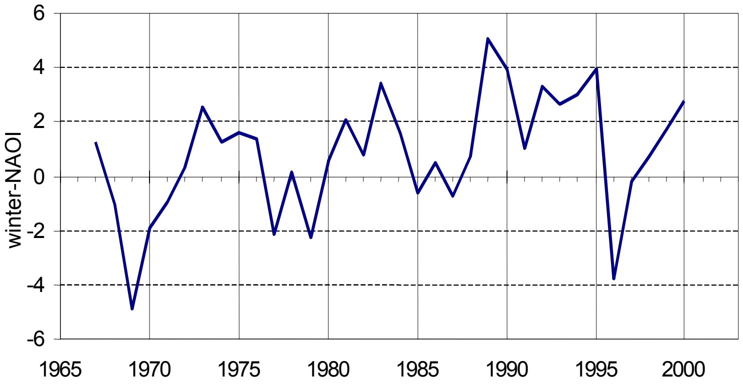

Fig. 4.5.2: Winter NAO-index 1967 – 2000.

Large negative values are reached from '68 to '71, in '77 and '79 and then again in '96. The values observed in '69 and '96 are amongst the lowest of the last 150 years (Fig. 4.5.1).

The longest period of a positive NAOI is between '88 and '95. Shorter periods appeared from '72 to '76 and again from '80 to '84 though mostly at a lower level than in the early 90ies. After the extremely low value from '96, the NAOI rose again to a high positive value in 2000.

4.5.2 Water temperature

The mean water temperature at Helgoland during winter (Dec. – Mar.) varies between 3 °C and nearly 7 °C (Fig. 4.5.3).

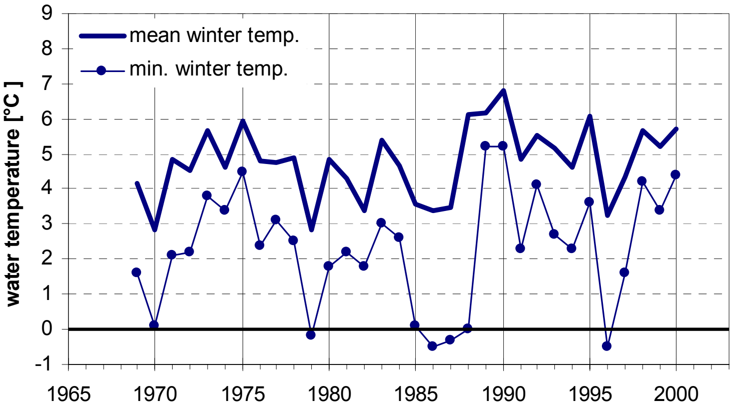

Fig. 4.5.3: Mean and minimum water temperature between December and March at Helgoland (BAH-data).

Cold winters with mean water temperatures below 3.5 °C were observed in 1970, '79, '82, '85-'87 and in 1996. Prolonged periods with mean temperatures above the average of 4.7 °C were observed between '71 and '78 and then again from '88 until '95.

This pattern is reflected in the minimum water temperatures with a slightly different emphasis. Minimum temperatures of 0 °C and below were observed in 1970, '79, '85 – '88 (!) and '96. The minimum water temperature in '82 was not lower than average, but in '88 a minimum temperature of 0 °C was reached although the mean winter temperature was well above average. Judged by the minimum temperature, the severest winters were those of '86 and '96 followed by '87 and the '79.

The mean water temperature during summer (Jul. - Sep.) varies between 15 and 17.5 °C (Fig. 4.5.4). Highest mean water temperatures were reached in 1974, '76, '83/'84, '92/'93, '95/'96, '98 and 2000. Lower than average temperatures were recorded in '79/'80 and between '85 and '88.

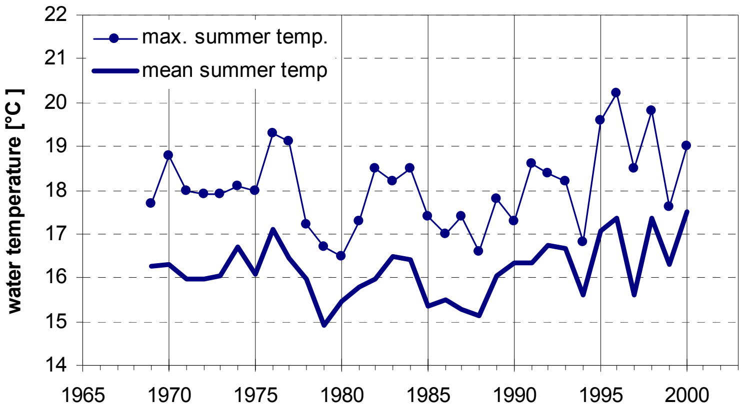

Fig. 4.5.4: Mean and maximum water temperature between July and September at Helgoland (BAH-data).

This pattern in mainly reflected by maximum water temperatures, that reach high values in a couple of additional years like 1977, '82 and '91, while not rising above 17.5 °C in the periods of '78-'81 and '85-'88 and in '90 and '94.

4.5.3 Wind

The frequency of stormy days was calculated for the main windy season from September to March preceding the benthos sampling. The mean number of days with a mean wind speed of Beaufort 7 or more is significantly higher during the 90ies (24.4 ± 3.8 SD) than during the 70ies and 80ies (10.1 ± 5.0 SD) (Fig. 4.5.5).

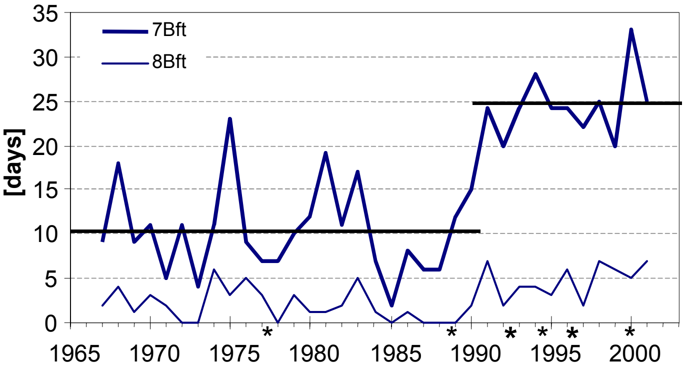

Fig. 4.5.5: Frequency of stormy days from September to March at Helgoland (DWD-data). (mean wind force of 7 or 8 Bft. or more); small and large asterisks mark single occurrences of 11 and 12 Bft. respectively. Broken horizontal lines indicate mean of periods '69-'90 and '91-2000.

Before 1990, peaks of over 15 days were reached in 1968, '75, '81 and '83. During the 90ies the stormiest season was that of 2000.

The general pattern of an increase in the 90ies is also visible for days with 8 or more Bft. with a few exceptions. In 1975 no higher number of days with 8 Bft. or more was observed than in '74 and '76 and only one day in '81. Mean wind speeds of 9 Bft. or more were only observed on single days during the seasons of 1967 - '69, '76, '82 and '84.

Regarding the timing of the windy season, a prolongation towards the early spring is visible in the 90ies. During the earlier years, the main windy season lasted mostly from September to January, while during the 90ies it is extended up to early April (Fig. 4.5.6).

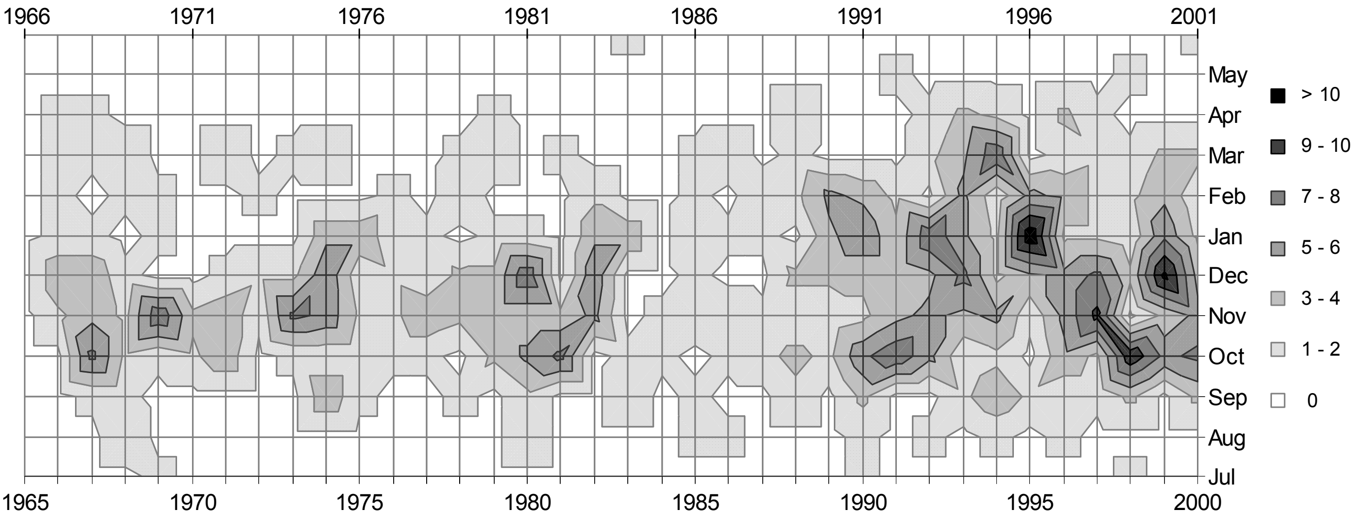

Fig. 4.5.6: Frequency of stormy days per month (mean wind force of 7 Bft. or more; DWD-data); the lower axis indicates the year preceding the winter.

Not only has there been a shift in timing, but also in the direction of strong winds. While the number of stormy days from westerly directions (SW, W, NW) is during the 90ies at a similar level as during the stormy seasons of '75 and '80, the number of days with storm from easterly directions (NE, E, SE) increases much stronger (Fig. 4.5.7).

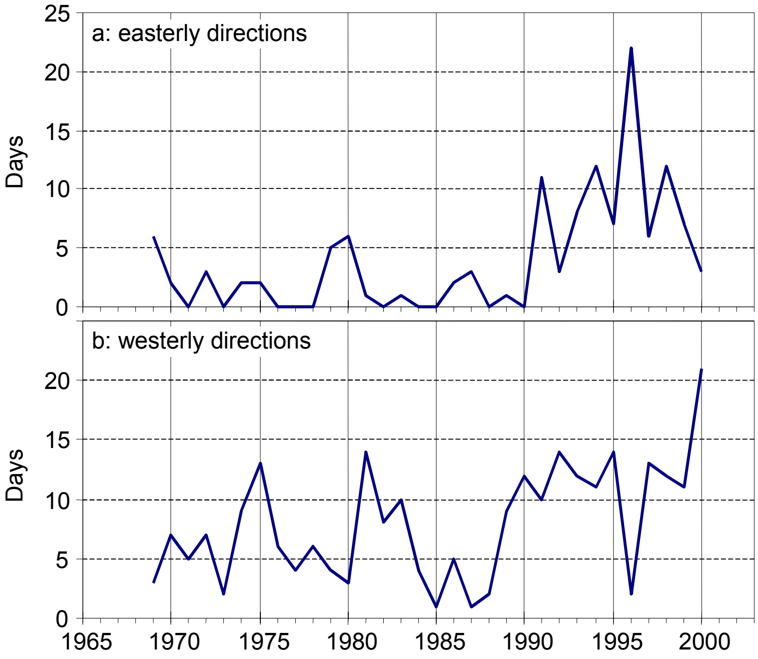

Fig. 4.5.7: Frequency of stormy days from September to March (mean wind force of 7 Bft. or more); a: westerly directions (SW, W, NW); b: easterly directions (NE, E, SE); (DWD-data).

An exception is 1996, when the storms came predominantly from easterly directions, while in 2000 they came mostly from westerly directions.

4.5.4 Salinity

The salinity at Helgoland is strongly coupled to the total annual discharge of the Elbe (Spearman's Rho = -0.75; $p < 0.001$) (Fig. 4.5.8).

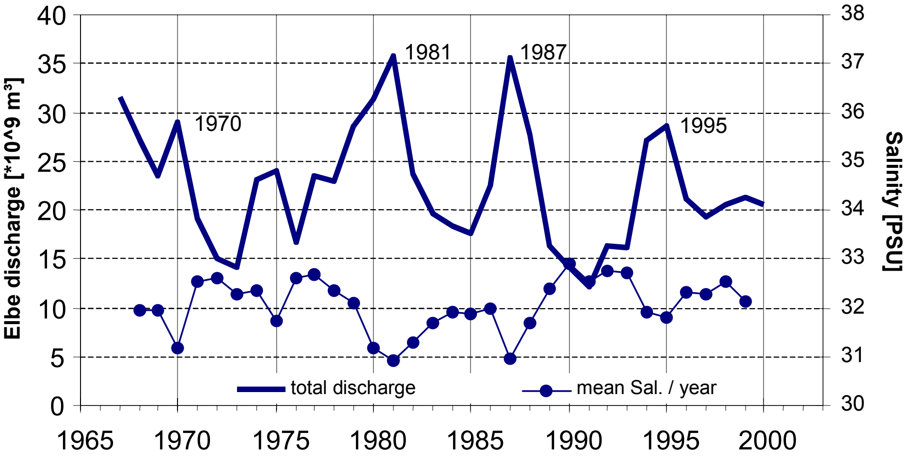

Fig. 4.5.8: Total annual discharge of river Elbe (Eggert 2002, left axis) and annual mean salinity at Helgoland (BAH-data, right axis).

The largest discharges coupled to the lowest salinity were observed in 1979, '81, '87 and '95. Low discharge volumes coupled to a high salinity appeared in '72/'73, '76, '83 - '85 and between '89 and '93.

4.5.5 Nutrients

The three main inorganic nutrients phosphate, nitrogen and silicate do not fluctuate in parallel, but rather show each a distinct pattern during the period from 1969 to 2000.

4.5.5.1 Phosphate

Mean annual concentrations of phosphate showed a strong increase during the early 70ies. All values between 1974 and '87 were well above the average of the period '69 – 2000 (Fig. 4.5.9).

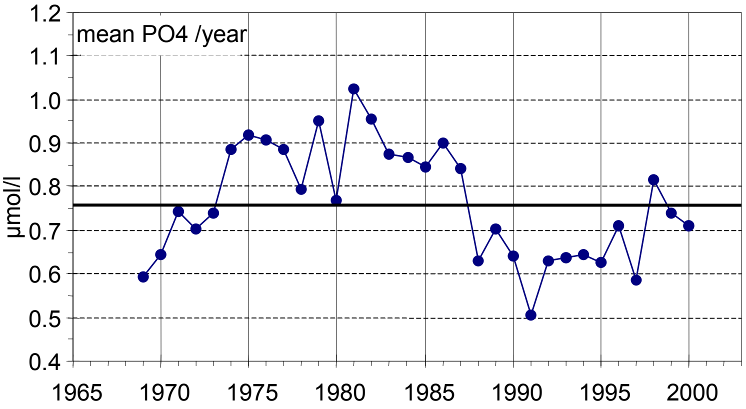

Fig. 4.5.9: Mean annual concentration of phosphate (PO_4) at Helgoland [µ mol/l] (BAH-data). Thick horizontal line marks the mean concentration of 1969 – 2000.

In the contrary, the period from '88 until '97 was marked by lower concentrations than average, with an increase in the late 90ies.

4.5.5.2 Nitrogen

Unlike phosphate, the concentration of the total inorganic nitrogen shows an increasing tendency over the whole period from '69 at least until the mid-90ies (Fig. 4.5.10).

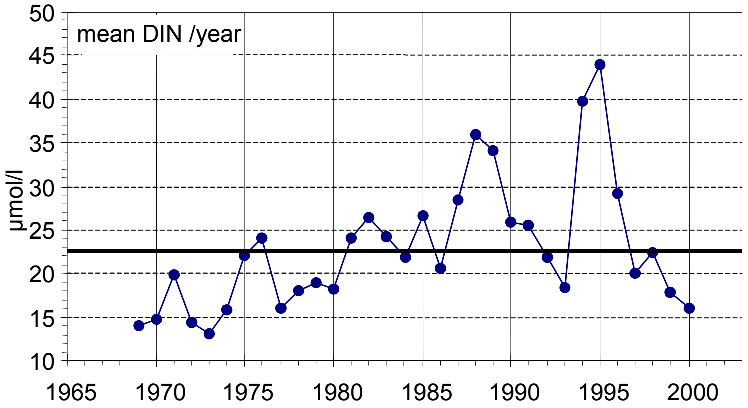

Fig. 4.5.10: Mean annual concentration of dissolved inorganic nitrogen (DIN = NO_3+NO_2+NH_4) [µ mol/l] at Helgoland (BAH-data). Thick horizontal line marks the mean concentration of 1969 – 2000.

The period between '88 and '96 is marked by large fluctuations in the nitrogen concentrations, reaching peak concentrations in '88/'89 and in '94/'95. In the end of the 90ies the concentrations start to decrease again to levels comparable to the (early) 70ies.

4.5.5.3 Silicate

The silicate concentration in the sea water at Helgoland is fluctuating around 5 µmol/l until 1987, followed by an extreme increase up to 20 µmol/l in 1988 (Fig. 4.5.11).

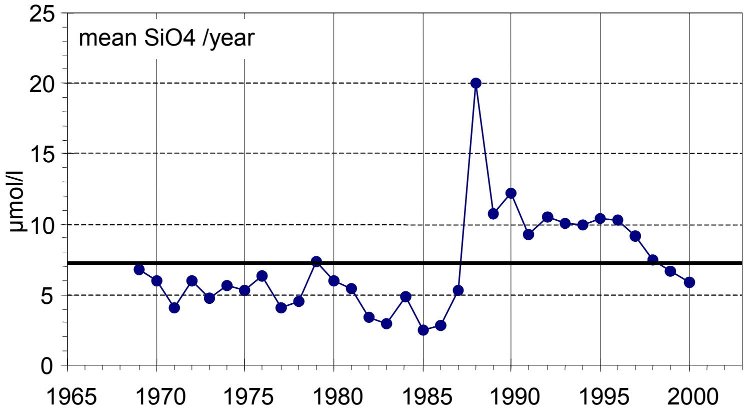

Fig. 4.5.11: Mean annual concentration of silicate (SiO_4) at Helgoland [µ mol/l] (BAH-data). Thick horizontal line marks the mean concentration of 1969 – 2000.

Following this peak, the mean concentration stays at around 10 µmol/l until 1996 and then declines again towards the end of the 90ies, reaching comparable levels to the 70ies in 2000. Before the dramatic change in '88, the highest mean concentrations were measured in '69 and '79 and lowest concentrations between '92 and '86.

4.4.6 Correlations between abiotic environmental data

Several of the environmental time series described in the previous chapter are correlated with each other.

The NAO as large-scale climatic pattern influences the European weather. The Winter-NAOI is highly significantly correlated to the frequency of strong *westerly* winds (Bft.7W) and to the mean winter temperature (T_w), consequently the latter two are also positively correlated (Tab. 4.5.1). The correlation to the overall frequency of strong winds (Bft.7) is lower but still significant. Winter- and the preceding *annual* NAOI (ANAOI) and consequently also winter and preceding summer temperature (T_s) are also correlated. The *annual* NAOI is not as strongly correlated to the frequency of windy days and to the winter temperature, but it shows a higher correlation to the summer temperature and the annual salinity (Sal.) and a negative correlation to the total river runoff of the Elbe. The salinity is highly correlated to the river runoff of the Elbe, but also to the frequency of easterly winds (Bft.7E). Both westerly and easterly winds are not significantly correlated with each other.

Phosphate (PO_4) concentrations are negatively correlated to easterly winds while silicate (SiO_4) concentrations are positively correlated to easterly winds. Consequently there is a strong negative correlation between both nutrients. The silicate concentration is also positively correlated to the overall wind frequency and to the winter temperature. The concentrations of both phosphate and dissolved inorganic nitrogen (DIN) are negatively correlated to the salinity, although only the latter correlation is significant (Tab. 4.5.1).

Tab. 4.5.1: Spearman's rank correlation between environmental factors. *R*: Spearmann's Rho; *p*: (unadjusted) error probability for *R* [p ≤ 0.05 in bold]. W-NAOI: winter-NAO-index; A-NAOI: annual NAO-index of the previous year; Bft.7: frequency of days between previous September and April with a mean wind of 7 Bft. or more; Bft.7E/Bft.7W: as Bft.7 but restricted to easterly (SE-NE) and westerly (SW-NW) directions; Tw: mean winter temperature; Ts: mean summer temperature of the previous summer; Sal.: mean salinity of the previous year; DIN: mean dissolved inorganic nitrogen concentration of the prev. year; PO$_4$: mean phosphate concentration of the prev. year; SiO$_4$: mean sililcate concentration of the prev. year; Elbe: total river discharge of the prev. year.

		W-NAOI	**A-NAOI**	**Bft.7**	**Bft.7W**	**Bft.7E**	**Tw**	**Ts**	**Sal.**	**DIN**	**PO4**	**SiO4**	**Elbe**
W-NAOI	R		0.539	0.450	0.642	-0.024	0.697	0.319	0.066	0.302	-0.133	0.290	-0.214
	p		**0.001**	**0.010**	**<0.001**	0.897	**<0.001**	0.075	0.721	0.093	0.467	0.107	0.240
A-NAOI	R	0.539		0.289	0.274	0.134	0.425	0.363	0.376	0.212	-0.094	0.030	-0.461
	p	**0.001**		0.108	0.129	0.465	**0.015**	**0.041**	**0.034**	0.245	0.609	0.869	**0.008**
Bft.7	R	0.450	0.289		0.774	0.734	0.311	0.525	0.283	0.196	-0.317	0.524	-0.133
	p	**0.010**	0.108		**<0.001**	**<0.001**	0.084	**0.002**	0.117	0.284	0.077	**0.002**	0.469
Bft.7W	R	0.642	0.274	0.774		0.305	0.469	0.440	0.220	0.058	-0.188	0.323	-0.181
	p	**<0.001**	0.129	**<0.001**		0.090	**0.007**	**0.012**	0.227	0.754	0.302	0.071	0.322
Bft.7E	R	-0.024	0.134	0.734	0.305		-0.074	0.251	0.382	0.038	-0.415	0.497	-0.178
	p	0.897	0.465	**<0.001**	0.090		0.689	0.166	**0.031**	0.838	**0.018**	**0.004**	0.331
Tw	R	0.697	0.425	0.311	0.469	-0.074		0.432	0.180	0.149	-0.336	0.383	-0.136
	p	**<0.001**	**0.015**	0.084	**0.007**	0.689		**0.014**	0.323	0.416	0.060	**0.030**	0.459
Ts	R	0.319	0.363	0.525	0.440	0.251	0.432		0.148	0.018	-0.188	0.255	-0.186
	p	0.075	**0.041**	**0.002**	**0.012**	0.166	**0.014**		0.417	0.924	0.304	0.159	0.308
Sal.	R	0.066	0.376	0.283	0.220	0.382	0.180	0.148		-0.376	-0.322	0.214	-0.753
	p	0.721	**0.034**	0.117	0.227	**0.031**	0.323	0.417		**0.034**	0.072	0.240	**<0.001**
DIN	R	0.302	0.212	0.196	0.058	0.038	0.149	0.018	-0.376		-0.037	0.306	0.246
	p	0.093	0.245	0.284	0.754	0.838	0.416	0.924	**0.034**		0.842	0.088	0.174
PO4	R	-0.133	-0.094	-0.317	-0.188	-0.415	-0.336	-0.188	-0.322	-0.037		-0.682	0.182
	p	0.467	0.609	0.077	0.302	**0.018**	0.060	0.304	0.072	0.842		**<0.001**	0.319
SiO4	R	0.290	0.030	0.524	0.323	0.497	0.383	0.255	0.214	0.306	-0.682		-0.044
	p	0.107	0.869	**0.002**	0.071	**0.004**	**0.030**	0.159	0.240	0.088	**<0.001**		0.810
Elbe	R	-0.214	-0.461	-0.133	-0.181	-0.178	-0.136	-0.186	-0.753	0.246	0.182	-0.044	
	p	0.240	**0.008**	0.469	0.322	0.331	0.459	0.308	**<0.001**	0.174	0.319	0.810	

4.6 Correlation between benthos and abiotic environment

Correlations between environmental factors and the benthic communities can be seen for sum parameters of the community as well as for the multivariate community composition.

Correlations of single species to environmental factors are weak and differ widely between stations. An analysis of the correlation of single species densities to environmental factors would imply the assumption of an influence of the respective factor on the population size of the species. For a reasonable estimate of the development of the population size of benthic organisms it would be necessary to sample the main area of their distribution. Single stations are not representative for the population size. An analysis of the environmental influence on single species' populations needs to consider a larger spatial scale and is therefore beyond the scope of the present study.

Local densities are likely to be strongly influenced by interactions between species and by local environmental influences. A detailed analysis of these factors and interactions responsible for the local densities requires more sophisticated models than simple correlations. The development of such models goes beyond the scope of the present study.

4.6.1 Sum parameters

The various environmental factors described in chapter 4.5 were correlated to sum parameters of the benthic communities such as species density (S), total organism density (N), Pielou's evenness index (J') and Shannon-Wiener diversity index (H'). Calculations were done with a time lag of up to three years for the environmental variables (denoted by an appended "_L*x*" to the factor name with *x* the lag in years).

Several correlations were detected that are statistically significant if tested for themselves. However the large number of combinations tested (38 for each parameter) strongly increases the probability of detecting accidental correlations. If the error probability is adjusted for this multiple testing, a single correlation remains significant: Between the frequency of strong winds two years before and the species density at WB (chapter 4.6.1.2). Nevertheless the highest detected correlations can be seen as the 'most probable correlations' at the respective stations.

4.6.1.1 SSd

The highest positive correlations at SSd are those of the species density to the winter-NAOI and the annual NAOI with a lag of one year. The species density is also negatively correlated to the Elbe river runoff with a time lag of two years (Tab. 4.6.1).

Tab. 4.6.1: The highest detected rank correlations between environmental factors and sum parameters of the benthic community at SSd.
S: species density; N: organism density; J': Evenness; H': diversity.
Factor names as in Tab. 4.5.1; "_L1" indicates a time lag of one year.
R: Spearmann's Rho; *p*: (unadjusted) error probability for *R* [p ≤ 0.01 in bold].

Parameter	Factor	*R*	*p*
S	A-NAOI_L1	0.509	**0.006**
	W-NAOI_L1	0.504	**0.006**
	Elbe_L2	-0.502	**0.006**
	A-NAOI_L2	0.435	0.021
	W-NAOI	0.380	0.046
N	Sal._L1	0.438	0.020
J'	Sal.	-0.413	0.029
	Sal._L1	-0.377	0.048
H'	DIN	0.391	0.040

The total organism density is positively correlated to the salinity with a lag of one year while evenness is negatively correlated to the salinity. The diversity is positively correlated to the DIN-concentration of the twelve months preceding the sampling.

4.6.1.2 WB

The strongest correlations of the community parameter to the environmental factors of all stations was detected at WB.

The negative correlation between the frequency of strong winds two years before and the species density at WB (*R* = -0.697) is the only one which is still significant after correction for multiple testing (Tab. 4.6.2).

Tab. 4.6.2: The highest detected rank correlations between environmental factors and sum parameters of the benthic community at WB.
S: species density; N: organism density; J': Evenness; H': diversity.
Factor names as in Tab. 4.5.1; "_L1" indicates a time lag of one year.
R: Spearmann's Rho (sign. correlation after error adjustment in bold);
p: (unadjusted) error probability for *R* [p ≤ 0.01 in bold].

Parameter	**Factor**	***R***	***p***
S	Bft.7_L2	**-0.697**	**0.001**
	Ts_L2	-0.607	**0.005**
	Bft.7E	-0.584	**0.007**
	Bft.7	-0.547	0.013
	Bft.7E_L2	-0.522	0.018
	W-NAOI_L3	-0.456	0.043
N	W-NAOI_L3	-0.653	**0.002**
	A-NAOI_L2	-0.490	0.028
	Sal._L2	-0.471	0.036
J'	A-NAOI_L3	0.605	**0.005**
	Sal._L2	0.534	0.015
	DIN	0.481	0.032
H'	A-NAOI_L3	0.608	**0.004**
	Sal._L2	0.564	**0.010**
	DIN	0.514	0.020

The species density is also strongly negatively correlated to the summer-temperature two years before (Ts_L2) and to the frequency of (easterly) windy days during the preceding winter (Bft.7E) and with a lag of two years.

With a lag of three years, the total density of organisms is negatively correlated to the winter-NAOI, and evenness and diversity are positively correlated to the annual NAOI. The mean salinity two years before is also negatively correlated to the total density of organisms and positively to the evenness and diversity indices.

4.6.1.3 Slt

The highest correlations at Slt were detected between the total density of organisms and the annual NAOI with a lag of two years. The correlation to the winter-NAOI is lower, even lower than the negative correlation to the Elbe river runoff, both with a lag of two years (Tab. 4.6.3).

Tab. 4.6.3: The highest detected rank correlations between environmental factors and sum parameters of the benthic community at Slt.
S: species density; N: organism density.
Factor names as in Tab. 4.5.1; "_L1" indicates a time lag of one year.
R: Spearmann's Rho; *p*: (unadjusted) error probability for *R* [p ≤ 0.01 in bold].

Parameter	**Factor**	***R***	***p***
S	DIN_L1	0.488	**0.005**
	DIN	0.394	0.026
	DIN_L2	0.386	0.029
	W-NAOI	0.385	0.029
	W-NAOI_L2	0.378	0.033
	Bft.7_L2	0.374	0.035
	Bft.7	0.370	0.037
	Bft.7W_L2	0.350	0.049
	Bft.7_L1	0.348	0.051
N	A-NAOI_L2	0.523	**0.002**
	Elbe_L2	-0.413	0.019
	W-NAOI_L2	0.359	0.044

The species density was most strongly correlated to the concentration of DIN (highest for a lag of one year). Further correlations were detected to the winter-NAOI and to the frequency of windy days with a lag up to two years.

No correlations of H' or J' to environmental factors was detected at Slt.

4.6.1.4 FSd

Relatively few correlations were detected at FSd. The highest ones are those of the species density to the winter-NAOI and the annual NAOI one year before (Tab. 4.6.4).

Tab. 4.6.4: The highest detected rank correlations between environmental factors and sum parameters of the benthic community at FSd.
S: species density; J': Evenness.
Factor names as in Tab. 4.5.1; "_L1" indicates a time lag of one year.
R: Spearmann's Rho; *p*: (unadjusted) error probability for R [p ≤ 0.01 in bold].

Parameter	**Factor**	***R***	***p***
S	W-NAOI	0.456	0.011
	A-NAOI_L1	0.441	0.015
	Tw	0.405	0.026
	Tw_L2	0.398	0.029
	Bft.7E	-0.379	0.039
J'	A-NAOI_L1	-0.371	0.044

Further correlations of the species density were detected to the mean winter-temperature of the previous winter and the winter two years earlier. A negative correlation was found between the species density and the frequency of easterly strong winds.

Evenness was negatively correlated to the annual NAOI one year before.

No correlations of the total density of organisms or of the evenness to environmental factors was detected at FSd.

4.6.2 Community composition

The temporal development of the benthic communities composition as reflected in the interannual faunal similarity is significantly correlated to the change of environmental factors. According to the specific environmental conditions at the stations, the main influential factors and the strength of the correlation differs between the stations.

4.6.2.1 SSd

At SSd the highest correlation to the development of the benthos was found for the factors time (reflection temporal autocorrelation) and the winter-NAOI from the year before (W-NAOI_L1). Further correlations were found to the concentration of DIN of one and two years before (Tab. 4.6.5).

Tab. 4.6.5: Largest correlations between benthos and environmental data at SSd; *R*: Spearman's rank correlation between distance matrix of environmental data (Euclidian distance, normalised data) and similarity matrix of benthos abundance data (Bray-Curtis similarity, 4th root transformation); Factor names as in Tab. 4.5.1; Bonferroni-adjusted significance level: * 5%, ** 1%; R.v. > *R*: percentage of random variables that result in a larger *R* than the last added factor.

Factors	*R*	Factor 1	Factor 2	Factor 3	R.v. > *R*
3	0.534**	Time	W-NAOI_L1	PO_4_L2	**0.4 %**
3	0.528	Time	W-NAOI_L1	DIN_L2	**0.5 %**
2	0.527**	Time	W-NAOI_L1		**< 0.1 %**
2	0.469**	Time	DIN_L2		**< 0.1 %**
2	0.431**	W-NAOI_L1	DIN_L2		**0.1 %**
2	0.418**	Time	Bft.7E_L1		**0.4 %**
1	0.415**	Time			**< 0.1 %**
1	0.395**	W-NAOI_L1			**< 0.1 %**
1	0.296	DIN_L2			**< 0.1 %**
1	0.216	DIN_L1			**0.4 %**
1	0.212	Bft.7E_L2			**0.6 %**
1	0.204	A-NAOI_L3			**0.8 %**
1	0.194	W-NAOI_L2			**1.0 %**
1	0.194	Tw_L1			**1.0 %**
1	0.187	Bft.7E_L1			1.3 %
1	0.174	Ts			1.4 %
1	0.145	PO_4_L2			3.2 %
1	0.145	Bft.7E_L2			3.2 %
1	0.143	Ts_L1			3.3 %
1	0.129	W-NAOI_L3			4.4 %

The correlations to a couple of further factors reach relatively low but still significant values of *R*. These include eastern winds (Bft.7E) from two and one years before, the winter-NAOI from two years before and the winter-temperature from the year before.

The largest increase of the correlation by addition of a second factor was achieved by the combination of time and W-NAOI_L1 (*R* = 0.525). The further addition of DIN_L2 or

PO_4_L2 yielded only a small increase to 0.528 and 0.534. These are the highest correlations with combinations of three factors and the only ones that reach a higher *R* than time and the NAOI alone.

To visualise how much of the structure in the temporal development of the benthic community is reflected by the three factors that reached the highest correlation, MDS-plots based on both similarity matrices are presented. The MDS-plot based on the three environmental factors (Fig. 4.6.1 b) displays a similar structure as that based on the benthos abundance data (Fig. 4.6.1 a).

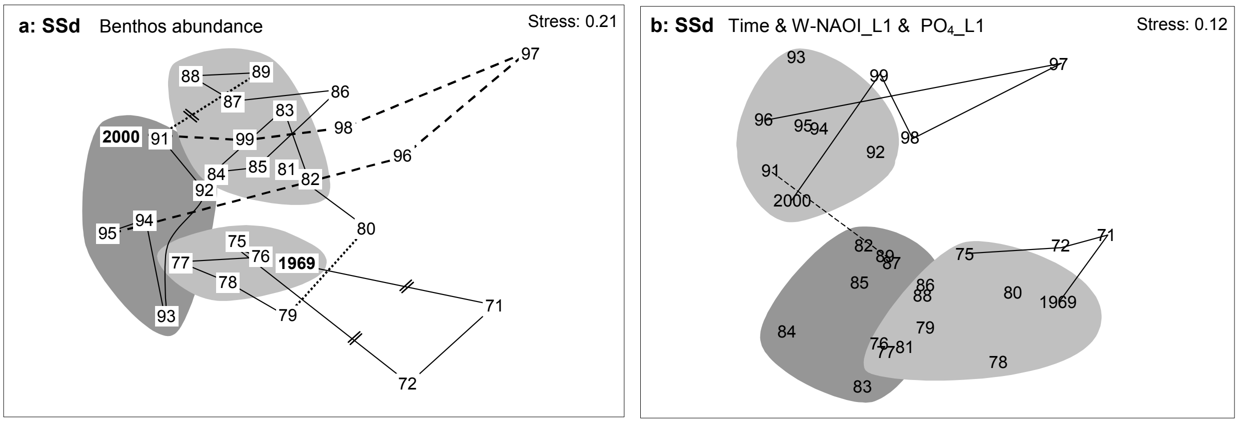

Fig. 4.6.1: a: Community development at SSd between 1969 and 2000. MDS-plot based on Bray-Curtis similarity of 4th root transformed densities [m^{-2}]. Consecutive years are connected by lines. Broken lines indicate major shifts in the community. Shaded areas indicate groups supported by cluster analysis (group average); b: MDS based on three environmental factors with the highest correlation to the benthos similarity matrix; Euclidian distance, normalised data.

The distinction between late 70ies and 80ies is less clear on the environmental MDS-plot, but 1971/'72 are separated from the other 70ies, the 90ies are clearly distinguished from the 80ies and '97 is very well separated from the 90ies. However, 1979, '86 and '96 are not separated from their respective periods as seen on the faunal MDS-plot.

4.6.2.2 WB

The highest correlation to the faunal data from WB for any of the environmental factors was found for the frequency of easterly winds (Bft.7E), which is also part of any combination of up to three factors. Even for the single factor the correlation of 0.636 is much higher than that of any factor or even a combination of factors at all other stations (Tab. 4.6.6)

Tab. 4.6.6: Largest correlations between benthos and environmental data at WB; *R*: Spearman's rank correlation between distance matrix of environmental data (Euclidian distance, normalised data) and similarity matrix of benthos abundance data (Bray-Curtis similarity, 4th root transformation); Factor names as in Tab. 4.5.1; Bonferroni-adjusted significance level: * 5%, ** 1%; R.v. > *R*: percentage of random variables that result in a larger *R* than the last added factor.

Factors	*R*	Factor 1	Factor 2	Factor 3	R.v. > *R*
3	0.724**	Bft.7E	Bft.7E_L1	Time	**0.5 %**
3	0.715*	Bft.7E	Bft.7E_L1	Bft.7E_L2	**0.9 %**
2	0.706**	Bft.7E	Bft.7E_L1		**0.1 %**
2	0.643**	Bft.7E	Time		**0.5 %**
1	0.636**	Bft.7E			**< 0.1 %**
1	0.430**	Time			**< 0.1 %**
1	0.384	Bft.7E_L2			**0.1 %**
1	0.373	Bft.7E_L1			**0.1 %**
1	0.309	W-NAOI_L1			**1.0 %**
1	0.296	DIN_L2			1.2 %
1	0.264	Bft.7_L2			1.7 %
1	0.231	Bft.7			2.9 %
1	0.212	W-NAOI			3.8 %
1	0.196	Ts			4.7 %
1	0.192	DIN_L1			5.0 %
1	0.189	PO4_L2			5.0 %

The second-highest correlation was again found for the factor time. All other correlations of single factors are not significant after Bonferroni-correction. However a number of factors did show higher correlations than most random variables. Amongst these are many wind related factors (mainly easterly winds), the winter-NAOI (most strongly with a lag of one year: W-NAOI_L1) and concentrations of DIN and PO_4 with a lag up to two years.

Out of all combinations of two factors, a combination of the frequency of easterly winds of the previous winter with that from the year before resulted in the largest increase of *R* to 0.706.

The further addition of the easterly winds from two years before resulted in a further increase to *R* = 0.715. The best correlation is attained by a combination of the frequency of easterly winds in the previous winter and the winter before with the time as third factor (R = 0.724).

One percent of 1000 random variables reach a correlation above 0.31 at WB, much higher than at the other stations (Slt: 0.13; FSd: 0.18; SSd: 0.2).

A MDS-plot based on the best combination of three factors (Fig. 4.6.2 b) shows many similarities to the one based on the faunal data (Fig. 4.6.2 a). The periods from '81-90 and '92-2000 are clearly separated and the prominent position of '96 and '97 is also reflected.

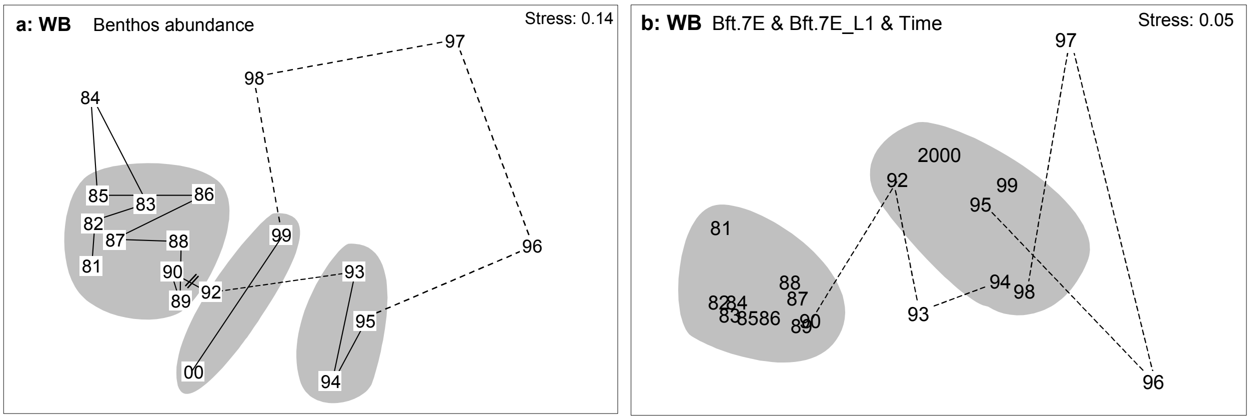

Fig. 4.6.2: a: Community development at WB between 1981 and 2000 ('91 omitted). MDS-plot based on Bray-Curtis similarity of 4th root transformed densities [m^{-2}]. Consecutive years are connected by lines. Broken lines indicate major shifts in the community. Shaded areas indicate groups supported by cluster analysis (group average); b: MDS based on three environmental factors with the highest correlation to the benthos similarity matrix; Euclidian distance, normalised data.

On the environmental plot, the year 1993 is isolated between the 80ies and the 90ies group. The larger variability during the 90ies that is visible on the faunal MDS-plot is also reflected in the environmental MDS-plot, but several properties of the faunal data can not be seen: in the environmental plot, '84 is in the middle of the 80ies and '98 is not separated from the remaining 90ies.

4.6.2.3 Slt

The correlations between the development of the benthic community and the environmental factors at Slt are much smaller than that observed at WB and SSd. The highest correlation for single factors was again found for the factor time (*R* = 0.318), followed by the phosphate-concentration. This correlation is even higher for the mean phosphate concentration two years ago (PO_4_L2; *R* = 0.285) than for that of the previous year (PO_4, *R* = 0.215; see Tab. 4.6.7).

Tab. 4.6.7: Largest correlations between benthos and environmental data at Slt; *R*: Spearman's rank correlation between distance matrix of environmental data (Euclidian distance, normalised data) and similarity matrix of benthos abundance data (Bray-Curtis similarity, 4th root transformation); Factor names as in Tab. 4.5.1; Bonferroni-adjusted significance level: * 5%, ** 1%; R.v. > *R*: percentage of random variables that result in a larger *R* than the last added factor.

Factors	***R***	**Factor 1**	**Factor 2**	**Factor 3**	**R.v. > *R***
3	0.402**	PO_4_L2	Time	Bft.7E_L1	**0.4 %**
3	0.393**	PO_4_L2	Time	A-NAOI_L2	**0.9 %**
3	0.392**	PO_4_L2	Time	PO_4	**0.9 %**
3	0.388**	PO_4_L2	Bft.7E_L1	A-NAOI_L2	1.1 %
2	0.387**	PO_4_L2	Time		**< 0.1 %**
2	0.363**	PO_4_L2	Bft.7E_L1		**< 0.1 %**
2	0.343**	PO_4_L2	Bft.7		**0.2 %**
2	0.337**	PO_4_L2	Bft.7_L1		**0.6 %**
2	0.323**	PO_4_L2	DIN		**0.7 %**
2	0.322**	PO_4_L2	A-NAOI_L2		**0.7 %**
1	0.318**	Time			**< 0.1 %**
1	0.285**	PO_4_L2			**< 0.1 %**
1	0.215*	PO_4			**< 0.1 %**
1	0.199	Bft.7E_L1			**< 0.1 %**
1	0.187	SiO_4			**< 0.1 %**
1	0.176	Bft.7			**0.1 %**
1	0.169	Bft.7_L1			**0.1 %**
1	0.134	SiO_4_L1			**0.8 %**
1	0.119	A-NAOI_L2			1.7 %
1	0.099	Bft.7W_L2			3.9 %
1	0.096	Sal.			4.2 %
1	0.092	Bft.7E_L2			4.6 %
1	0.092	SiO_4_L2			4.6 %

Several of the lower correlations of single factors, though not statistically significant after Bonferroni-correction, are still higher than that of 99% of the random variables ("R.v. > *R*" in Tab. 4.6.7). Most prominent amongst these are the (eastern) winds one year before (Bft.7(E)_L1) but also the silicate concentration of the previous year (SiO_4) and one year before (SiO_4_L1).

A combination of time and PO_4_L2 yields the highest correlation of any two factors (*R* = 0.387) and a further addition of the frequency of easterly winds one years ago

(Bft.7(E)_L1) further increases the correlation to the highest value found for any combination of up to three factors (*R* = 0.402).

Although the correlation between the combination of these three environmental factors and the community development is with 0.4 not very high, the MDS plots based on the similarity matrices of the benthos data and the environmental factors show some similarities. The majors groups delineated on the faunal MDS-plot (Fig. 4.6.3) are also visible on the environmental MDS-plot but separated more clearly (Fig. 4.6.3).

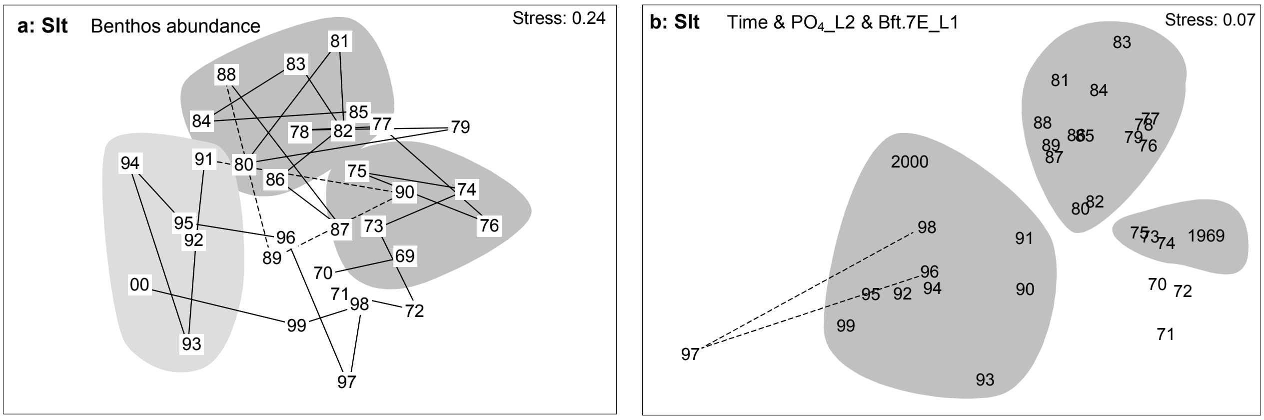

Fig. 4.6.3: a: Community development at Slt between 1969 and 2000. MDS-plot based on Bray-Curtis similarity of 4th root transformed densities [m^{-2}]. Consecutive years are connected by lines. Broken lines indicate major shifts in the community. Shaded areas indicate groups supported by cluster analysis (group average); b: MDS based on three environmental factors with the highest correlation to the benthos similarity matrix; Euclidian distance, normalised data.

Some details of the faunal MDS are however not reflected in the environmental plot, such as the distinction of '79 from the 80ies and the position of '96 to '99 closer to the 70ies. The extreme position of '97 on the MDS from environmental data is not as pronounced on the faunal MDS although '97 is positioned at the periphery in this plot as well.

4.6.2.4 FSd

By far the largest correlation of any single factor to the benthic community development at FSd is found for the factor time (*R* = 0.464; the only statistically significant single factor after correction). The correlation to the winter-NAOI with a lag of three (!) years (W-NAOI_L3; *R* = 0.283) and one year (W-NAOI_L1; *R* = 0.207) are much lower but still higher than 99% of the correlations to random variables (Tab. 4.6.8)

Tab. 4.6.8: Largest correlations between benthos and environmental data at FSd; *R*: Spearman's rank correlation between distance matrix of environmental data (Euclidian distance, normalised data) and similarity matrix of benthos abundance data (Bray-Curtis similarity, 4th root transformation); Factor names as in Tab. 4.5.1; Bonferroni-adjusted significance level: * 5%, ** 1%; R.v. > R: percentage of random variables that result in a larger *R* than the last added factor.

Factors	*R*	Factor 1	Factor 2	Factor 3	R.v. > *R*
3	0.518**	Time	W-NAOI_L3	W-NAOI_L1	**0.8 %**
3	0.494**	Time	W-NAOI_L3	A-NAOI_L1	1.7 %
2	0.489**	Time	W-NAOI_L3		**< 0.1 %**
1	0.464**	Time			**< 0.1 %**
1	0.283	W-NAOI_L3			**< 0.1 %**
1	0.207	W-NAOI_L1			**0.5 %**
1	0.134	A-NAOI_L1			3.6 %
1	0.128	Bft.7E_L2			4.2 %
1	0.123	Bft.7W_L1			5.0 %
1	0.116	Bft.7_L1			5.8 %
1	0.116	Bft.7E_L1			5.8 %
1	0.096	W-NAOI			8.1 %
1	0.090	Bft.7_L2			9.3 %
1	0.073	A-NAOI_L3			13.0 %

Besides time, only the NAOI with various lags and the frequency of strong winds show any correlation to the benthic community development at FSd.

A combination of the time with the W-NAOI_L3 yields a correlation of 0.489 and a further inclusion of W-NAOI_L1 as third factor the largest correlation found for any combination of up to three factors of 0.518.

A MDS-plot based on this combination of three factors (Fig. 4.6.4 b) also separates roughly three major groups similar to those delineated on the faunal MDS (Fig. 4.6.4 a).

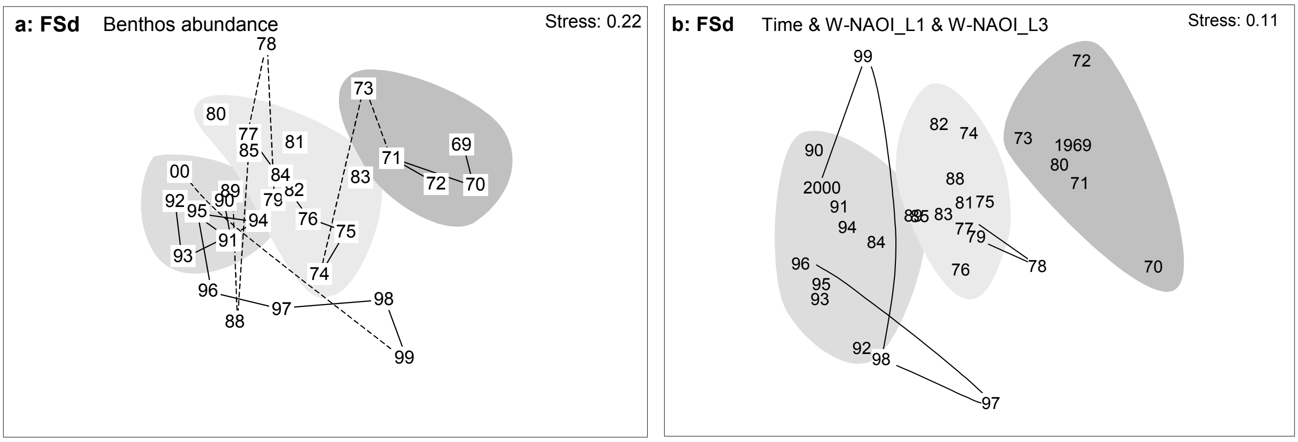

Fig. 4.6.4: a: Community development at FSd between 1969 and 2000. MDS-plot based on Bray-Curtis similarity of 4th root transformed densities [m^{-2}]. Consecutive years are connected by lines. Broken lines indicate major shifts in the community. Shaded areas indicate groups supported by cluster analysis (group average); b: MDS based on three environmental factors with the highest correlation to the benthos similarity matrix; Euclidian distance, normalised data.

1978 is positioned at the periphery of the 80ies on both plots, but '88 is on the environmental plot in the middle of the group of the 80ies while it is clearly separated on the benthos plot. 1997 and '99 are clearly separated from the group of the 90ies on both plots, but '96 and '98 are not separated on the environmental plot.

5. Discussion

5.1 Sampling gear and penetration depth

For long-term studies, the sampling methodology and especially the sampling gear should ideally be kept constant over the whole period of investigation (e.g. Dybern et al. 1976; Van der Meer 1997). If changes are necessary, the previous methodology should at least be continued for a certain period in parallel to the new methodology, to allow an estimation of the bias introduced by the change (Rumohr 1999). Unfortunately, this has not been carried out constantly during the sampling of the time series presented here. A rough comparison of the effects of different sampling gears can be achieved by the analysis of the extensive sampling with various gear types carried out in July 1976 at the FSd-station (see chapter 4.3.2).

A combination of two van Veen grabs (vV) with six Reineck box corers (RBC) resulted in a lower number of species and a lower diversity index, while evenness estimates were about the same as calculated from five vVs. The lower total area sampled by this gear combination (2 vVs + 6 RBCs = 0.3 m²) explains the lower species number compared to that of five vVs (0.5 m²). However, the wider spatial spread of the cores increases the species number to values comparable to that found in four vVs.

In contrast to the species number, the estimate of overall density of organisms was higher in the gear combination. Several species were found in significantly different numbers in the RBCs and the vVs (Tab. 4.3.2). Some of these differences can be explained by the higher penetration depth of the RBCs, like the higher densities of *Goniada maculata* or *Tellina fabula*, larger individuals of which may live deeper in the sediment than the mean penetration of the vV of only 6 cm, although *T. fabula* inhabits the upper 5 - 7 cm, like most small bivalve species (Birkett 1958). The larger numbers of e.g. *Urothoë poseidonis* could also be related to the bow wave of the vV that may push away small organisms on the surface (Andersin & Sandler 1981). The *lower* density in the RBCs of *Ophiura albida* and juvenile ophiuroids living on the sediment surface, as well as of *Nephtys hombergii* and *Echinocardium cordatum*, which are often found deep in the sediment (Beukema 1974) cannot be explained by these differences in the performance of the gear, but must be attributed to real spatial differences in the area sampled for the comparison.

The type and magnitude of bias introduced by the change of gear types will vary between the stations, as each one is characterised by a different sediment type and macrozoobenthic community. The penetration depth of the gear is influenced by sediment granulometry (Beukema 1974; Christie 1975; Ankar 1977; Eleftheriou & Holme 1984) as well as by differences in compactness associated with biogenic structuring of the sediments (Buchanan 1984). Because of the low penetration depth of the light vV especially at the FSd- and SSd-station (Fig. 4.3.1), a combination of vVs and RBCs was used at these stations to benefit from the significantly higher penetration depth of the RBC and of the higher number of smaller samples, which was expected to improve the spatial spread and the precision of population density estimates.

Under the assumption that the difference in species numbers is mainly a function of the sampled area, a correction of the species number was tentatively applied for the long-term comparison.

The bias in density estimates differs widely between species and will therefore vary strongly with changes in the community structure. A correction for the different sampling efficiency does therefore not make sense for other community parameters and is impossible for multivariate methods.

The largest proportion of the infaunal organisms inhabits the upper 5 – 10 cm of the sediment (Molander 1928; Holme 1964; Kaplan et al. 1974). These species should for most of the time at most stations have been appropriately collected. Only in samples from the early years at FSd their density estimates may be negatively biased because of the low penetration depth of the old vV. Especially larger organisms often live deeper in the sediment. Species like the mudshrimps *Callianassa subterranea* or *Upogebia deltaura*, larger polychaetes such as *Nereis* spp., *Nephtys* spp. or *Lanice conchilega,* and echinoids like *Echinocardium cordatum* commonly appear in 15 – 20 cm depth and some have been recorded to more than 50 cm depth (Kaplan et al. 1974; Beukema 1974; Thayer et al. 1975; Santbrink & Bergman 1994). As larger organism mostly occur in small numbers per sample, their influence should be less pronounced for community analyses based on density estimates. Their large size would more strongly affect analyses of biomass (Lie & Patamat 1965; Thayer et al. 1975), which are not covered in the present study because of the relatively few available biomass data from the present time series (see chapter 3.2.3).

The lighter vV-grabs used until 1985 were not warp rigged and most of them did not have a sieve covered upper lid. Compared to the new vV introduced in 1986, this resulted in a lower penetration depth and in a greater bow wave when approaching the bottom, leading to a loss of deeper living species as well as small surface dwelling species (Ankar 1977; Bhaud & Duchene 1977; Andersin & Sandler 1981). The new modified and heavier vV achieved a penetration depth comparable to that of the RBC and the bow wave has been reduced significantly using the sieve-covered lid (Andersin & Sandler 1981).

The gear type and penetration depth surely have an influence on the community analyses, which can not be exactly estimated, but seem to be less pronounced than the common interannual variations of the benthic communities.

Sampling gear changes were not accompanied by larger changes in the faunal data than the common interannual community changes between other years. The observed changes are in all cases the result of *increasing* densities of some species as well as of *decreasing* densities of other species and therefore reflect real changes in the communities beyond sampling influences.

The low densities of several deeper dwelling species and of small species living on the sediment surface found in the early 1970ies may partly be due to the less efficient sampling, especially at FSd and SSd.

The changes in sampling gear need always to be considered when interpreting increasing abundances of deep living or surface dwelling species in the present time series.

5.2 Spatial variability of the benthic communities at the sampling stations

When investigating temporal changes of macrozoobenthic communities, it is essential to have a good estimate of the spatial sampling variability (Thrush et al. 1994; Underwood 1994). The precision of estimates of community attributes is determined by the size of the sampling units and the number of replicates as well as by the spatial distribution pattern of the respective community (Krebs 1998). Spatial patterns in the distribution of the benthic community around the sampling stations at a larger scale than the actually sampled area can confound temporal comparisons (Thrush et al. 1994). Small-scale patterns may reduce the power of the comparisons but will not cause errors (Morrisey et al. 1992; Stewart-Oaten et al. 1995), as long as several grab samples are combined to adequately reflect the benthic communities with their inherent variation (Gray 2000).

In addition to this, descriptors of community structure such as the species number or diversity and evenness indices are generally a function of sample size (Hill 1973; Colwell & Coddington 1994; Gray 2002). Theoretical studies have so far only investigated the *systematic* dependency in simulated samples (Wolda 1981; Smith & Wilson 1996). This systematic relation is superimposed on the effects of an aggregated distribution of organisms. The sample size dependency of diversity measures found in real samples can therefore differ from the predictions of theoretical simulations.

The main intention of the analysis of the spatial variability is threefold:

- To detect any spatial structuring of the community in the sampling area that might confound long-term results.
- To assess the small-scale distribution of the benthic organisms and the resulting variability of the sampling units. Based on this variability we can estimate the sample size (number of replicates) needed to adequately describe the local benthic community with its natural spatial variability.
- To evaluate the sample-size-dependency of community descriptors based on real data and the consequences on the interpretation of these measures.

5.2.1 Spatial patterns

If large scale patterns in the spatial distribution of the benthic community were present in the sampling area, i.e. sub-areas with slightly different types of communities, a deviation from the exact sampling location might result in a sampling of a different community (Morrisey et al. 1992). Such patterns should be discernible as spatial autocorrelation or as large-scale gradients across the area.

Neither a clear spatial pattern, nor a significant spatial autocorrelation or a gradient was found in the multivariate analysis of the benthic communities.

A hint towards a large-scale pattern or gradient was indicated by a (non-significant) decreasing spatial autocorrelation at the FSd-station with longitude (Fig. 4.2.2). The significant correlation of the species density with latitude as well as with longitude may support the idea of such a gradient (Fig. 4.2.3). Considering the low number of grabs and the fact that this supposed gradient is not reflected in the normally very sensitive MDS, it may also be an accidental result of a small-scale variability. On rare occasions, coarse sediments with pebbles or small stones have been found at FSd (unpublished data from other sampling occasions, not included in the present analysis) and even large stones were recorded on photographs of the sea bottom in the area (Fig. 5.1). With the present data no clear statement about the size and distribution of stones or coarse sediment "islands" is possible.

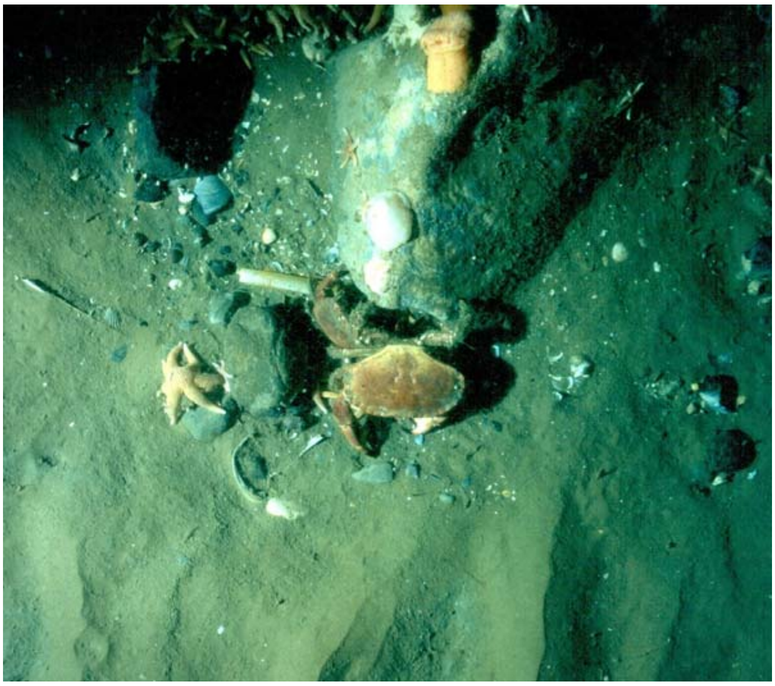

Fig. 5.1: Large boulder found in the direct vicinity of the FSd station with associated fauna of *Cancer pagurus*, *Asterias rubens*, *Metridium senile*. The fine sand with ripples at a wavelength of 10 to 20 cm at the lower edge represents the usual sediment surface in the area. (Picture covering an area of appr. 60 x 70 cm taken in July 2002 by I. Suck)

A forthcoming analysis of bottom photographs, video footage and side-scan sonar investigations of the area around the long-term sampling stations may help to clarify this question. With the present number of sampling positions it cannot be finally concluded whether a real gradient exists at FSd, but even *if* it existed at longer distances, a distance from the centre position of 0.5 nm (which will hardly ever be reached during the sampling) did not result in significant differences in the benthic communities. None of the other three stations showed hints towards the presence of larger scale patterns of gradients.

The non-significant positive correlations to the first distance class, as observed in the Mantel-correlograms at all stations (see Fig. 4.2.2), may indicate a patchiness at a smaller scale than the mean distance between grabs from the same position (90-150m). Patterns in macrozoobenthic soft bottom communities commonly reach a patch size of 40 to 160 m (Kendall & Widdicombe 1999; Somerfield & Gage 2000; Parry et al. 2003). The actual scale of the spatial community pattern causing the observed variability is not determinable with the present sampling design (Thrush et al. 1994). (Stewart-Oaten et al. 1995)To overcome this small-scale variability, it is advisable to take the replicates randomly around the specified position, covering an area larger than the largest suspected spatial patterns in the area. Under the conditions found in the offshore communities of the German Bight, this spacing of replicates is likely to be automatically realised by the observed precision of sampling. If great care is taken in the positioning, a precision of ± 30 to 50 m would surely be possible, but this is not desirable to avoid the confounding effects of spatial autocorrelation.

The combination of the estimated accuracy of the recorded position, and the distance observed between desired and actual sampling position show that even with today's technical possibilities the expected precision under standard offshore conditions will be about ± 100 m while some samples may be taken more than 200 m from the desired position. This spatial spread is large enough to overcome any suspected confounding effects of spatial autocorrelation for the present sampling stations.

As no clear distribution patterns of the benthic communities were detected, the observed variability is taken as the medium scale local variability of the communities. Samples can be assumed as random samples of a patchily distributed benthic community.

5.2.2 Medium-scale spatial variability and the precision of estimates

Most macrozoobenthos organisms are spatially aggregated and often associated with other species (Wiens 1989; Gray 2002). This leads to a high variability of samples, and single sampling units are not sufficient to characterise a benthic community. With an increasing number of replicates, the precision of most estimates increases. This is the most important aspect for a determination of an appropriate sample size. The decreasing variance of the pooled samples is an indication of the amount of local spatial variability included between the replicates.

5.2.2.1 Organism densities and biomass

The mean density and biomass estimates as well as their variances differ largely between the stations. The mean density of organisms is five times higher at WB than at Slt. In opposition to this, the mean biomass at WB is only a fifth of the biomass recorded at Slt. The variability of the mean density is much higher at these two stations compared to the other two stations FSd and SSd, which have an intermediate biomass and organism density. The total organism density at Fsd is not significantly higher than at Slt, but the variability of this estimate at FSd is the lowest of all stations. Obviously the variability is not dependent on the mean, but rather related to either external factors or to the community structure.

The communities at the more variable stations are characterised by a strong numerical dominance of a single species, *Amphiura filiformis* at WB (76%) and *Nucula nitidosa* at Slt (59%), which is also reflected in the lower evenness at these stations. The dominance of the most abundant species at the other two stations is much lower (*Tellina fabula* 27% at

FSd; *Nucula nitidosa* 16% at SSd), and consequently both stations have a high evenness value.

The larger variability of total abundance estimates at WB and Slt could be explained by the numerical dominance of a single species. The variability in the population density of this species dominates the variance of the total abundance.

This is not to say that the dominant species are the most variable, quite the contrary, the more abundant species have generally the lower CV. With a larger evenness, however, high densities of one species in a grab are often levelled out by lower densities of other species, leading to a lower variability of total organism density. The same mechanism could also explain the lower variability of biomass estimates at SSd compared to the other three stations, which are stronger dominated by one or two species in terms of biomass.

It is common practice to exclude the largest species from biomass analyses because they are poorly represented when taking only a few grab samples, since they are often widely dispersed and/or live deeper in the sediment than the usual penetration depth of the grab. This procedure reduces the differences in mean biomass between the stations and leaves only SSd with a significantly higher biomass, while the reduced biomass of the other three stations is not significantly different. The exclusion of these large species does not increase the precision of the biomass estimate but rather decreases it. It does in fact decrease the standard deviation of the biomass estimate, but as the mean value decreases even more, the result is a loss of precision as measured by the ratio between SD and mean (CV). The stronger the reduction of the mean, the stronger is the loss of precision. This procedure can therefore not be recommended as such. Even if the real population density and biomass of these species may not be accurately reflected by the sampling, those specimens that are found in the samples are an integral part of the local community. Most sublittoral benthic communities of the North Sea are generally regarded as food-limited (Kuenitzer et al. 1992; Heip & Craeymeersch 1995; Rosenberg 1995). The area covered by one grab sample (0.1 m²) is small enough to allow direct interaction between the species present. Apart from direct negative impacts of large predatory species or of active bioturbation, a few large specimens in the area covered by one grab sample are likely to reduce the available food (and space) for the remaining species. This would lead to a lower biomass of the smaller species compared to adjacent areas without large specimens. This effect might also be reflected in the increased skewness of the biomass distribution after reduction (Annex: Fig. A.6.3), indicating a more clumped distribution. Single large specimens, that are regarded as outliers, should therefore only be disregarded after careful consideration.

Sample size effects

The increase of the precision of the mean biomass and organism density with increasing sample size is very similar at all stations. The precision at a certain sample size is in the first place a reflection of the variability of single grabs.

The largest reduction of variability in mean density of organisms and biomass estimates is reached by the first three to five grabs. With five grabs the size of the empirical confidence interval of the mean is reduced by more than 50% compared to single grabs.

Nevertheless, even with five grabs, the precision of the mean density estimate at WB and Slt is rather low and the empirical confidence interval (C.I.) is as large as the mean itself Fig. 4.2.4). At the two less variable stations SSd and FSd, the precision is much better and the confidence interval with five replicates is only half as large as the mean. This level of precision could only be reached with more than 20 grabs at WB or Slt. An increase to 10 replicates results in a 30% gain of precision relative to five replicates. A further increase of replicate number results only in a small improvement of the precision.

These *relative* improvements of precision are similar for the mean biomass estimates, but the precision is lower than for total density estimates at FSd and SSd (Fig. 4.2.5). Five replicates result in a C.I. as large as the mean at all stations but SSd, where it is only about 80% of the mean. The variability of the total biomass estimates at WB and Slt is similar to that of total organism density.

Most species are significantly spatially aggregated. The spatial variability (reflected in the CV of the mean density) of most species is even higher than that of the sum parameters.

Only species with a low density are characterised as randomly distributed (chapter 4.2.2), but especially for these species a much higher number of replicates would be necessary (i.e. 50 to 200 replicates) to achieve a reliable estimate of their spatial distribution (Andrew & Mapstone 1987; Krebs 1998).

As the investigation of single species populations is not the aim of this study, explicit calculations on the precision of density or biomass estimates in dependence of sample size are not presented here. As each species has its own spatial distribution, these calculations have to be done for each species separately. Many species also show seasonal changes in their spatial variability, while other species show the same spatial pattern throughout the year (Dittmer 1977). A large proportion of these differences in spatial variability can be explained by the increasing variance (s^2) with the mean described by a power function $s^2=a*mean^b$ known as "Taylors power law" (Taylor 1961; McArdle et al. 1990; Legendre & Legendre 1998). Some species that are present at several stations show a different variability at each station, therefore the results may even differ between stations. Suffice it to say that for most species five grab samples would result in an asymmetric confidence interval (C.I.) that is considerably larger than the mean. Under the assumption of a random distribution of organisms, a (symmetric) C.I. is calculated as

$$\bar{x} \pm \frac{t_{(\alpha,n-1)}}{\sqrt{n}} CV$$

where $\bar{x}$ is the mean density, *n* the sample size, $t_{(\alpha,n-1)}$ the value of Student's t-distribution for error probability α and n-1 degrees of freedom and *CV* the coefficient of variation. Especially for small sample sizes, this estimate is smaller than the C.I. for aggregated distributions (Krebs 1998). Nevertheless even this (underestimated) C.I. is larger than the mean (for n = 5) as long as the CV is larger than 0.4 ($t_{(0.05,4)}/\sqrt{5}$ = 1.24). Only a single species reaches such a small CV at a single station (*Scoloplos armiger* at FSd) while the CV of most species is considerably larger. A larger number of ten or more replicates is therefore recommended for studies of population density and spatial variability of single species (see also Rachor 1976; Dittmer 1977). Such an effort is often not possible because of practical limits in sample processing time.

A sample size of five replicate 0.1 vVs may be regarded as acceptable for an analysis of the *community* development but not for an appropriate description of single species population densities.

5.2.2.2 Community structure

Besides the sum parameters, the community structure is summarised by the species number per area (*species density* [for a definition of terms see methods chapter 3.4.1.2]) and the "evenness" reflecting the dominance structure. Diversity indices, such as H', combine aspects of species density and dominance structure.

The species density is at all stations much less variable than e.g. estimates of total organism density or biomass. The variability of the evenness and diversity indices J' and H' is generally even lower, but this depends on the dominance structure. At SSd and FSd, the two stations with the highest evenness (0.83), the variability of the evenness is much lower than that of the species density. The variability of H' is consequently intermediate between the two. At WB and Slt the evenness is much lower and has a much higher variability, similar to the variability of the species density. As H' is a product of J' and the *logarithm* of the species density, which has an inherently lower SD, the variability of H' is at WB and Slt lower than that of J' but still much higher than at the other two stations. The high dominance of single species at WB and Slt increases the variability also of the community structure. Fluctuations in the abundance of this species directly influence the value of J' and consequently H'.

The spatial variability seems to be linked closer to the community structure than to the total organism density and species density. It is not the station with the largest species density and the highest organism density (WB), that has the lowest spatial variability, but rather those stations with the highest evenness in the species distribution (SSd & Fsd).

Slt, the station with the lowest organism density and the poorest species spectrum is also the most spatially variable station. This could be seen as a result of a temporally variable environment (see chapter 5.4.4), as spatial variability is commonly seen as an indication of disturbance (Warwick & Clarke 1993). The second highest spatial variability was found at WB, the station with the highest organism density and the largest species spectrum. This station, the furthest offshore and deepest of all four stations, would, however, normally be seen as the most environmentally stable station. However, it is the only station which is outside the area of the "plaice box", which is partially protected from bottom trawling. Therefore WB is presumably subjected to the highest intensity of demersal trawling, which is also known to be patchily distributed in the area (Rijnsdorp et al. 1998; see chapter 5.4.2.1). Although both communities are not dominated by typically opportunistic species, the spatial variability could be caused by a higher frequency of disturbance. Without detailed information on the small-scale spatial distribution of disturbances at the stations, it is difficult to distinguish between the contributions of biotic interactions and community structure and those of environmental conditions to the development of the spatial variability of the community (see also chapter 5.4.4.1).

Sample size effects

Even though species densities and organism densities differ widely between the stations, there is one point in which all species accumulation curves (Fig. 4.2.6) are similar:

At all stations the number of species continues to rise even for 20 samples or more and there is no sign of it reaching an upper level within the range of samples at hand.

The total number of species found does not appear to be a good indication for an appropriate sample size. If the main aim of a study is the species spectrum of the local community, a deliberate limit has to be set for the expected number of additional species per additional replicate. In the species-poor community at Slt, nine replicates would have been enough to reach a point where each additional sample would yield less than one additional species, while in the species-richer community at WB more than 17 grabs would have been necessary. Because this measure is highly dependent on the number of rare species, it is not an appropriate limit when the temporal development of the community is the focus of the analysis.

The variability of the number of species for a certain sample size seems more informative for a decision of an appropriate reflection of the species spectrum of the community. At SSd and Slt, this curve stayed rather constant after an initial decrease up to a sample size of three to five grabs. The decrease in variability at a sample size larger than half the total replicate number is biased because of the decreasing number of possible combinations and cannot be interpreted (Bros & Cowell 1987). This variability in species number is a result of the spatial distribution especially of the rare species in the community.

Beyond the initial decrease for very small samples the variability in species number does not seem an appropriate measure either to determine sufficient sampling, but rather one of spatial heterogeneity in the local species composition of the community.

For analyses of community development an appropriate reflection of the community structure seems more important.

For single grabs the variability of J' and consequently H' is rather large. The decrease of the variability is most pronounced for the first three to five grabs.

Nevertheless the remaining variability differs between the stations. The large variability at Slt especially for J' indicates that a larger sample size of 10 to 15 grabs would be necessary to achieve a precision in the estimates of diversity at this station that is comparable to the level of precision reached at the three other stations with a much smaller sample size. However, such an effort is not realistically feasible in most cases, taking into account the costs of ship-time and personnel. A fixed level of precision may also not be necessary, as the variability also reflects the spatial heterogeneity, which is an attribute of the local community and as such a useful characteristic itself.

5.2.2.3 Community composition

Beyond the variability of sum parameters, spatial *community* variability is reflected in the similarity between samples, which includes the species identities and their densities. The frequency distribution of similarities (Fig. 4.2.13) gives a good impression of the homogeneity of the community.

The *mean* similarities between samples reflect the natural spatial variability of the communities. Consequently the community at SSd with the highest mean similarity exhibits the lowest community variability, followed by FSd, Slt and finally WB with the highest variability of the four stations.

The coefficient of variation (CV) of these similarities goes one step further and indicates how evenly the similarity values are distributed. This could be interpreted in terms of the spatial distribution of the community. Following this hypothesis, in an area with a patchy distribution of the benthic community, some pairs of samples should be found with an especially high similarity and others with extremely low similarities. The resulting CV of the mean similarity will be larger than in areas where the observed similarities result simply from random variability. It may therefore serve as a multivariate indicator of patchiness. This hypothesis should be further investigated by simulation studies. According to this hypothesis, the patchiness is also lowest at SSd, followed by Fsd. The communities at WB and Slt exhibit not only a higher spatial variability but also a higher patchiness. However, while the mean similarity at Slt is higher than at WB, the larger CV indicates a more patchy distribution of the community at Slt compared to WB.

Multivariate methods have shown to be more powerful for the detection of environmental impacts on benthos (Clarke & Warwick 1994) and to detect subtle changes in the community (Legendre & Legendre 1998). They are more powerful means of describing the community but still require replicate samples to distinguish between local spatial variability and temporal changes. In each area one to two exceptional samples occurred amongst the total of 20-21 samples per station, with a low similarity to the remaining samples (Annex: Fig. A.6.5), which must be expected in any sampling. Single samples may thus well be misleading. Not only for the possibility of statistical inference, but also for the recognition of community differences, replicates are clearly needed.

The spatial variability of the community at any single station is significantly lower than the difference between the benthic communities. The *temporal* variability of the benthic community at each station is also in all cases lower than the community differences between the stations. Each station represents a clearly distinct benthic community.

In both the spatial and the temporal MDS ordinations, SSd is positioned between the three other stations. The axis between the Slt and FSd can be interpreted in terms of increasing sediment grain size while the perpendicular axis is related to an increasing distance from shore. Correspondingly the largest differences in the benthic community are found between Slt and FSd (finest and largest grain size) and between Slt and WB (in- vs. offshore). The community at SSd shows aspects of all other stations, but is in all cases clearly distinct.

Sample size effects

As the precision of mean density estimates of all species rises with sample size, the differences between the abundance in the samples decrease and the similarity of the samples increases. For the same reason the variance of the similarities is also related to the sample size. The smaller the samples, the larger is the variance not only of univariate measures but also of the similarity between samples. A low variability and high similarity is indicative of an appropriate reflection of the benthic community by the respective sample size. Most (dis-) similarity indices are influenced by sample size (Wolda 1981; Streever & Bloom 1993; Schleier & van Bernem 1998; Kohn & Riggs 1982; Walsh 1997; Cao Yong et al. 1997; Kobayashi 1987). The systematic influence has been investigated in simulation studies (e.g. Wolda 1981) based on a theoretical community with a species composition according to a log-series and an independent random distribution of all species. Under these assumptions, the expected similarity must be higher than in reality, which is characterised by spatially clumped distributions and interspecific correlations. The expected similarity, its sample size dependence and variability for real communities can therefore only be realistically estimated using real data.

A similarity of 100% for the Bray-Curtis (BC) index can only be reached if the compared samples contain exactly the same species in exactly the same abundance. With the natural variability in species composition and organism density, the mean similarity between replicates from the same community is usually lower (Bray & Curtis 1957). Values of 70% to 80% BC similarity have been proposed as an indication of a sufficient sample size (Weinberg 1978; Kronberg 1987). With the present data, a level of 70% would be achieved with only two grabs at most stations, which seems an unrealistically small sample considering the observed variability of sum parameters. A level of 80%, however, is in 1998 not reached at Slt even with a sample size of ten grabs. Nevertheless, in certain years the mean similarity even between single grabs at Slt can be as high as 80% or even 90%, as visible in the comparison of spatial variability over time (Fig. 5.2.15).

An absolute similarity level for all communities seems not realistic as indication of a sufficient sample size, as the mean similarity is also a measure of spatial variability of the community. Instead, an adequate sampling can be assumed at the point where the average similarity does not increase remarkably with a further increase in sample size. The very shallow slope of the similarity-area curves above five grabs indicates that only minor improvements can be achieved by increasing the number of replicates above five.

For a remarkable increase in similarity and reduction in variability, the sample size would have to be doubled to ten replicates (Fig. 4.2.14). The influence of sample size on the mean inter-sample similarity results from two effects: The increase in species number and the increase in precision of mean abundance estimates with increasing sample size.

Some authors claim that similarity indices should be independent of sample size, which is in this context generally expressed as the number of organisms per sample (Wolda 1981). Because the number of species in the samples influences most indices, only similarity measures that are based mainly on the comparison of the dominant species can be relatively free from sample size influences (Krebs 1998). Beyond the variability for small samples, a sensitivity for changes in organism density in general is also a desirable property. Comparing standard samples of equal areas, density differences of the present populations *do* reflect something going on. Differences in the abundance of the species between samples will lead to a lower Bray-Curtis similarity even if the number of species and the proportional composition remain the same.

5.2.2.4 Temporal changes in spatial variability

The main intention of the spatial sampling was to examine the spatial variation at these permanent stations as a background for the analysis of the temporal development of the benthic communities. However, the spatial variability of communities does also vary over time. The small number of usually five replicates taken for the long-term series does not allow good estimates of the spatial distribution of single species or the spatial variability of community parameters. The multivariate similarity between five replicates results in ten similarity values per sampling occasion. The mean similarity between replicates is the most inclusive measure for a comparison of the spatial *community* variability between years, combining changes in species composition and abundance.

The large differences in mean similarity observed over the years show that the spatial variability at any station is not constant over time. In a study of the spatial distributions of polychaetes near the FSd-station, Dittmer (1977) found that the spatial distribution of many species varied also seasonally. The values calculated from the samples taken in 1998 can therefore not be generalised, although the observed community variability in 1998 is close to the mean variability over time (Fig. 4.2.15). Just like the species number and dominance structure vary between years, so does the spatial variability. Therefore the temporal differences between years can only be compared to the spatial variability estimates of the respective years (ANOSIM results: Annex Tab. A.5.2 - A.5.5).

The community differences between years are in all cases significantly larger than the respective spatial variability at the station.

Replicate samples are necessary at any sampling time to get an estimate of the spatial variability. The actual precision of community parameters cannot be exactly predicted from the analysis of the data from 1998. The *relative* changes of the respective measures in relation to sample size and their decreasing variance should however be valid also for other years.

5.2.2.5 Sample size needed for statistical inferences

As power analysis for nonparametric and multivariate methods is not available, the desirable sample size for various measures is defined by a compromise between the increasing effort and the achieved improvement of the precision of the estimate.

If any statistical inference is intended, replicates are needed to assess the *within*-sample variability and compare it to the *between*-sample differences. Because frequency distributions of sample parameters are hard to estimate from small samples and are unknown for most diversity and similarity indices, nonparametric methods are more appropriate and with small sample sizes often even more powerful than parametric methods (Zar 1996). For small sample sizes the error probability of nonparametric tests is calculated by a permutation procedure comparing the observed value to all possible values for the given sample size. In multivariate analyses, difference of the "between" and "within" group (rank) similarities is also tested for statistical significance by permutation (Moore et al. 1984; Clarke & Warwick 1994). The number of replicates restricts the number of possible permutations and thus the maximum possible significance level for these tests (Clarke & Warwick 1994).

For statistical inferences about community changes, a minimum of four, five or seven replicates is needed to allow for a significance level of 5%, 1% or 0.1%, respectively.

An exact calculation of the sample size needed for the detection of a certain effect size based on the observed variability of samples is possible for parametric tests (Zar 1996; Thomas 1997; Sheppard 1999; Underwood 2000) and specialised software is readily available (Thomas & Krebs 1997). Statistical power analysis for nonparametric tests, however, is a very new field of research and can only be realised by simulation (Mumby 2002). Although nothing is known about the formal relationship between power and sample size for multivariate methods (Clarke & Green 1988), it clearly depends on the variability of the data and on the effect size that needs to be detected. A quantifiable measure of power to detect a community change of a certain size would need a detailed simulation study using artificially created and exactly defined levels of difference between samples, which would be an interesting topic, but is beyond the scope of the present study.

5.2.3 Systematic sample size influence on measures of community structure

All measures that are related to the number of species or the community structure also show a systematic dependency on sample size. The systematic dependency implies that these measures should only be compared between samples of the same size, but it also contains information about the spatial homogeneity of the sampled community.

The species number, diversity and evenness indices as well as most similarity indices are strongly influenced by the sample size (Hill 1973; Colwell & Coddington 1994; Krebs 1998; Gray 2002). However, the sample size dependency found in this study differs in several aspects from the predictions of theoretical simulations (Wolda 1981; Smith & Wilson 1996). These differences allow some interesting conclusions about the properties of the respective measures as well as about the studied communities.

The term "diversity" has been used in so many different ways that Hurlbert (1971) even declared it a non-concept. Unless one is willing to describe the whole community structure, a combination of indices may still be useful for comparisons, provided that their specific information content and focus are borne in mind. Diversity includes two components, the number of species present and their frequency distribution (Legendre & Legendre 1998). Diversity indices such as Shannon-Wiener's H' are heterogeneity measures incorporating both aspects of species number and evenness (Hill 1973).

5.2.3.1 Species number

The species accumulation curves of all four stations do not approach a constant value but rather continue to rise even for large samples (Fig. 4.2.6). For marine communities, this seems to be the general rule even for much larger samples (Rumohr & Karakassis 1999; Gotelli & Colwell 2001; Gray 2002). It is in most cases impossible to determine or even estimate an absolute number of species for these open communities delimited by gradients rather than borders. Various methods have been developed to estimate the total number of species in a community (see e.g. Colwell 2000), but all estimates increase for marine benthic communities almost as much with sample size as the species number itself (Ellingsen 2001; Melo & Froehlich 2001; Rumohr et al. 2001; Gotelli & Colwell 2001) and therefore seem not very helpful.

Just like abundance or biomass values, which are always related to a certain area, the species number should be related to the sampled area and rather be referred to as "*species density*".

Comparing species density between the stations, WB has with 56 species the highest number of species per m², followed by SSd (50) and FSd (43) and Slt has the lowest species density with only 25 species per m² (Fig. 5.2). This relation is only changed at samples of less than three grabs. Although there is generally a positive relation between sample and total species number, the mean number of species per grab at WB (21 spp.) is smaller than at SSd (23 spp./grab) while the total number of species collected at WB is larger than at SSd (69 spp. vs. 60 spp. in 21 grabs). This highlights the importance of taking a large enough number of replicates to overcome small-scale spatial variability and to appropriately reflect the community at a station; in this case five grabs seem sufficient, as a larger number of replicates does not change the results.

Species richness and *species density* measure two different things, analogue to *diversity* (heterogeneity) indices that incorporate aspects of *species density* and *evenness*:

Species richness incorporates aspects of *species density* and *organism density*. It is as such rather a measure of diversity (heterogeneity) while *species density* and *organism density* are the basic numbers measured independently of one another.

In the context of spatial analyses, *species density* is the appropriate measure. Whenever theoretical predictions and models are formulated in terms of organisms, *species richness* would be more appropriate (Gotelli & Colwell 2001).

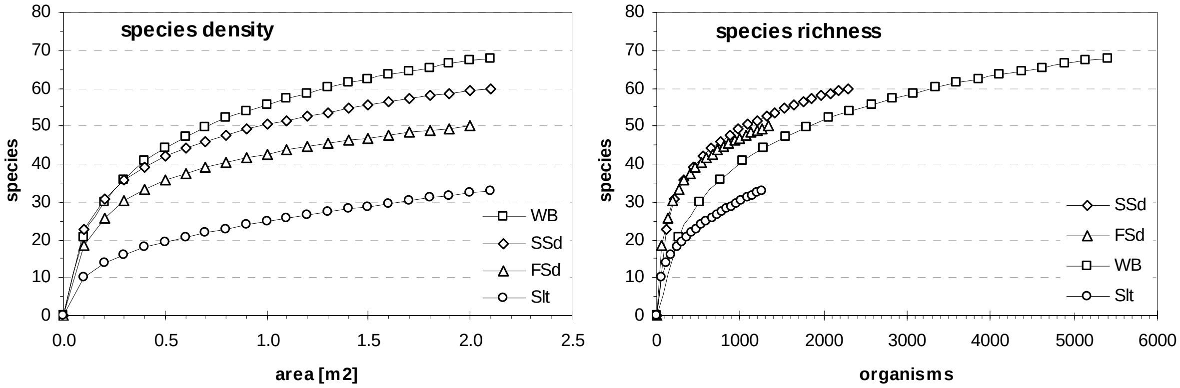

Fig. 5.2: Comparing species density (left) and species richness (right).

Comparing *species richness*, at SSd and FSd the highest number of species were found in relation to the number of organisms (Fig. 5.2). Over the range of samples available, WB has a clearly lower species richness, at low sample sizes even comparable to the otherwise much lower species richness at Slt. This highlights the strong influence of the large numerical dominance of *A. filiformis* at WB, leading to a completely different assessment of the species richness compared to the species density.

Sanders' rarefaction method (Sanders 1968; improved by Hurlbert 1971) calculates the number of species expected for a specified fraction of the total number of organisms to remove the density dependence. In this case the comparison is one of *species richness*. These individual-based rarefaction curves, however, often overestimate species numbers

(Simberloff 1972). They rely on the assumption of randomly distributed organisms, and that dominance does not vary with sample size. The fact that almost all benthic species are spatially aggregated and dominance usually decreases with sample size has been made responsible for the reported overestimation for rarefied samples (Gray 2002).

In contrast, sample-based species accumulation curves incorporate the actual spatial variability of the community and allow more precise estimates and comparisons between communities (Loehle 1990; Kronberg 1987; Gotelli & Colwell 2001). The sample-based curve depends on the spatial distribution of the organisms and of the size and placement of samples (Hurlbert 1990) and can therefore not be theoretically derived.

The difference between individual-based and sample-based species accumulation curves is seen as an indication of the patchiness in the distribution of the organisms (Colwell & Coddington 1994; Gotelli & Colwell 2001). Following this interpretation, the very small difference between these curves observed in this study would be seen as an indication of nearly randomly distributed organisms. This is, however, not the case, as most species showed a significantly aggregated distribution at all stations studied here.

A high dominance of a few species may lead to an underestimation of the species number by rarefaction (Gray 2000). This influence is not apparent for the present samples, as the rarefaction curve for WB overestimates the species number although the community is strongly dominated by a single species. The deviation between the rarefaction curve and the empirical species accumulation curve is even smaller at other stations with a lower dominance.

A possible explanation for this phenomenon could be a question of species associations. The difference between the curves could reflect a possibly scale-associated spatial heterogeneity of the community (Wiens 1989) but not in terms of *independently* clumped distributions of the species but rather in terms of spatial correlation between species. In larger and/or heterogeneous areas species will tend to occur together leading to an over-estimation of the species density for smaller samples because not all species have the same probability of being found in any sample. In smaller and/or homogeneous areas the overall probability is the same for any sample. The question in how far spatial distribution or species associations are responsible should be analysed in simulation studies that go beyond the scope of the present study.

5.2.3.2 Evenness

The evenness of the species' frequency distribution is summarized by Pielou's J' relating the observed diversity to the maximum value obtained when all species are present in equal abundances (Pielou 1966). Like several other evenness indices it has been criticised for its sample size dependence (e.g. Krebs 1998).

The systematic dependence between evenness and sample size is an *increase* with sample size found in theoretical simulation studies (Smith & Wilson 1996). The behaviour observed in this study is just the opposite: Evenness *decreases* with sample size at all stations. This effect is strongest at small sample sizes, whereas the mean evenness value for larger sample sizes is almost constant.

Dominance is commonly measured by (1-J') and is the opposite of evenness. Most studies of larger spatial scales found that dominance decreases with sample size and increasing species number (Fager 1972; Gage & May 1993; Gray et al. 1997). A possible positive relation between dominance and species density was proposed by Birch (1981).

This apparent contradiction may not be a question of the relation between dominance and species number itself, as the above-mentioned authors implied, but rather a question of sample size and sampling scale or homogeneity of the sampled area:

A possible explanation for the systematic increase in dominance observed in this study may be found in the distribution of rare species. Especially at smaller sample sizes, the number of species that are present as single individuals usually increases with sample size (Rumohr et al. 2001; Gray 2002). A doubling of the sample size will result in a mean doubling of the abundance of all species except for the rare species. A number of the latter will still be present with a single individual while other rare species are added. This results in a (small) decrease of evenness respectively an increase in dominance. This effect will only be observed if all samples are taken at random from a generally homogeneous community. It is most pronounced in species poor communities and at small sample sizes when the increase in species number is largest. The higher the proportion of rare species, the stronger will be the decrease of evenness with sample size.

A different mechanism can be proposed to cause the decrease in dominance if samples are taken on a larger spatial scale. The larger the scale, the more slightly different habitat types will be included. Each of these will have a slightly different dominance structure, i.e. a different species may be dominant. A combination of two systematically different samples will not result in a doubling of the abundance of the dominant species in the first sample but rather in a larger increase in a subdominant species, which is dominant in the second sample. The larger the differences between the samples, the stronger will be the increase in evenness respectively the decrease in dominance.

Following this hypothesis, a decreasing evenness with increasing sample size can be seen as an indication of a homogeneous area and thus, community. An increasing evenness with increasing number of pooled sampling units can be interpreted as an indication of a heterogeneous area including several differing types of benthic community.

5.2.3.3 Heterogeneity diversity

The Shannon-Wiener diversity index H' has a low variability of estimates and reaches quite a constant value at rather low sample sizes. The systematic increase of H' with sample size is pronounced only for less than five grabs. The sample size influence is much lower than for the species number (S) or even for the evenness (J'). While the number of species strongly rises with sample size, evenness declines. Because H' is a combination of both aspects [$H' = J' * \log(S)$], the opposing trends of species density and evenness cancel each other out and lead to rather constant values of H' for larger sample sizes.

Despite the highest total species number found at WB, the strong numerical dominance of *Amphiura filiformis,* reflected in the low evenness value, is the reason for the lowest "diversity" of all stations. The influence of the evenness on H' seems stronger than that of the species number. The combination of both aspects of diversity is intended to combine statements on the diversity of faunal communities into one value. As a higher species number can be cancelled out by a lower evenness (or vice versa), the result of comparisons of only heterogeneity indices between samples may be misleading. An additional comparison of the species number and evenness is advisable in any case.

In practise, a presentation of S and J' is the most informative way to summarise the diversity of faunal communities. Because of the systematic dependency of both measures on the sample size, they should only be stated in relation to the sample size (area).

5.2.4 An optimal sample size ?

As the variability of all measures is the result of the local spatial variability, which is an inherent property of the examined community, changes in the community will also cause changes in the precision of the estimates. A fixed limit of precision cannot be reached without adjusting the number of replicates depending on the respective situation, which is not feasible in most instances. The relative change and increase in precision in relation to sample size of the here-examined measures may still be assumed similar. If this is the case, some general assumptions can be derived.

There is no absolute sample size that is appropriate for all studies. Depending on the aims of the study, a sample size has to be found that achieves a sufficient precision of the studied measures. For specific types of analyses and an *a priori* fixed effect size, the required sample size can be calculated by power analysis using the observed variance of representative samples. However, the precision achieved by a certain replicate number differs not only for the different parameters and between the stations, but varies also in time. Therefore to be sure to achieve a certain power, the maximum variability observed in time would have to be assumed.

In practise a compromise has to be found between feasibility and power. Although power analysis has not been developed yet for multivariate methods, these methods have proven to be very powerful in detecting even small changes in benthic communities. For such analyses even a definition of an effect size is very difficult and simulation studies based on null-models would be necessary. The practical choice of sample size for community studies will mostly rely on an evaluation of the improvement achievable by an increase in sample size, compared to the expended effort (Bros & Cowell 1987).

As often the number of replicates goes at the expense of the number of stations, two to three replicate 0.1 m^2 vVs may be a compromise for studies of large-scale spatial distribution of communities. If spatial or temporal comparisons are intended, a larger number of replicates per area are required, depending on the spatial variability of the area. A sufficient characterisation of a local community of small homogeneous areas (like those around the long-term stations) for long-term studies may be assumed with a standard number of five replicates as a practical compromise to detect the main trends. This is, however, still a rather crude measure and a sample size of ten or more grabs would be desirable for an analysis of the local densities of the dominant species.

5.3 Temporal development of benthic communities

At all stations, a large interannual variability of the benthic communities was combined with a variation on a roughly decadal scale and a couple of unusual years presumably following disturbances. A general description of the temporal development will be followed by a more detailed discussion of the effects of influential factors in subsequent chapters.

The multivariate community analysis identified several groups of years with a similar community composition at all stations and a couple of exceptional years. The groups represent roughly the 70ies, 80ies and 90ies, but they are not distinctly separated by strong changes. Exceptional community compositions were recorded in most cases following extremely cold winters (see e.g. Fig. 4.3.4a).

The transitions between the periods are rather gradual changes in species composition and dominance structure, and each period is itself subject to large interannual community fluctuations.

The periods correspond roughly to the observed shifts in various compartments of the biological system of the North Sea in the late 70ies and the late 80ies (Lindeboom et al. 1994; Reid et al. 2001). Major transitions in benthic communities were recorded in various parts of the North Sea around 1979-81 and 1986-89 (Austen et al. 1991; Kröncke et al. 2001; Warwick et al. 2002). While some indications of changes as early as 1987 may also be seen at WB and SSd, large changes followed between 1989 and 1990 and again 1992/93 and make a clear identification of a "point of change" in the German Bight difficult. Apart from the poor communities found at all stations during the early 70ies, which are suspected to be at least partly due to methodological changes, the above-mentioned periods do not differ significantly in total density of organisms, species number or community structure. Major changes of these parameters are reflections of short-term fluctuations often related to disturbances rather than persistent changes over longer periods. The largest changes in the benthic communities follow severe winters, which strongly influence macrofaunal communities in coastal areas (Ziegelmeier 1964; 1970; Gerdes 1977; Buhr 1981; Dörjes et al. 1986; Arntz & Rumohr 1986; Beukema 1989; Kröncke et al. 1998; Armonies et al. 2001).

The clearest development can be seen at the two deeper stations, the Silty-Sand-station (SSd) and the station east of the White Bank (WB).

The most prominent feature of the community development at **SSd** are the changes following the severe winters of 1970, '79, '86 and '96 (Fig. 4.4.4). Following all of these winters, the densities of many species decline markedly and a few opportunistic species, mostly small polychaetes, increase, as already found in earlier years by Ziegelmeier (1964; 1970). While the community during 1993-95 approached a similar composition as already found during the 70ies, the change initiated in 1996 is followed by a recovery from 1997 to '99 that results in a similar community composition as found during the 80ies. In 2000, the community approaches the situation of the early 90ies again, although *A. filiformis* has not regained its former densities, while several small bivalve species (*Nucula nitidosa, Mysella bidentata, Montacuta ferruginosa, Tellina fabula, Abra* spp.) reach extremely high densities.

A similar temporal development is visible in the shorter series from **WB**. Here, most of the 80ies represent a rather persistent community dominated by *Amphiura filiformis*, only interrupted by 1984 with a low species number and lower density of many species indicating a possible influence of the hypoxic bottom waters recorded in the area in 1983 (Niermann et al. 1990; 1997). Similar low oxygen contents recorded in the area already in 1981 and '82 (Rachor & Albrecht 1983) are, however, not reflected in the benthic communities. A low density of *A. filiformis* in 1989 may be seen as a beginning of a gradual change in the community over the following years, but a major change in the community occurs in 1992/93. Strong decreases of the dominant species, especially *A. filiformis*, lead to a more even community structure, which persists until 1995. The severe winter of 1995/96 initiates the largest changes observed at this station, with a strong decrease of most species. This is followed by a massive recruitment mainly of the species that were dominant during the 80ies, and by 1999 the community has reached a similar composition as during the early 90ies.

Although a roughly similar temporal development is discernible at the shallower Silt-station (Slt) and Fine-Sand-station (FSd), large interannual fluctuations render the picture less clear.

The community at **Slt** is characterised by the lowest interannual similarity of all stations, with very large fluctuations of most species. The community composition following the cold winters is not as clearly different from other years, although most of these years are to some extent separated from the respective periods, with generally low species numbers and abundances. The community development following 1996 is similar to the development after 1970, and the community approaches in the 90ies the situation of the 70ies again. Both periods are characterised by a dominance of *Nucula nitidosa*, which was less abundant during the 80ies, when *Diastylis rathkei* dominated the community.

Although interannual similarity is higher at **FSd**, the community is dominated by opportunistic species like *Magelona mirabilis* and other small polychaetes during most years. Therefore, the years following most severe winters are not as clearly separated from the remaining years. However, marked changes are visible following 1996, and a situation similar to the early 90ies is only reached again by the year 2000.

The separation of roughly decadal periods should not be interpreted as periods of relative stability separated by major transition.

Each of these periods is characterised by strong fluctuations and often a development within the period. Periods without major changes are the exception, and significant inter-annual changes are the rule.

Whenever enough replicates are available, nearly all years are significantly different in community composition from all other years (Annex Tab. A.5.2 – A.5.5).

Large inter-annual changes and interruptions by "exceptional" years make a statistical detection of temporal trends difficult. An application of regression analysis or smoothing methods or filters to extract long-term development against interannual ("random?") variability would also ignore the occurrences of distinct disturbances, which are a characteristic feature of these shallow-water systems. Therefore, the simple visual inspection and description of the development of the communities and nonparametric correlation analyses with environmental factors are probably the best way to interpret the present data.

As each station represents a clearly distinct type of community, the nature of the community changes differs. Fluctuations in total abundance or species density are not in parallel between the stations, except for a few common features. Lower total abundance and species number found at most stations during the early 70ies may in part by related to low penetration depth of the grab especially at FSd and SSd. As the increasing species number in the late 70ies was also observed at Slt, where it is not correlated to methodological changes, it should be based on real increases in species density. From then until 1995, no major trends in the species number are observed. The development during the 90ies is remarkably similar between the stations, with a relatively high species number until '95 (with the exception of a low species number in '93). At all stations, species number drops after the severe winter of 1995/96 with a recovery after two to three years.

Beyond these similar development of the species density, the temporal development of the benthic communities at the different stations does not run very much in parallel and a couple of species do even exhibit opposing trends at different stations. While large inter-annual fluctuation make a detection of long-term trends difficult, a number of significant correlations to environmental variables was detected at all stations.

5.4 Internal dynamics and external forcing

Temporal fluctuations of shallow water benthic communities are mainly the result of environmental fluctuations including abiotic factors as well as a variable food supply from pelagic production, while the nature of the response of the community depends on the type of community present and on interactions between species.

5.4.1 Environmental forcing

A persistent community structure can only develop under stable environmental conditions. However, the environmental factors examined here exhibit large inter-annual variations and some decadal changes.

Most notable are the increasing tendency of the NAOI (Fig. 4.5.1 & 4.5.2), with its consequences on higher winter temperature (Fig. 4.5.3) and the increasing frequency of strong winds observed in the German Bight (Fig. 4.5.5). An increasing concentration of phosphate during the 70ies was reversed in the late 80ies (Fig. 4.5.9), while nitrogen concentrations continued to increase (Fig. 4.5.10).

Several of these variables were correlated to changes in the benthic communities. Correlations cannot be used to infer direct functional relations, but if known mechanisms (e.g. from experimental studies) are tested on the long-term data, correlations can give evidence for the relevance of these mechanisms for community ecology.

5.4.1.1 Correlations between environmental factors

The NAO index (NAOI) reflects the main weather pattern over the northeast Atlantic and therefore summarises several climatic factors, but also all other environmental variables presented here are correlated to several others (see Tab. 4.6.1):

The North Atlantic Oscillation (NAO) strongly influences the weather in northern Europe especially in winter. Positive values of the winter-NAOI are associated with westerly weather and thus a stronger oceanic influence and mild winters (Hurrell 1995). This is reflected very well in the strong, positive correlation between the NAOI and the frequency of strong westerly winds as well as the winter water temperature at Helgoland. Negative NAOI values are associated with easterly weather, which results in a continental influence on northern Europe and, consequently, often cold winters (Hurrell 1995). Cold winters are however not always connected to a very low NAOI. The very cold winter of 1979 has a low but not exceptional NAOI. The winters between 1985 and '87 were amongst the coldest of the last thirty years, and water temperatures at Helgoland declined even below 0°C (Fig. 4.5.3), while the NAOI was around zero. The frequency of stormy days is also correlated to the NAOI, especially for westerly directions, but the frequency of easterly winds shows a development that is not reflected in the NAOI. Local water temperatures and storms are those factors that may directly influence benthic communities whereas the NAOI is a summarising factor for the large-scale weather development. It may therefore incorporate signals from larger scale processes that are not necessarily reflected in local abiotic factors.

The main windy season in the German Bight is between September and April. The annual NAOI is therefore not so closely correlated to the frequency of strong winds, but it shows a significantly negative correlation to the river runoff of the Elbe and consequently a positive correlation to the salinity at Helgoland. A positive annual NAOI is associated with lower precipitation and river runoff (Hurrell 1995). The large rivers entering the North Sea are the main sources of inorganic nutrients such as phosphate and nitrogen (OSPAR Commission 2000), which are important factors for the primary production by phytoplankton. While nitrate concentrations in river waters increase during phases of higher precipitation and associated leaching from agricultural areas, concentrations of phosphate, originating mainly from waste water discharges, are generally rather diluted (Hickel et al. 1997). Nevertheless, the total amount of nutrients entering the German Bight increases with higher river runoff (OSPAR Commission 2000). The actual concentrations of these nutrients at Helgoland are negatively correlated to the salinity, but this correlation is not very high, as the nutrient concentrations are also influenced by the actual uptake by phytoplankton and by the relation between the amount of nutrients that is recycled in the pelagic system or exported to the benthos. The correlation between nutrients and Elbe river runoff is even lower, as variable hydrographic conditions may alter the amount of riverine waters reaching Helgoland (Hickel et al. 1997).

The concentration of silicate is only correlated to the frequency of strong winds, especially from easterly directions and to the mean winter temperature. Strong winds mix the water and bring nutrients from deeper layers to the euphotic zone. In the German Bight, especially easterly winds result in an offshore transport of surface waters, which is replaced by an onshore transport of deeper waters through the Pleistocene Elbe valley. This and/or an export from the Wadden Sea may explain an increasing supply of silicate.

5.4.1.2 Effects of environmental variation on benthic communities

Even if the temporal development of the benthic communities shows similar features for all stations, the environmental factors that show the highest correlation to the benthos differ between the stations (see chapter 4.7). The winter-NAOI shows a correlation to the development of the benthic communities at all stations.

Except for the deepest and most offshore station WB, a positive correlation of the species number to the winter NAOI was found at all other stations. This is a common phenomenon, which has also been found in other studies and is presumably mostly mediated by the water temperature (Kröncke et al. 1998). The fact that nearly no direct correlation to the mean winter temperature or the possibly even more important minimum winter temperature has been found at any of the stations does not question the strong influence of severe winters on the benthic communities. Clear changes have been found at all stations following these cold winters. A correlation between the benthic community and the water temperature may not be detected because it is not a monotonic one, but rather a form of disturbance that only happens when a certain threshold has been surpassed. In these severe winters the survival of less cold-adapted species is low, leading to a decreasing species number (Kröncke et al. 1998). Especially when some of the dominant species are affected, such as *A. filiformis* at SSd and WB, major changes in the community structure may result, which are only reversed after several years.

The effects of the severe winter 1995/96 were clearly visible at **WB** and correlations of the abundance and community structure to the NAO were also observed at WB (Tab. 4.7.2 & 4.7.6). The strong correlation of the benthos development at WB to the frequency of easterly winds is mainly caused by the strong increase of the latter seen in 1991 and from '93 onwards. During the years '92/'93 the most pronounced changes occurred in the benthic community at WB including a dramatic decrease of *Amphiura filiformis* and several related species. These started to recover, however, already in 1998, while eastern storms still occurred frequently with a decrease in frequency only visible in 2000. This indicates that the observed correlation cannot be seen as a direct influence, but might rather hint at some indirect mechanisms like changes in hydrographic conditions.

A conspicuous feature of the benthos-environment correlations at **SSd** is - besides the influence of the NAOI - the prevalence of factors related to nutrient concentrations and the lag of two years (Tab. 4.7.1 & 4.7.5). This indicates a possible influence via the planktonic system (see below). The fact that neither salinity nor the river discharge of the Elbe shows any correlation to the benthic community development makes a direct influence of the river water unlikely.

The species density at **Slt** is most closely correlated to the concentration of nitrogen. The correlation of the benthic community development to the phosphate concentration also indicates a connection to the phytoplankton development. Besides the correlations to the NAO and the frequency of storms, the community at Slt is correlated to all nutrient concentrations in some way (Tab. 4.7.3 & 4.7.7).

At **FSd**, the total abundance is not correlated to any of the environmental variables. However, the species density is significantly correlated to the NAOI, the winter temperature and the frequency of easterly storms (Tab. 4.7.4). A low NAOI and winter temperature as well as a high frequency of easterly storms result in a reduction of the species density. Also the community development at FSd is significantly correlated mainly to the winter NAOI and to the frequency of storms (Tab. 4.7.8). Winter temperature and storms seem to be the main influential factors for the community development at FSd, although the correlations with lags up to three years and the factor time indicate the importance of biotic interactions (see chapter 5.4.3).

The development of the benthic communities at all stations shows correlations to the winter-NAOI and exhibits clear changes following severe winters.

In addition to this, the local communities are also influenced by differing factors:

- at WB by easterly storms, which may hint at some indirect mechanisms like changes in hydrographic conditions;
- at FSd and Slt by storms;
- at SSd and Slt a correlation to nutrient concentrations indicates influences of the planktonic system.

While some of the detected correlations and large time lags are difficult to interpret with the present data, they may be seen as indications of indirect effects and biological processes producing a delayed perception in the benthic community. In many cases, these are presumably related to changes in the planktonic system, which may in turn be driven by nutrient supply. These connections are further discussed in the context of eutrophication (chapter 5.4.2.3).

5.4.2 Anthropogenic influences

5.4.2.1 Fisheries

Relating the observed long-term changes in benthic communities over the last century (Rachor 1990; Kröncke 1990; 1992; 1995; Rumohr et al. 1998; Reid & Edwards 2001) to the direct effects of demersal fisheries (Bergman & van Santbrink 1994; Bergman & Hup 1992; Bergman et al. 1990) and to the differences found between fished and unfished areas (Tuck et al. 1998) has led to the conclusion that 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; Kröncke 1995; Lindeboom & de Groot 1998; Jennings & Kaiser 1998; Frid et al. 1999; 2000; Piet et al. 2000; Kaiser & de Groot 2000). However, a clear identification of the contribution of bottom trawling to the observed changes is still difficult. On the one hand this is due to the relatively high natural variability of the communities of the North Sea and their elasticity against short-term and localised disturbances (Rachor & Gerlach 1978; Niermann et al. 1990; Rachor 1990). On the other hand it is often not possible to distinguish the influence of fisheries from the multiple influences of pollution and eutrophication (Rachor 1990; Duineveld et al. 1991; Rachor & Schröder 2003).

In 1989, a partially closed area in the coastal waters of the southeastern North Sea, the "plaice box", was established, to reduce the trawling effort of large beam trawlers (>300 hp) and thereby to protect the main nursery areas of plaice (*Pleuronectes platessa*). The beam trawl effort has decreased in two phases. During 1989–1993, when the "plaice box" was closed only during the second and third quarter, effort was reduced to around 40% of the original level. When the box was also closed in the fourth (1994) and first quarter (1995 onwards), effort decreased to around 6% (Pastoors et al. 2000). Following the establishment of the "plaice box", the effort in the adjacent areas increased.

The station WB is situated outside the "plaice box" in one of the most intensively fished areas in the southern North Sea with an annual trawling frequency of four to eight times per year by the Dutch fleet alone, although a rather patchy distribution of effort (Rijnsdorp et al. 1998). Detailed information on other fleets is not available. The strong decline of *Amphiura filiformis* at WB in 1989 and from 1992 until 1995 could be related to an increased fishing effort in the area. The fact that the low density in 1989 is followed by a high density in the next year may indicate some localised influence at this station, followed by an immigration of adult individuals from the vicinity, as *A. filiformis* is a relatively mobile species (47m/h) (Rosenberg et al. 1997). However, community changes between 1992 and 1993 are also evident at the other stations, suggesting an influence of other, large-scale factors.

The three other stations are situated within the area of the "plaice box" and should therefore have experienced a decreasing effort since 1989. An intensive eel fishery in the inner German Bight was also cancelled in July 1988 when the catches were not worth the effort any more (15-20kg / 12h) (Lozán 1990). This may have contributed to the changes observed at the stations in the inner German Bight during the 90ies such as the increasing density of *Lanice conchilega* or *Callianassa subterranea,* but these could also be related to changes in climatological factors or the planktonic system. However, smaller vessels are still fishing in the area and as detailed information on the spatial distribution of fishing effort is not available, any inferences about the influence on the communities at the sampling stations remains speculative.

Frequent disturbances favour the establishment of small, opportunistic species, while the densities of larger long lived species are reduced (Rachor & Gerlach 1978; Riesen & Reise 1982; Kröncke & Rachor 1992). Apart from the influence of eutrophication, which generally induces a similar effect, this may be seen as an indication for an increase in the frequency of disturbance from the increased fishing pressure. This may contribute to the explanation of the frequently observed extremely high numbers of *Phoronis* spp., *Magelona* spp., *Owenia fusiformis*, *Spiophanes bombyx* and other opportunistic species. These species can colonise disturbed areas very quickly, and they are not very dependent on a specific type of sediment, leading to a wide spread dominance of this group. Mostly, the increased eutrophication had been used to explain this trend (Pearson & Rosenberg 1978; Rachor 1990), but a general increase in the supply of organic matter within certain limits should also result in better conditions for filter and suspension feeders such as most bivalves and several echinoderms. However, the numbers and especially the biomass of these species declined, while that of the above mentioned opportunistic species increased. This provides evidence for an increased frequency of disturbance (see chapter 5.4.4), affecting longer-lived species more strongly and putting the faunal communities back to an earlier successional stage.

Bottom trawling has been shown to have strong impacts on benthic organisms. However, from the benthic community data analysed here, a distinction of the trawling effects from the often similar effects of various other factors is not possible. Inferences about the fishing effects on the benthic communities without detailed information on the development of the local trawling intensity at the sampling stations remain speculative.

5.4.2.2 Pollution

Changes in benthic communities due to pollution have been shown for estuarine and coastal regions and in the vicinity of oil or gas platforms (Rees & Eleftheriou 1989; Davies et al. 1984; Kingston 1992; Kröncke et al. 1992; Tapp et al. 1993; Olsgard & Gray 1995). Also in the open North Sea, elevated levels of many heavy metals and other contaminants have been found in sediments as well as in the fauna (OSPAR Commission 2000; Kröncke & Bergfeld 2001). The physiological effects of several contaminants like e.g. Tributyltin (TBT) on gastropods are well documented, leading to "imposex" with subsequent reductions of the populations (Spence et al. 1990; Cadée et al. 1995). Organic toxicants and TBT may also negatively affect zooplankton grazing and thereby contribute to larger phytoplankton blooms (OSPAR Commission 2000) and enhancing several effects of eutrophication. Nevertheless, it is still difficult to prove a correlation between contaminant levels and benthic community changes in open waters (Kröncke 1995).

The most probable pollution effects on the communities of the long-term stations in the German Bight should be expected from the former dumping of wastes at the FSd station and east of the Slt station.

About 4.5 nm east of the Slt station sewage sludge from Hamburg was disposed until 1980 (Rachor 1982). A trend of impoverishment of the fauna at Slt in the 70ies with a decrease of the dominant bivalve *Nucula nitidosa* has been attributed to the development of anaerobic conditions, favoured by thermohaline stratifications of the water during summer in combination with the sewage sludge disposal (Rachor 1977; 1980). The dumping ceased in 1980 and species numbers have since been higher, although the densities of several bivalves remained low until the mid- to late 80ies. However, the dominant bivalve *N. nitidosa* is able to tolerate anaerobic conditions for several days and its mobility allows unburying itself if covered by sediments during stormy weather. *N. nitidosa* was also abundant in the direct area of the sewage sludge disposal (Rachor 1976). Although some changes of the local community in the dumping area have been attributed to the disposal, a lasting effect could not be proven due to the frequent occurrence of mass developments of several species and population breakdowns, which reflect the natural variability of the community structure (Muehlenhardt-Siegel 1981; Muehlenhardt-Siegel 1988; Muehlenhardt-Siegel 1990). The effects of dumping are difficult to distinguish from eutrophication and pollution effects and presumably cannot be separated, as the observed effects are the result of the combination of all factors.

The FSd-station is situated in the centre of a former disposal area of acid-iron wastes from titanium dioxide production, which had been used from 1969 to 1989 (Rachor 1972; Rachor & Gerlach 1978). However, no reduction in species number or in abundance was detected during the dumping phase (Fig. 4.3.32). Instead, an increase in species number and in the abundance of many species, not only of opportunistic nature but also including bivalves like *Tellina fabula,* has been observed at Fsd during the 80ies, which is most likely an effect of increased food supply due to eutrophication. Despite the harmful effects shown in experimental studies, no ecological effects on the macrozoobenthos were detectable (Rachor 1972; Rachor & Dethlefsen 1976). In the water, the iron is oxidised and sinks to the bottom (together with other heavy metals), where it was observed floating above the sediment as ferric hydroxide flakes (Rachor 1972). The fact that no biological effects were detectable in the benthos has been attributed to rapid dilution and hydrographic conditions in the area that result in a wide dispersion (Rachor 1972; Rachor & Dethlefsen 1976). High natural fluctuations of the community and the effects of wave erosion during heavy storms (Rachor & Gerlach 1978) further complicate the distinction of possible effects.

A considerable input of environmental chemicals (notably DDT) at the end of 1995 and the beginning of 1996 (ARGE Elbe 1997) was made responsible for dramatic effects on the health of the whole ecosystem in the German Bight (Schmolke et al. 1999). This may have contributed to the drastic changes observed for the benthic communities in 1996/97, which have so far been mostly explained mainly by the severe winter of 1995/96, highlighting again the problems of attributing observed changes to a specific factor.

No effects of the former dumping of wastes at the FSd station and east of the Slt station were obvious for the benthic communities. High natural fluctuations and the simultaneous (and possibly synergistic) effects of eutrophication or other factors complicate the distinction of possible pollution effects.

5.4.2.3 Eutrophication

An influence of eutrophication on the benthic communities of the German Bight can be inferred from the high number of correlations found between nutrient concentrations and the benthic communities at Slt, SSd and Fsd.

Nutrient concentrations do not directly influence benthic organisms, but they are the most important factor limiting primary production (Van Beusekom & de Jonge 2002), determining the amount of organic material reaching the sea bottom as primary source of energy for the benthic system. Food availability is a major structuring factor for sublittoral benthic communities, which are generally regarded as food limited (Pearson & Rosenberg 1987; Rosenberg 1995). An increasing food supply may result in an increased biomass (Josefson 1998) or in communities of small individuals (Pearson et al. 1985). However, large phytoplankton blooms in combination with unfavourable hydrographic conditions may also lead to oxygen deficiency resulting in a reduction or elimination of macrobenthos (Rachor 1977; 1980; Rachor & Albrecht 1983; Niermann et al. 1990; Heip 1995; Gray et al. 2002). New production in coastal waters may have increased by about 25% in recent decades (Richardson & Pedersen 1998), and hypoxia in stratified waters is becoming a widespread phenomenon of growing concern (Diaz et al. 1995).

The benthic community at Slt receives large amounts of high quality organic matter resulting in often high numbers of organisms inhabiting mainly the upper sediment layers (Dauwe et al. 1998). The high input of organic matter also leads to hypoxic conditions in the sediment and occasionally in near-bottom water, sometimes accompanied by enrichment of hydrogen sulphide, and may result in sudden breakdowns of population density, mainly during late summer (Rachor 1977; 1980). The period from the late 70ies until the early 90ies is characterised by mass occurrences of the highly mobile cumacean *Diastylis rathkei* and several polychaetes with strong interannual fluctuations. *N. nitidosa* starts to increase again in abundance during the mid 80ies and regains a dominant role in the community in the 90ies accompanied by *Abra alba* and several other species that were rare during the 80ies, which might indicate an amelioration of the local conditions. The impoverishment of the fauna at Slt in the 70ies has been attributed to frequent anaerobic conditions (Rachor 1977; 1980). These result in large interannual changes in the community and in the prevalence of opportunistic species and species that are able to tolerate or actively avoid hypoxic conditions (Arntz & Rumohr 1986).

During warm, calm weather periods with a stable thermocline, hypoxic conditions may also develop in large parts of the outer German Bight. Low oxygen concentrations of less than 4 mg/l have been recorded in the north-eastern part of the German Bight in 1981, '82, '83, '89 and '94 (Rachor & Albrecht 1983; Niermann et al. 1990; Heip 1995; Van Beusekom et al. 2003). While no effects on the macrofauna were observed in 1981 (Rachor & Albrecht 1983), a widespread mass mortality of macrozoobenthos was documented in 1982 and 1983 (Dyer et al. 1983; Dethlefsen & Westernhagen 1983; Niermann et al. 1990). Although many populations were extinguished at single stations, a very quick recovery of the community composition by next spring at most stations was facilitated by their survival at other stations (Niermann et al. 1990).

The decline of several species at WB in 1984 could be related to the low oxygen concentrations observed in 1983 in the area, although these effects were not very severe as the community returned to a similar composition as in the previous years already after one year. Many species such as *A. filiformis* or *N. nitidosa,* which are able to tolerate moderate hypoxic conditions, were not affected. An influence of hypoxic conditions on the community at FSd or SSd was not discernible. These stations lie west of the main areas where hypoxic conditions were recorded. Especially the community at FSd that is adapted to frequent disturbances may also allow a rapid recovery after the hypoxic conditions in summer, such that minor community alterations may not persist until the following spring.

The impoverishment of the fauna at Slt may be a result of frequent hypoxic conditions. Only at WB an indication of effects of low oxygen conditions was observed on a single occasion. These shallow-water communities with large interannual changes and the prevalence of opportunistic species are presumably adapted to frequent disturbances and may rapidly recover after hypoxic conditions.

However, the "pelagic-benthic coupling" is not simply a one-way interaction, but benthic communities influence pelagic processes in many ways (Arntz et al. 1999). Benthic suspension feeders may directly influence primary and secondary pelagic production of shallow areas (Officer et al. 1982; Loo & Rosenberg 1989; Hily 1991). In addition, most benthic organisms have pelagic larvae that live for a certain period as meroplankton. During this phase larvae are dependent on the type and amount of food supplied by phytoplankton, but the larvae themselves may also change the planktonic food web and alter the species composition of the plankton (Lindley et al. 1995). The relative composition of nutrients may also strongly influence the species composition of the phytoplankton (Sommer et al. 2003). Species composition and density as well of phytoplankton as of planktonic predators may thus severely affect the larval supply of the benthic communities. In the absence of a comprehensive analysis of the phytoplankton and (mero-) zooplankton development, nutrient concentrations may be used as proxies for shifts in the planktonic system even though functional relations remain as yet obscure.

From the development of temperature, salinity, nutrients and phytoplankton observed at Helgoland (Hickel et al. 1997), Radach (1998) suggested that "the states of the ecosystem in the inner German Bight in the 70ies and 80ies have abandoned the situation of the 60ies, but are possibly returning in the 90ies to the situation of the 70ies". This is supported by the development of the benthic communities, which in the early 90ies, especially at SSd and Slt, show a tendency towards the situation in the 70ies as indicated by the MDS-results. The hypotheses about connection between benthic and pelagic systems in the German Bight can only be analysed further in combination with the time-series of phyto-, zoo- and meroplankton e.g. from the "Helgoland Reede" data when these are ready for a combined analysis, which is beyond the scope of the present study.

5.4.3 Biological interactions

The influence of biological interactions on population development of the community is not necessarily reflected in simple correlations between species. More knowledge about indirect effects and complex models are needed to describe the population development in the presence of density dependence, interspecific interactions and external forcing (Van der Meer et al. 2000). Interactions may only become obvious in certain situations or especially high densities.

An example is the relation between the deposit feeding polychaete *Scoloplos armiger* with benthic larval development and the generalist predator *Nephtys hombergii* with pelagic larvae (Schubert & Reise 1986; Hartmann-Schröder 1996). In the Wadden Sea, a negative influence of *N. hombergii* on the population density of *S. armiger* was found without a direct feedback on the population development of *N. hombergii* (Van der Meer et al. 2000). In accordance with this, the density of *S. armiger* declined following peak densities of *N. hombergii* at Slt and Fsd. At the other two stations, where *S. armiger* occurs in lower abundances, no such relation was observed. The absence of a direct feedback on the density of *N. hombergii* can be explained by the wide prey spectrum of *N. hombergii* and its reproduction via pelagic larvae, which reduces the dependency of its abundance fluctuations on the local prey abundance.

The invasion of *Ensis directus* in an "*Abra-alba*-community" in the southern bight of the North Sea coincided with a remarkable change in the community (Carpentier et al. 1997).

The first appearance of *E. directus* in the inner German Bight in 1979 may have contributed to the changing community at Slt between 70ies and 80ies. However, local populations of *E. directus* fluctuate interannually and mostly only develop for one year reaching a size of only 10 cm (Dörjes 1992). Because of the very variable community in the area, an influence of *E. directus* is not obvious and hardly separable from effects of other factors.

At SSd, *Abra* spp. and *Amphiura filiformis* both are common species and no clear correlation between their densities is visible during most years. However, a high density of *Abra* spp. only occurred in years when *Amphiura filiformis* was rare or absent. At high densities, both species inhibit the settlement of pelagic larvae (Eagle 1975; Crowe et al. 1987). A less stringent but still negative effect can be expected also at lower densities, especially considering the presence of numerous other additional species, many of which may exert additional negative effects. This may contribute to the lower settlement of *Abra* when *Amphiura* was present, but also possibly to the delayed recovery of the *Amphiura* population after the severe winters observed at SSd. At WB, *Abra* occurred only in low densities, and juvenile *Amphiura* were found in the first year following the severe winter of 1995/96. However, the delayed recovery of the *Amphiura* population at SSd may also be related to hydrographic conditions in the German Bight and their effects on the advection of pelagic larvae of *A. filiformis* (Gerdes 1977).

Parallel fluctuations of *Amphiura filiformis* and *Mysella bidentata* at SSd and WB reflect the known commensalism between these species (Ockelmann & Muus 1978), but this association is only facultative, and high densities of *M. bidentata* occur at SSd during many years when *A. filiformis* is absent. A similar commensalism has been described for *Montacuta ferruginosa* and *Echinocardium cordatum* (Gage 1966), which is more clearly visible at WB than at SSd, while at SSd *M. ferruginosa* varies very much in parallel to *Nucula nitidosa*. Such an association can however not be seen at WB and may just be a parallel response to a common factor.

These cases may serve as a few examples for known interaction between pairs of species. Density-dependent inhibition of recruitment by adult deposit-feeders or predators is a common regulatory mechanism and post-larval settlement processes may have a much more critical influence on benthic community structure than any variability in larval recruitment levels (Crowe et al. 1987; Olafsson et al. 1994; Osman & Whitlatch 1998).

However, complex interactions between species within a developed community often lead to more positive than negative correlations between species on a small scale (Woodin 1978; Josefson 1986; Schaffner 1990). Large and deep-burrowing species create a three-dimensional sediment structure of tubes, burrows etc. providing a variety of microhabitats for other, small species (Pearson 2001). Several species like *A. filiformis* or tube-building polychaetes are able to rapidly collect food supplied on the sediment and to subduct it several cm into the sediments (Rosenberg et al. 1997),(Levin et al. 1997) where it becomes available also for other deep-burrowing species. Beyond the enlargement of oxygenated sediment surface, the increased habitat complexity itself often leads to a higher diversity of benthic communities (Johnson et al. 2003). Bioturbation and irrigation of the sediment increase the depth of the oxygenated sediment layer and modify fluxes of particles as well as dissolved substances across the sediment-water interface (Graf & Rosenberg 1997; Pearson 2001; Rosenberg 2001). Bioturbation can reduce sediment stability by feeding movements or the accumulation of loose material in fecal mounds with negative effects on other species. Other species, especially tube builders (e.g. *Lanice*) may stabilise the sediment and provide additional structures that lead to a diversification of the community (Rhoads & Young 1970; Posey et al. 1991; Hall 1994; Widdicombe & Austen 1999; Berkenbusch et al. 2000; Solan & Kennedy 2002).

It is evident from these examples that biotic interactions are amongst the most important determinants for benthic community composition. In most cases, they will tend to stabilise the community, which is reflected in the temporal autocorrelation found at all stations. The major antagonistic factor are disturbances that tend to destabilise the web of biotic interactions.

5.4.4 Disturbances

The most dramatic changes in the benthic communities are related to "disturbances" resulting from "extreme" conditions of environmental factors or from anthropogenic inferences and can lead to "catastrophic" reductions of benthic communities. For the communities in the German Bight, the most common forms of disturbances are extremely cold winters, hypoxia following algal blooms in stratified waters, feeding of large predators and physical disturbance of the sediment by wave erosion during strong storms or by demersal fishing gear.

With the exception of WB, the three stations in the inner German Bight are dominated by short-lived species and recovery of the community composition following localised disturbances is very quick. The effects of the severe winters were most clearly notable at the two deeper stations SSd and WB.

Nevertheless, the largest changes of the benthic communities are observed following severe winters, especially that of 1995/96, possibly aggravated by a pollution event (see chapter 5.4.2.2). While the direct effects of the severe winter of 1979 were discernible for less than two years, those following the cold winter of 1996 lasted at least until 1999 and some species like *A. filiformis* at SSd did not even reach the previous densities by 2000.

In shallow waters, most bivalve species are affected by cold temperatures (Ziegelmeier 1964), but this effect was not observed for *N. nitidosa* at Slt, while other species like *Abra alba* declined markedly. Other especially larger, long-lived species may permanently remain rare because of the increased frequency of various disturbances. However, most long-lived species (except for e.g. ophiuroids) are too rare to be adequately sampled by five 0.1 m^2 vV-grabs, and inferences about their long-term development can therefore not be drawn from the present data.

Although the effects may differ in severity and spatial extent, the main result of any disturbance is mostly a reduction of species number, abundance and biomass. Subsequently, a process of succession will develop towards "mature ecosystems" (Margalef 1968) with a pattern of species numbers, abundance and biomass changing in a predictable way (Pearson & Rosenberg 1978), which is similar for many kinds of disturbances (Arntz & Rumohr 1986). A general scheme for succession from azoic sediments to a diverse benthic community has been proposed by Pearson & Rosenberg (1978) and Rhoads & Germano (1986). The pioneer species, usually small opportunistic worms, may quickly dominate a community. Lack of intraspecific interference competition and the subsequent depletion of food often cause sudden outbreaks followed by sudden breakdowns in these populations (Chesney 1985). Dominant species are often represented by mainly a single year class, adding to the instability of the community (Eagle 1975). As gradually larger and deep-burrowing species establish, a three-dimensional structure of tubes, burrows etc. provides a variety of microhabitats for other species, finally leading to a "mature" community.

For many communities, the frequent occurrence of disturbance events is an inherent feature of the "normal" environmental regime and leads to the "typical" appearance of the respective community.

At FSd, the dominance of small opportunistic and mostly mobile worms results from the unstable sediments. The relatively poor community at Slt can be seen as a result of frequent hypoxic conditions. The "normal" community composition in this case reflects the general disturbance regime (in terms of type, intensity and frequency) rather than a mature community.

Parallels can be found in many areas (e.g. Baltic Sea, Peruvian Coast etc. see Diaz et al. 1995), where frequent or even persistent hypoxic conditions are characteristics of the environmental regime (comp. e.g. Arntz 1981; Arntz & Rumohr 1986; Tarazona et al.

1996). Changes in the community are therefore likely to occur when the disturbance regime changes. The quality of the disturbance by e.g. a beam trawl is different from that of wave-induced erosion, cold water temperature affects other species than hypoxic conditions. Different species are susceptible to other factors. Not only the type of disturbance will affect different species in a different way, but also the timing of a disturbance may have a significant effect on succession (Zajac & Whitlatch 1982a; 1982b).

Hypoxia has become one of the most severe disturbances for benthic communities in the German Bight (as already discussed in the context of eutrophication; chapter 5.4.2.3). Depending on the severity of hypoxia, the recovery may reach an almost identical community structure within less than two years (Nilsson & Rosenberg 2000) or even quicker in areas where hypoxia is a common phenomenon and benthic communities are suggested to be pre-adapted and mainly composed of opportunistic species (Arntz 1981). In more severely affected areas, with long-lived species and where biogenic sediment structuring is important for the development of the community, recovery may take five years or longer (Rosenberg 1976).

Although there are natural factors of disturbance like oxygen deficiency situations, strong storms causing sediment movements or extremely cold temperatures, fishery has become a very important disturbing factor since several decades. Mechanical disturbances caused by natural events (sediment movements) may expose or bury organisms, but will rarely result in mechanical damage or destruction of animals. None of the naturally occurring events produces the same effects as bottom fisheries, physically crushing or damaging many benthic animals (Arntz & Weber 1970; Rumohr & Krost 1991; Bergman & van Santbrink 1994; 2000; Bergman & Hup 1992; Kaiser & Spencer 1995; Bergman et al. 1998). Thus, the additional disturbance caused by bottom fishery not only increases the frequency of disturbances but also adds a different quality of disturbance.

5.4.4.1 Spatial heterogeneity as symptom of stress

Changes in the benthic community do not only affect the abundance of organisms and the dominance structure, but also their spatial distribution and therefore the spatial heterogeneity of the community. Increased spatial variability is interpreted as a symptom of stress in benthic communities (Warwick & Clarke 1993).

Spatial variability caused by biotic interactions within the benthic community (Schaffner 1990; Posey et al. 1991; Berkenbusch et al. 2000; Bergstrom et al. 2002) or from other organisms in the ecosystem (Arntz 1980; 1986; Hall et al. 1991) will change with variations in the dominance structure and possibly more drastically with changes in the species composition. Within the community, predation and competition create a spatial structuring (Ambrose 1991). In addition to this, especially those species that alter their environment by creating hard structures or reworking the sediment have pronounced effects on the community structure of their immediate vicinity (Brenchley 1981; Schaffner 1990; Graf & Rosenberg 1997; Widdicombe & Austen 1999; Pearson 2001; Solan & Kennedy 2002). These biologically caused spatial variability may also be destroyed by disturbances. Especially severe disturbances that lead to more or less defaunated sediments may subsequently be recovered by mass settlements of planktonic larvae and thus lead to lower spatial variability.

An evaluation of the question whether spatial variability increases after disturbances at the investigated stations would imply an *a priori* knowledge when these disturbances were present at the respective stations. While many years with presumably disturbed situations from e.g. cold winters exhibit increased spatial variability, at some stations just the opposite phenomenon arises, like at FSd, where the spatial variability in 1996 was the lowest of all years (Fig. 4.2.15). Also in 1979 the spatial variability was low at all stations. In 2000, the spatial variability of all stations was one of the lowest values except at Slt.

No clear correlation between stress and dispersion is visible. However, this may also point to the fact that we do not really know when disturbances occurred at a specific station. Especially physical disturbances from fishing gear or from natural sediment movements create a spatial variability that cannot be detected by the present explanatory data.

The spatial variability in 1993 is amongst the highest at all stations, which seems to represent a disturbed situation, supported by a low total number of organisms and low species densities. This effect is most pronounced at Slt, where also the evenness and the diversity are extremely low during this year. At Slt, this results from the fact that the dominant *Nucula nitidosa* is the only species that is still abundant. At WB, 1993 represents the beginning of a phase of high spatial variability with low densities of the otherwise dominant *Amphiura filiformis* but also several other species. This phase ended after the severe winter of 1995/96, when many species, including *A. filiformis*, decreased further in abundance. Subsequent recovery led to a similar community as that found in the beginning of the 90ies. The responsible factors for the change observed in 1993 remain as yet obscure, as no extreme environmental conditions are visible in the present explanatory data.

5.5 Local vs. regional community development

Local densities of single species are a product of local conditions, and are not representative for the population development of the respective species. If observed population densities and changes from single stations are referred to a large area, the estimate of the mean for the whole area is biased and the variance is underestimated (Van der Meer 1997). For a serious description of populations in the German Bight, sampling would be necessary on a wider spatial scale to encompass the major habitat patches that may fluctuate out of phase (Reise 1991; Thrush et al. 1997; Armonies 2000; 2001).

Beyond the small-scale spatial variability within the area of a sampling station, each benthic community includes a large-scale variability between parts of the total area. The Dutch sector of the North Sea contains similar communities as those found in the German Bight (Craeymeersch et al. 1997; Heip & Craeymeersch 1995). The temporal development of single species in the Dutch area (Holtmann et al. 1999), however, is very different. No similar development in species density, total abundance or H' is visible between SSd or WB and the Oyster Ground that have a generally very similar community composition or between the Dutch "offshore area" and FSd (Holtmann et al. 1999). The only obvious similarity between the Dutch area and the stations in the German Bight is the drop in species number and abundance after the severe winter of 1995/96, which is apparent in most areas.

But even within the relatively small area of the German Bight, remarkable differences in community development can be observed. Almost none of the pattern found for single species by Kröncke et al. (2002) is seen at the FSd station, although the species composition is very similar. The general pattern observed on the MDS for the second quarter of the year in their paper (Fig. 10 in Kröncke et al. 2002) is, however, very similar to the pattern observed during the present study especially at SSd and WB.

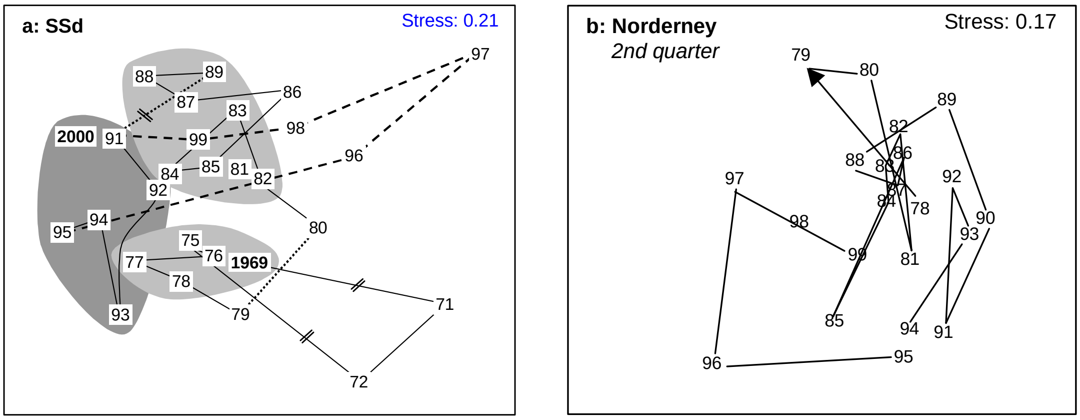

Fig. 5.3: MDS plots for community development at the silty sand station (**a:** SSd, this study) and off Norderney (**b:** modified from Kröncke et al. 2001: Fig. 10, 2nd quarter); based on Bray-Curtis similarity of 4th root transformed organism densities.

In an earlier study at the same location, Kröncke et al. (1998) found fluctuations in species number, abundance and biomass to be correlated to the NAOI. A significant correlation of the species number to the winter-NAOI was evident at FSd, whereas no correlation could be detected for the abundance.

These differences between local assemblages are a common feature observed in many areas, and fluctuations are not in parallel, but local conditions play a key role (Gray & Christie 1983; Fromentin et al. 1997a; 1997b). The agreement of the development of species density between the stations examined here is larger than compared with investigations from other areas (comp. e.g. Holtmann et al. 1999; Kröncke et al. 1998; 2001; Warwick et al. 2002). This reflects the relative proximity of the stations and influences of the same environmental factors, possibly related to the special situation of the German Bight with its high productivity (Dauwe et al. 1998).

Also for geographically more distant communities of a generally very similar composition, a correlation of community changes to climatic and oceanographic factors has been observed (Warwick et al. 2002; Carpentier et al. 1997). If regarded in more detail, the temporal development of the respective communities shows little similarity to the development in the German Bight. Species density, abundance or the densities of single species often even show opposite developments. Local biological interactions may decouple systems from direct physical determination by introducing temporal or spatial lags in system dynamics or creating webs of indirect effects (Wiens 1989).

While local communities exhibit large interannual fluctuations, different patterns may emerge at larger scale. A fine-scale instability may be part of a long-term persistence and stability at the scale of the larger metapopulation (Wiens 1989). The large fluctuations of several opportunistic species but also of species numbers observed at FSd and SSd are characteristics of a short-term and possibly scale-dependent variability, while the overall species composition remains relatively stable. This is only possible within a larger mosaic of habitat elements, where a regional species pool persists, which contains all species that could eventually colonise a location if competitive exclusion was unimportant (Gray 2002). Benthic soft-bottom communities are characterised as a mosaic of patches at various spatial scales that may exhibit differing temporal development following the mosaic-cycle concept (Aubreville 1936; see also Remmert 1991). This may lead to an overall stability of loosely coupled elements, dispersed over habitat patches, and local stability is no longer relevant. Instead, temporal and spatial scaling of the cycling communities and processes driving the cycles come into focus (Reise 1991).

Within benthic communities biological interactions (predation, spatial interference, bioturbation etc.) cause a small-scale patchiness and a mosaic-cycle on a scale of a few centimetres to a few metres (Reise 1991). In addition, on a larger scale of several kilometres not only the community composition changes, but also the spatial patterns shift seasonally and between years (Eagle 1975). The observed changes in local densities at the stations in the German Bight may also reflect spatial shifts of populations. While the local population density of *Nucula nitidosa* at Slt was lower during the 80ies and then increased again, *N. nitidosa* was more abundant at SSd during the 80ies and then declined again. Following cold winters, the local populations of *Amphiura filiformis* in the inner German Bight collapse and may take several years before reaching higher densities again (like at SSd), which was explained by hydrographic conditions by Gerdes (1977). In deeper parts of the area, recovery can be much faster, and high densities are reached already after two years, as observed at WB. A slow return to the inner parts, whether caused by hydrography or biotic interactions, leads to the perceived outward shift of the limit between the *Amphiura-filiformis*-association and the *Nucula-nitidosa*-association in the Pleistocene Elbe valley (Rachor & Nehmer 2003). In several parts of the Oyster Grounds west of the German Bight, *A. filiformis* was present in high densities during the 90ies (Holtmann et al. 1999). According to the main easterly direction of the residual current, this should allow a supply of larvae to the German Bight. The actual current conditions are, however, depending on the wind and conditions during the larval phase and may not have allowed an advection of the larvae into the inner German Bight. Effects related to this question can only be solved in combination with meroplankton and hydrographic data.

The spatial distribution of benthic organisms on a regional scale within the southern North Sea is different between studies (Duineveld et al. 1987; Craeymeersch et al. 1997). Meroplanktonic larvae of many benthic species allow a dispersal over wide areas and the use of habitat mosaics at very large spatial scales. So they can shift to other geographic regions when confronted with an adverse phase of a long-term environmental periodicity (Reise 1991)

The highly significant correlation between the similarity matrices of the temporal development of the communities at several stations indicates a parallel development of the communities. This applies to similar periods and similar "unusual" years indicating a possible dependence on the same factors acting on a large scale. The lower correlation between stations separated by the furthest geographical distance (WB/Slt), or with the most different sediment composition (FSd/Slt) respectively, indicates the importance of local conditions and/or of the community composition for the temporal community development.

The *timing* of changes in communities is similar between different parts of the North Sea and may be a result of climate and oceanographic features. However, the *local* community development is a product of *local* environmental variation and biotic interactions, and both differ between areas.

Therefore, a direct correlation between large-scale environmental factors and population changes in the wider area may not lead to consistent results. However, the local development, influenced by interactions and in relation to local abiotic conditions, could possibly be further analysed using advanced mathematical models if local environmental conditions can be adequately quantified.

5.6 Implications for offshore monitoring of soft-bottom benthos

The power to detect trends in community composition depends on the sample size, the magnitude of the trend, and the magnitude of random variation, just as it does with univariate analyses (Philippi et al. 1998). The present design with five replicate van-Veen grabs at four selected stations seems sufficient to follow the *local* community development. However, as discussed in the previous chapter, single stations do only allow inferences about the local development, which may be only one element in a large scale mosaic cycle. To differentiate between the natural fluctuations of mosaic elements and long term trends, a repeated mapping of the area would be needed (Reise 1991).

For studies of the development of the benthic communities in larger heterogeneous areas, a stratified random sampling is presumably the most powerful design (Krebs 1998). Under the assumption that each stratum represents a homogeneous area (which can adequately be represented by e.g. a mean density per species), randomly selected stations with only a single replicate per station provide the largest power to detect community differences (Cuff & Coleman 1979; Van der Meer 1997). These strata should not include heterogeneous communities and borders between strata should be avoided, because this would greatly reduce the power to detect changes (Philippi et al. 1998). For marine community studies, formal random selection of sites is less important since the spatially stochastic distribution of populations will probably generate an appropriate randomness from evenly spaced sites (Milne 1959; Clarke & Green 1988). Random selection may sometimes even lead to an uneven distribution of effort across an area and an appropriate spatial dispersion of sites across the area needs to ascertained (Hurlbert 1984).

Once the stations are selected, the same stations should be revisited in succeeding years to reduce the confounding effects of spatial variation and increase the power to detect temporal changes (Thrush et al. 1994; Stewart-Oaten et al. 1995; Van der Meer 1997). The appropriate number of stations depends on the size of the area and its spatial variability. A larger extent will incorporate greater spatial heterogeneity (Wiens 1989; Philippi et al. 1998).

Such a large-scale stratified random sampling is realised in the Dutch offshore monitoring program BIOMON (Van der Meer 1997; Holtmann et al. 1999). This approach includes all spatial variation on all scales within the designated strata and therefore leads to very large variability of the data especially with small-sized sampling gear (e.g. Holtmann et al. 1999; Armonies 2000). Apart from this, it precludes comparisons among stations, and changes in the spatial distribution within the stratum are likely to pass unnoticed. The variability of single grab samples is too high to detect differences between sub-areas except for the most extreme ones as, e.g., between different communities. If any comparison between sampling sites is intended, replicates are needed to assess the within-site similarity between replicates (Clarke & Green 1988; Philippi et al. 1998). Two replicates are the minimum, but more replicates allow a more precise description of the local community and greatly enhance the power of comparisons by increasing the possible number of permutations in randomisation tests (see chapter 5.2.2).

A nested design over different spatial scales allows a distinction of the variability and relevant processes at different scales (Morrisey et al. 1992; Thrush et al. 1997; Kendall & Widdicombe 1999; Paiva 2001; Hewitt et al. 2002). In nested designs, it is important to allocate the effort across the levels efficiently to maximise the power for the most important questions of the study. The optimal balance can be calculated when the variability at the respective scales is known (Clarke & Green 1988). A selection of sites for the German Bight could be realised by analysing the spatial distribution of benthic communities within the designated communities from large scale surveys (Salzwedel et al. 1985; Rachor & Nehmer 2003) and comparing it to the local variability analysed here.

Time series of benthic communities are mostly characterised by a considerable seasonal variation (Arntz & Rumohr 1982; 1986; Muehlenhardt-Siegel 1988; Frid et al. 1996;

Kröncke et al. 1998). For long-term observations of benthic communities, the late-winter or early spring situation is preferred as the communities are reduced to those species that are able to survive in the area over longer periods. In summer many species settle in the area, sometimes in very large numbers, but may not be able to survive until the next year. When interspecific interactions control the community development, the establishment of large densities often of opportunistic species may be impaired or even inhibited (Crowe et al. 1987; Olafsson et al. 1994) and the development may mainly be characterised by density increases of the species already present (Weigelt 1991). While this general pattern occurs in most years, the identity of the successful species varies and is not predictable. It may be a question of which species happens to be in the area at the right time (Reise 1991). This seasonal variation adds to the spatial variation and complicates the identification of long-term trends. While single sampling occasions in early spring are appropriate to document long-term changes in benthic communities, each change observed to the previous year's situation is a result of various processes including recruitment and mortality over the whole year. If inferences about processes were intended, biannual sampling in spring and autumn would be necessary (Alden et al. 1997).

Beyond the description of community variability, inferences about responsible factors can only be made if appropriate data of possibly influential variables are available. As several of these factors also vary on various spatial and temporal scales, measurements should ideally be directly connected to the sampling of the benthic communities. Values for all relevant variables should be determined from each replicate sample (on the appropriate scale for the respective variable), thus matching the biological, physical and chemical data as closely as possible (Clarke & Green 1988).

A general statement about the regional community development beyond the local conditions would require a larger extent of sampling within each community. Any conclusions about changes in the spatial distribution would require several stations with replicate samples. A more functional analysis would only be possible with a higher frequency of sampling to identify the exact timing of changes in benthic communities in relation to fluctuations of environmental variables and a continuous recording of the relevant environmental factors locally at the benthos sampling stations.

If annual sampling of numerous stations is not feasible, information on the long-term development of benthic communities beyond local conditions could be derived by a combination of annual sampling at selected stations with extensive large-scale surveys at longer intervals (e.g. every ten years). A combined analysis of the large-scale spatial and local temporal variability may be seen as a compromise to investigate the spatial distribution of the communities and their long-term development.

5.7 Open questions and further analyses

Spatio-temporal definition of benthic communities

The definition of benthic communities from spatial surveys can identify the spatial extent of relatively similar associations. Consecutive surveys covering the same area have often found other species to be characteristic of a certain area. This depends partly on the sampling grain and extent of the survey, but also on the temporal variability of the benthic communities, which should be incorporated, leading to a spatio-temporal definition of the community. At the same time, the temporal variability could be compared to the spatial variability on a larger scale to evaluate the local fluctuations in relation to the large-scale spatial variability.

Combined analyses of benthic and planktonic time series

Information on planktonic primary production in combination with hydrodynamic models might allow an estimate of the interannual variations in food supply at the stations. A more comprehensive study of the connections between nutrients, primary production, the planktonic food web and the benthos is a very challenging problem, which needs expertise from specialists. It could be tackled in a scientific cooperation using e.g. the data presented here in combination with nutrient and phyto- and (mero-)zooplankton community time series from Helgoland, when these are available for analysis.

Predictive models

The correlations between multivariate community structure and several environmental factors weight each factor equally. A more differentiated weighting may further increase the fit. Rank correlations detected in this study can only be used for qualitative predictions. A further investigation using more quantitative models and advanced techniques (e.g. distance-based redundancy analysis (Legendre & Anderson 1999)) may lead to *predictive* models. Such models do not necessarily have to incorporate the exact knowledge about functional relationships, but may on the basis of empirical correlations allow predictions about changes in the ecological system under various scenarios of environmental change.

Sample size sensitivity of diversity and dominance indices based on real samples

The analysis of the sample size dependency of the Shannon-Wiener diversity (H') and Pielou's evenness (J') indices has shown that the dependency found in real samples can differ from predictions of theoretical simulations. Each index has a slightly different focus and its own properties regarding sample size sensitivity and variability (Hurlbert 1971; Hill 1973; Smith & Wilson 1996; Krebs 1998). The choice of index may have profound effects on the interpretation of the results. The sample size dependence and variability of indices using real data will not only serve to better understand the properties of the respective indices applied to real, naturally variable communities, but may also allow implications on community structures and spatial variability.

Species richness vs. species density

The use of *species richness* instead of *species density* (or even the total species number found irrespective of sampling effort) may have interesting influences on comparisons of "diversity" between published studies. An interesting application was shown in the study of Oksanen (1996) accounting for the "hump-shaped" diversity curve in relation to productivity by variation in total density. An investigation of the effects on the predictions of e.g. the "intermediate disturbance hypothesis" (Connell 1978; Huston 1979) would merit further investigations.

A potential pitfall in the term "*species density*" is that it has even in recent literature often been interpreted as the simple ratio of species per total sampled area (S_{total}/A_{total}) (e.g. Gray 2002). However, this implies a linear relation between species and area and may lead to misinterpretations (Gotelli & Colwell 2001), as demonstrated in Fig. 5.4.

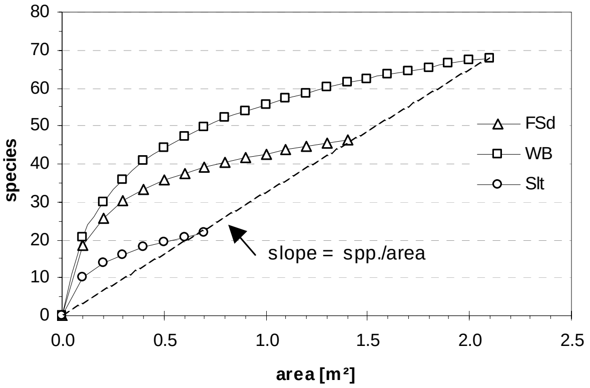

Fig. 5.4: Potential misinterpretations of the species per area ratio from different sample sizes

If no information on the dominance structure or even single samples is available, rarefaction cannot be applied to standardise *species density*. In the case where only the total number of species (S_{total}) and the total number of organisms (N_{total}) or the total sampled area (A_{total}) are available, a better approximation of the species density may be reached by assuming a functional relationship like a semi-logarithmic relation or a power function (depending on the heterogeneity of the investigated area). Based on this function, the species richness or species density can be standardised and published results can be compared between studies of different sampling effort. While international across-latitude studies of benthic diversity with identical methods are not available (Arntz et al. 1999), these calculations could be interesting in the context of hypotheses on depth- or latitude-related differences in diversity (Gray 2001; 2002).

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Annex

A.1 Species list

For each station the mean densities ([m^{-2}] ± SD) from the data selected for the long-term analysis are given for all species found.

Species found only outside the selected data sets as well as outdated synonyms that appear in the database are marked by an "x".

	Slt	FSd	SSd	WB
Phylum				
Class				
SubClass				
Ordo				
SubOrder				
Family				
Genus				
SpeciesName Author Status				
[= *Synonym*]				
Annelida				
Clitellata				
Hirudinea				< 1
Oligochaeta	< 1		x	
Polychaeta	x	< 1	x	< 1
Polygordiidae				
Polygordius appendiculatus Fraipont, 1887		< 1		
Capitellida				
Arenicolidae				
Arenicola marina (Linnaeus, 1758)	< 1			
Capitellidae	x			6 (±15)
Capitella spp.		< 1	1 (±7)	
Capitella capitata (Fabricius, 1780)	< 1	12 (±36)	< 1	< 1
Capitella minima (Langerhans, 1880)	< 1	5 (±20)	2 (±7)	< 1
[= *Capitomastus minimus* (Langerhans, 1880)]	x	x	x	x
Heteromastus filiformis (Claparède, 1864)	< 1	< 1	2 (±5)	< 1
Mediomastus fragilis Rasmussen, 1973				< 1
Notomastus latericeus M. Sars, 1850	< 1	3 (±5)	29 (±33)	4 (±6)
Magelonidae				
Magelona alleni Wilson, 1958		< 1	< 1	< 1
Magelona filiformis Wilson, 1959	< 1	< 1	< 1	< 1
Magelona minuta Eliason, 1962	< 1	70 (±140)	< 1	< 1
Magelona mirabilis (Johnston, 1865)	< 1	849 (±748)	1 (±2)	< 1
[= *Magelona papillicornis* (Johnston, 1865)]	x	x	x	
Chaetopterida				
Chaetopteridae				
Chaetopterus variopedatus (Renier, 1804)			3 (±5)	7 (±10)
Cirratulida				
Cirratulidae	x			
Aphelochaeta marioni (Saint-Joseph, 1894)		< 1		
[= *Tharyx marioni* (Saint-Joseph, 1894)]	x	x		
Chaetozone setosa Malmgren, 1867	< 1	40 (±40)	< 1	23 (±30)
Paraonidae				
Aricidea spp.		< 1		
Aricidea minuta Southward, 1956		3 (±7)		
Levinsenia gracilis (Tauber, 1879)				34 (±48)
[= *Paraonis gracilis* (Tauber, 1879)]				x
Eunicida				
Dorvilleidae				
Protodorvillea kefersteini (McIntosh, 1869)	< 1	x		
Lumbrineridae				
Lumbrineris	< 1			2 (±4)
Lumbrineris latreilli Audouin & Milne-Edwards, 1833		< 1		11 (±13)
Lumbrineris tetraura (Schmarda, 1861)				6 (±7)

	Slt	**FSd**	**SSd**	**WB**
Flabelligerida				
Flabelligeridae				
Diplocirrus glaucus (Malmgren, 1867)		x	5 (±10)	19 (±20)
Opheliida				
Opheliidae				
Ophelia limacina (Rathke, 1843)	< 1	2 (±4)		
Ophelina acuminata Oersted, 1843	x	< 1	5 (±5)	4 (±4)
Scalibregmatidae				
Polyphysia crassa (Oersted, 1843)				< 1
Scalibregma inflatum Rathke, 1843	36 (±149)	< 1	87 (±208)	< 1
Orbiniida				
Orbiniidae				
Orbinia sertulata (de Savigny, 1822)				< 1
Scoloplos armiger (O.F. Müller, 1776)	6 (±11)	92 (±128)	45 (±79)	5 (±8)
Oweniida				
Oweniidae			< 1	
Myriochele oculata Zachs, 1922			5 (±13)	5 (±15)
[= *Galathowenia oculata* (Zachs, 1922)]			x	
Owenia fusiformis Delle Chiaje, 1841	71 (±371)	32 (±61)	87 (±106)	26 (±43)
Phyllodocida				
Glyceridae				
Glycera spp.				6 (±17)
Glycera alba (O.F. Müller, 1776)	< 1			5 (±5)
Glycera lapidum Quatrefages, 1865	< 1			< 1
[= *Glycera capitata* non Oersted, 1843] (sensu Fauvel, 1923 and Hartmann-Schröder, 1971)	x			
Glycera rouxi Audouin & Milne-Edwards, 1833				3 (±5)
Goniadidae				
Glycinde nordmanni (Malmgren, 1865)		8 (±20)	6 (±14)	7 (±9)
Goniada maculata Oersted, 1843	< 1	26 (±29)	38 (±41)	8 (±6)
Goniadella bobretzkii (Annenkova, 1929)				< 1
Hesionidae		x		< 1
Gyptis spp.		< 1		
Gyptis rosea (Malm, 1874)		< 1		
Ophiodromus flexuosus (Delle Chiaje, 1827)	< 1		< 1	7 (±7)
Podarkeopsis helgolandica (Hilbig & Dittmer, 1979)	< 1	< 1	5 (±9)	2 (±4)
[= *Gyptis helgolandica* Hilbig & Dittmer, 1979]	x	x	x	x
Nephtyidae				
Nephtys spp.	66 (±118)	21 (±41)	31 (±42)	33 (±27)
Nephtys assimilis Oersted, 1843	< 1	2 (±4)	< 1	< 1
Nephtys caeca (Fabricius, 1780)	< 1	3 (±4)	3 (±5)	< 1
Nephtys ciliata (Fabricius, 1776)		< 1		
Nephtys cirrosa Ehlers, 1868	< 1	4 (±17)	x	< 1
Nephtys hombergii Savigny, 1818	61 (±91)	45 (±48)	71 (±29)	13 (±10)
Nephtys incisa Malmgren, 1865 ?		< 1	< 1	2 (±3)
Nephtys longosetosa Oersted, 1843	< 1	< 1	< 1	x
Nereididae	< 1			
[= Nereidae]	x			
Eunereis longissima (Johnston, 1840)	< 1	1 (±2)	2 (±3)	< 1
[= *Nereis longissima* Johnston, 1840]	x	x	x	x
Neanthes succinea (Frey & Leuckart, 1847)				
[= *Nereis succinea* (Frey & Leuckart, 1847)]			x	
Neanthes virens (Sars, 1835)	< 1	x		
[= *Nereis virens* (Sars, 1835)]	x			
Nereis spp.		< 1	< 1	< 1
Nereis elitoralis Eliason, 1962			x	

	Slt	FSd	SSd	WB
Phyllodocidae		x	< 1	< 1
Anaitides spp.	< 1	< 1	< 1	
Eteone spp.		x	< 1	
Eteone flava (Fabricius, 1780)			< 1	< 1
Eteone foliosa Quatrefages, 1865		< 1	< 1	< 1
[= *Eteone lactea* (Eliason, 1920)]		x	x	
Eteone longa (Fabricius, 1780)	< 1	16 (±30)	2 (±4)	< 1
Eteone spetsbergensis Malmgren, 1865		< 1		
Eumida spp.		1 (±4)	< 1	
Eumida bahusiensis Bergström, 1914		< 1	1 (±5)	
Eumida punctifera (Grube, 1860)	< 1	3 (±7)	2 (±4)	
Eumida sanguinea (Oersted, 1843)	< 1	< 1	< 1	
Phyllodoce spp.	x		< 1	< 1
Phyllodoce groenlandica Oersted, 1843	7 (±16)	5 (±12)	< 1	4 (±13)
[= *Anaitides groenlandica* (Oersted, 1843)]	x	x	x	x
Phyllodoce lineata (Claparède, 1870)				
[= *Anaitides lineata* Claparède, 1870]		x		
Phyllodoce maculata (Linnaeus, 1767)	< 1	< 1	< 1	
[= *Anaitides maculata* (Linnaeus, 1767)]	x	x	x	
Phyllodoce mucosa Oersted, 1843	< 1	< 1		
[= *Anaitides mucosa* (Oersted, 1843)]	x	x		
Phyllodoce rosea (McIntosh, 1877)		4 (±9)	5 (±16)	
[= *Anaitides subulifera* Eliason, 1962]		x	x	
Pilargiidae				
Synelmis klatti (Friedrich, 1950)				3 (±5)
Pisionidae				
Pisione remota (Southern, 1914)	x	3 (±18)		
Sphaerodoridae				
Sphaerodorum flavum Oersted, 1843	x	< 1	3 (±4)	
[= *Sphaerodorum gracilis* Eliason, 1962]			x	
Syllidae				
Autolytus spp.	x	x		
Autolytus prolifer (O.F. Müller, 1776)		< 1	< 1	
Exogone hebes (Webster & Benedict, 1884)				5 (±8)
Tomopteridae				
Tomopteris helgolandica Greeff, 1879				x

	Slt	**FSd**	**SSd**	**WB**
Aphroditoidea				
Aphroditidae				
Aphrodita aculeata Linnaeus, 1761	< 1	x	2 (±2)	2 (±3)
Pholoidae				
Pholoe minuta (Fabricius, 1780)	31 (±66)	8 (±14)	48 (±38)	244 (±263)
Polynoidae		< 1		
Bylgides sarsi (Kinberg, 1856)	4 (±7)	< 1	< 1	< 1
[= *Harmothoe sarsi* (Kinberg, 1856)]	x	x	x	x
[= *Harmothoe sarsi sarsi* (Kinberg, 1856)]	x		x	
Enipo kinbergi Malmgren, 1865			< 1	< 1
[= *Polynoe kinbergi* (Malmgren, 1865)]			x	x
Eunoe nodosa (M. Sars, 1861)		< 1	< 1	3 (±7)
[= *Harmothoe nodosa* (M. Sars, 1861)]		x	x	x
Gattyana cirrosa (Pallas, 1766)	< 1	< 1	4 (±7)	3 (±5)
Harmothoe spp.	< 1	< 1	< 1	< 1
Harmothoe glabra (Malmgren, 1865)	< 1	< 1	1 (±2)	2 (±3)
[= *Harmothoe longisetis* (Malmgren, 1865)]	x	x	x	x
Harmothoe imbricata (Linnaeus, 1767)		< 1		
Harmothoe impar (Johnston, 1839)	< 1	x	< 1	< 1
Harmothoe ljungmani (Malmgren, 1867)		< 1		
Lagisca extenuata (Grube, 1840)		x		
Malmgrenia spp.				
[= *Malmgreniella*]		x	x	
Malmgrenia andreapolis McIntosh, 1874				< 1
[= *Malmgreniella andreapolis* (McIntosh, 1874)]				x
Malmgrenia castanea (McIntosh, 1876)		< 1	< 1	< 1
[= *Malmgreniella castanea* (McIntosh, 1876)]		x	x	x
Malmgrenia lunulata (Delle Chiaje, 1830)		< 1	2 (±3)	< 1
[= *Harmothoe lunulata* (Delle Chiaje, 1830)]		x	x	x
[= *Malmgreniella lunulata* (Delle Chiaje, 1830)]		x	x	x
Sigalionidae				
Sigalion mathildae Audouin & Milne-Edwards, 1830		1 (±3)		
Sthenelais spp.			< 1	
Sthenelais boa (Johnston, 1833)			< 1	
Sthenelais limicola (Ehlers, 1864)	x	6 (±7)	3 (±4)	4 (±4)
Sabellida				
Sabellidae				
Chone spp.		x		
Chone duneri Malmgren, 1867		< 1	< 1	
Chone infundibuliformis Krøyer, 1856		< 1	x	

	Slt	**FSd**	**SSd**	**WB**
Spionida				
Poecilochaetidae				
Poecilochaetus serpens Allen, 1904		3 (±5)	1 (±3)	< 1
Spionidae	x	x		< 1
Aonides paucibranchiata Southern, 1914		x		
Polydora ciliata (Johnston, 1838)		x		
Polydora cornuta Bosc, 1802	< 1			
[= *Polydora ligni* (Bosc, 1802)]	x		x	
Polydora pulchra Carazzi, 1895	x	x	2 (±4)	
[= *Pseudopolydora pulchra* (Carazzi, 1895)]			x	
Prionospio cirrifera Wirén, 1883				< 1
Pygospio elegans Claparède, 1863			< 1	
Scolelepis bonnieri (Mesnil, 1896)		10 (±16)	< 1	
Spio spp.	x			
Spio filicornis (O.F. Müller, 1776)	< 1	25 (±80)	< 1	< 1
Spiophanes bombyx (Claparède, 1870)	< 1	228 (±766)	139 (±317)	< 1
Terebellida				
Ampharetidae			< 1	1 (±3)
Ampharete spp.	x		< 1	
Ampharete acutifrons (Grube, 1860)	< 1		x	x
Ampharete falcata Eliason, 1955		< 1	< 1	
Ampharete finmarchica (M. Sars, 1864)	< 1	< 1	17 (±29)	< 1
Anobothrus gracilis (Malmgren, 1865)			< 1	5 (±8)
[= *Sosane gracilis* (Malmgren, 1865)]		x	x	
Pectinariidae				
Pectinaria auricoma (O.F. Müller, 1776)		< 1	< 1	25 (±43)
[= *Amphictene auricoma* (O.F. Müller, 1776)]				x
Pectinaria koreni (Malmgren, 1865)	19 (±61)	1 (±3)	14 (±19)	3 (±5)
[= *Lagis koreni* Malmgren, 1866]			x	x
Terebellidae		x		
Lanice conchilega (Pallas, 1766)	x	9 (±14)	26 (±31)	< 1
Lysilla loveni Malmgren, 1866		< 1	1 (±4)	1 (±2)

	Slt	**FSd**	**SSd**	**WB**
Arthropoda				
Crustacea				
Malacostraca				
Amphipoda	1 (±5)	< 1	< 1	
Caprellidea				
Caprellidae				
Pariambus typicus (Krøyer, 1845)	2 (±6)	2 (±5)	2 (±5)	< 1
Gammaridea				
Ampeliscidae				< 1
Ampelisca spp.			< 1	< 1
Ampelisca brevicornis (Costa, 1853)	< 1	11 (±12)	10 (±16)	2 (±3)
Ampelisca diadema (Costa, 1853)			< 1	
Ampelisca tenuicornis Liljeborg, 1856			< 1	3 (±4)
Amphilochidae				
Amphilochus spp.		< 1		
Amphilochus neapolitanus Della Valle, 1893				1 (±3)
Paramphilochoides odontonyx (Boeck, 1871)			< 1	< 1
Aoridae				
Autonoe longipes (Liljeborg, 1852)				< 1
[= *Lembos longipes* (Liljeborg, 1852)]				x
Unciola planipes Norman, 1867		x		
Argissidae				
Argissa hamatipes (Norman, 1869)	< 1	x		
Atylidae				
Atylus falcatus Metzger, 1871	< 1	< 1	< 1	
[= *Notoropis falcatus* (Metzger, 1871)]	x	x		
Atylus guttatus (Costa, 1851)	< 1			
Atylus swammerdami (Milne-Edwards, 1830)	< 1	< 1	< 1	
[= *Notoropis swammerdami* (Milne-Edwards, 1830)]	x	x	x	
Atylus vedlomensis (Bate & Westwood, 1862)				
[= *Notoropis vedlomensis* (Bate & Westwood, 1862)]		x		
Corophiidae				
Corophium spp.	< 1	< 1		< 1
Corophium crassicorne Bruzelius, 1859		< 1		
Siphonoecetes krøyeranus Bate, 1856				
[= *Siphonoecetes colletti* Boeck, 1871]		x		
Gammaridae				
Gammarus spp.	< 1			< 1
Haustoriidae				
Bathyporeia spp.	< 1	5 (±16)	x	
Bathyporeia elegans Watkin, 1938	< 1	41 (±50)	< 1	
Bathyporeia guilliamsoniana (Bate, 1856)	< 1	27 (±38)	< 1	
Bathyporeia nana Toulmond, 1966		< 1		
Bathyporeia pelagica (Bate, 1856)			< 1	
Bathyporeia pilosa Lindström, 1855		< 1		
Bathyporeia tenuipes Meinert, 1877		3 (±8)		
Urothoe spp.				
Urothoe poseidonis Reibisch, 1905		76 (±91)	< 1	< 1
[= *Urothoe grimaldi* (Reibisch, 1905)]		x	x	
Iphimediidae				
Iphimedia obesa Rathke, 1843		< 1		

	Slt	**FSd**	**SSd**	**WB**
Isaeidae	< 1			
Gammaropsis nitida (Stimpson, 1853)			< 1	
[= *Podoceropsis nitida* (Stimpson, 1853)]	x		x	
Microprotopus maculatus Norman, 1867	< 1	< 1		
Photis longicaudata (Bate & Westwood, 1863)		x	2 (±9)	
Photis reinhardi Krøyer, 1842	x			
Ischyroceridae				
Jassa falcata (Montagu, 1808)	x			
Lysianassidae				< 1
Hippomedon denticulatus (Bate, 1857)		< 1		
Orchomene minutus (Krøyer, 1846)	< 1	< 1	< 1	
[= *Orchomenella minuta* (Krøyer, 1846] (Identification in NS doubtfully valid)	x	x	x	
Orchomene nana (Krøyer, 1846)	< 1	< 1	1 (±5)	< 1
[= *Orchomenella nana* (Krøyer, 1846)]	x	x	x	
Scopelocheirus hopei (Costa, 1851)				< 1
Megaluropidae				
Megaluropus agilis Hoek, 1889	< 1	2 (±4)	< 1	
Melitidae				
Abludomelita obtusata (Montagu, 1813)		< 1	< 1	< 1
[= *Melita obtusata* (Montagu, 1813)]		x	x	x
Cheirocratus intermedius Sars, 1894				< 1
Melita dentata (Krøyer, 1842)			x	
Oedicerotidae		< 1		
Monoculodes carinatus (Bate, 1857)	< 1	< 1	x	
Perioculodes longimanus (Bate & Westwood, 1868)	< 1	17 (±19)	2 (±2)	4 (±5)
Pontocrates spp.		< 1		
Pontocrates altamarinus (Bate & Westwood, 1862)		< 1		
Pontocrates arenarius (Bate, 1858)	< 1	5 (±11)		< 1
Synchelidium haplocheles (Grube, 1864)	x	9 (±14)	< 1	< 1
Synchelidium maculatum Stebbing, 1906		< 1		
Phoxocephalidae				
Harpinia spp.				< 1
Harpinia antennaria Meinert, 1890				33 (±36)
Harpinia crenulata (Boeck, 1871)				35 (±63)
Harpinia pectinata Sars, 1891				4 (±8)
Podoceridae				
Dyopedos monacanthus (Metzger, 1875)				< 1
Stenothoidae				
Hardametopa nasuta (Boeck, 1871)			< 1	
[= *Metopella nasuta* (Boeck, 1871)]			x	
Metopa spp.		x		
Stenothoe marina (Bate, 1857)		< 1	< 1	< 1
Hyperiidea				< 1

	Slt	FSd	SSd	WB
Cumacea	x		3 (±16)	
Bodotriidae				
Bodotria scorpioides (Montagu, 1804)	< 1		< 1	< 1
Cumopsis goodsiri (van Beneden, 1861)	< 1		x	
Iphinoe trispinosa (Goodsir, 1843)	< 1	4 (±7)	< 1	< 1
Diastylidae				
Diastylis spp.	173 (±378)	< 1	< 1	23 (±57)
Diastylis bradyi Norman, 1879	6 (±17)	2 (±4)	2 (±5)	5 (±5)
Diastylis laevis Norman, 1869	7 (±35)	< 1	< 1	5 (±10)
Diastylis lucifera (Krøyer, 1841)	x		x	25 (±38)
Diastylis rathkei (Krøyer, 1841)	582 (±2373)	< 1	3 (±8)	3 (±5)
Lampropidae				
Lamprops fasciata Sars, 1863	< 1	< 1	x	
Leuconidae				
Eudorella spp.			< 1	
Eudorella emarginata (Krøyer, 1846)	< 1		19 (±37)	9 (±12)
Eudorella truncatula (Bate, 1856)	1 (±4)		29 (±48)	24 (±32)
Nannastacidae				
Campylaspis costata G.O. Sars, 1865	x			
Pseudocumatidae				
Pseudocuma spp.		< 1		
Pseudocuma longicornis (Bate, 1858)	10 (±42)	2 (±4)	< 1	2 (±3)
Pseudocuma similis Sars, 1900	x	1 (±5)	x	
Decapoda				
Pleocyemata				
Callianassidae				
Callianassa spp.			< 1	
Callianassa subterranea (Montagu, 1808)		< 1	12 (±16)	12 (±9)
Corystidae				
Corystes cassivelaunus (Pennant, 1777)		< 1	x	< 1
Crangonidae				
Crangon spp.	< 1	< 1	< 1	
Crangon allmani Kinahan, 1857	< 1	x	< 1	< 1
Crangon crangon (Linnaeus, 1758)	< 1	< 1	< 1	
Philocheras bispinosus (Hailstone, 1835)				x
Galatheidae				
Galathea intermedia Liljeborg, 1851	x			
Leucosiidae				
Ebalia cranchii Leach, 1817		< 1		< 1
Paguridae				x
Pagurus spp.				
[= *Eupagurus* spp.]		x		
Pagurus bernhardus (Linnaeus, 1758)	< 1	< 1	< 1	< 1
[= *Eupagurus bernhardus* (Linnaeus, 1758)]	x	x	x	x
Pinnotheridae				
Pinnotheres pisum (Linnaeus, 1767)		< 1		
Portunidae		< 1		
Liocarcinus holsatus (Fabricius, 1798)	< 1	< 1	< 1	
[= *Macropipus holsatus* (Fabricius, 1798)]	x	x	x	
[= *Portunus holsatus* (Fabricius, 1798)]	x	x	x	
Processidae				
Processa canaliculata Leach, 1815	x		x	
Processa nouveli holthuisi Al-Adhub & Williamson, 1975			< 1	< 1
Upogebiidae				
Upogebia deltaura (Leach, 1815)			x	< 1

	Slt	**FSd**	**SSd**	**WB**
Isopoda				
Asellota				
Pleurogoniidae				
Pleurogonium rubicundum (Sars, 1864)				< 1
Epicaridea				
Bopyridae				
Pleurocrypta longibranchiata (Bate & Westwood)				< 1
Pseudione borealis Caspers, 1939			< 1	< 1
Flabellifera				
Limnoriidae				
Limnoria lignorum (Rathke, 1799)			x	
Valvifera				
Idoteidae				
Idotea linearis (Linnaeus, 1767)	x			
Leptostraca				
Nebaliidae				
Nebalia bipes (Fabricius, 1780)				1 (±5)
Mysidacea	< 1	< 1	< 1	
Lophogastridae				
Lophogaster typicus Sars, 1857		x		
Mysidae				
Gastrosaccus sanctus (van Beneden, 1861)			< 1	
Gastrosaccus spinifer (Goes, 1864)	< 1	< 1	< 1	
Mesopodopsis slabberi (van Beneden, 1861)		x		
Paramysis arenosa (G.O. Sars, 1877)	x			
Schistomysis kervillei (G.O. Sars, 1885)	< 1			< 1
[= *Paramysis kervillei* (G.O. Sars, 1885)]	x	x		
Schistomysis ornata (Sars, 1864)	< 1		< 1	
[= *Paramysis ornata* (G.O. Sars, 1864)]	x	x	x	
Tanaidacea	< 1	< 1		< 1
Tanaidomorpha				
Tanaidae		< 1		
Pycnogonida				
Pantopoda		< 1	< 1	
Nymphonidae				
Nymphon gracile Leach, 1814	< 1			
Phoxichilidiidae				
Anoplodactylus petiolatus (Krøyer, 1884)	< 1		x	

	Slt	FSd	SSd	WB
Echinodermata				
Asteroidea	x			
Forcipulatida				
Asteriidae				
Asterias spp.			x	
Asterias rubens Linnaeus, 1758	x	x	x	
Paxillosida				
Astropectinidae				
Astropecten irregularis (Pennant, 1777)				< 1
Echinoidea		x	x	
Clypeasteroida				
Fibulariidae				
Echinocyamus pusillus (O.F. Müller, 1776)		< 1		
Echinoida				
Echinidae				
Psammechinus miliaris (P.L.S. Müller, 1771)	x	x	x	
Spatangoida				
Brissidae				
Brissopsis lyrifera (Forbes, 1841)				< 1
Loveniidae				
Echinocardium spp.	x	x	< 1	4 (±19)
Echinocardium cordatum (Pennant, 1777)		16 (±20)	22 (±12)	20 (±21)
Echinocardium flavescens (Müller, 1776)				4 (±8)
Spatangidae				1 (±4)
Spatangus purpureus O.F. Müller, 1776		x		
Holothuroidea			x	
Apoda				
Synaptidae				
Labidoplax buskii (McIntosh, 1866)				< 1
Leptosynapta inhaerens (O.F. Müller, 1776)				7 (±9)
Dendrochirota				
Cucumariidae				
Trachythyone elongata (Düben & Koren, 1846)				3 (±4)
[= *Cucumaria elongata* Düben & Koren, 1846]				x
Ophiuroidea		< 1	x	16 (±36)
Ophiurida	x			
Amphiuridae	1 (±6)	1 (±4)	4 (±16)	115 (±513)
Acrocnida brachiata (Montagu, 1804)	< 1	< 1	< 1	
[= *Amphiura brachiata* (Montagu, 1804)]			x	
Amphiura spp.		< 1	1 (±4)	154 (±472)
Amphiura chiajei Forbes, 1843			< 1	
Amphiura filiformis (O.F. Müller, 1776)	2 (±8)	< 1	35 (±70)	1234 (±1072)
Ophiuridae	2 (±11)	5 (±24)	6 (±33)	9 (±42)
Ophiura spp.	29 (±48)	20 (±38)	29 (±43)	64 (±177)
Ophiura albida (Forbes, 1841)	5 (±15)	43 (±63)	176 (±99)	24 (±28)
Ophiura ophiura (Linnaeus, 1758)	97 (±124)	2 (±4)	4 (±6)	< 1
[= *Ophiura texturata* (Linnaeus, 1758)]	x	x	x	x

	Slt	**FSd**	**SSd**	**WB**
Mollusca				
Bivalvia	2 (±10)	< 1	4 (±18)	< 1
Anomalodesmata				
Pholadomyoida				
Periplomatidae				
Cochlodesma praetenue (Pulteney, 1799)		x		
Thraciidae				
Thracia papyracea (Poli, 1791)		2 (±4)	1 (±4)	< 1
[= *Thracia phaseolina* (Lamarck, 1818)]		x	x	x
Thracia pubescens (Pulteney, 1799)		x		
Heterodonta				
Myoida				
Corbulidae				
Corbula gibba (Olivi, 1792)	1 (±3)	3 (±13)	5 (±20)	80 (±103)
[= *Aloidis gibba* (Olivi, 1792)]		x		
Hiatellidae				
Hiatella arctica (Linnaeus, 1767)				
[= *Saxicava arctica* (Linnaeus, 1767)]			x	
Saxicavella jeffreysi Winckworth, 1930	x		1 (±3)	
Myidae				
Mya spp.		x	< 1	
Mya arenaria Linnaeus, 1758		< 1	< 1	
Mya truncata Linnaeus, 1758		< 1	< 1	< 1
Veneroida				
Arcticidae				
Arctica islandica (Linnaeus, 1767)	1 (±8)	1 (±3)	< 1	< 1
[= *Cyprina islandica* (Linnaeus, 1767)]		x	x	
Cardiidae				
Acanthocardia echinata (Linnaeus, 1758)		< 1	< 1	
[= *Cardium echinatum* (Linnaeus, 1758)]		x		
Cerastoderma edule (Linnaeus, 1758)	< 1			
[= *Cardium edule* (Linnaeus, 1758)]	x			
Mactridae				
Lutraria lutraria (Linnaeus, 1758)			< 1	
Mactra stultorum (Linnaeus, 1758)	< 1	2 (±5)	< 1	< 1
[= *Mactra corallina* (Montagu, 1808)]	x	x	x	x
Spisula spp.		< 1	< 1	2 (±3)
Spisula elliptica (Brown, 1827)		x	< 1	
Spisula solida (Linnaeus, 1758)		< 1	< 1	< 1
Spisula subtruncata (da Costa, 1778)	5 (±17)	7 (±15)	8 (±12)	
Montacutidae				
Montacuta ferruginosa (Montagu, 1808)	2 (±6)	26 (±28)	29 (±23)	12 (±17)
[= *Tellimya ferruginosa* (Montagu, 1808)]		x	x	x
Mysella bidentata (Montagu, 1803)	31 (±79)	11 (±14)	112 (±118)	321 (±413)
[= *Montacuta bidentata* (Montagu, 1803)]		x		
Pharidae				
Ensis spp.	< 1	< 1		
Ensis directus (Conrad, 1843)	17 (±40)	< 1		
Ensis ensis (Linnaeus, 1758)		< 1		
Phaxas pellucidus (Pennant, 1777)		5 (±8)	8 (±16)	1 (±2)
[= *Cultellus pellucidus* Pennant, 1777]	x	x	x	x
Semelidae				
Abra spp.	14 (±72)		1 (±4)	2 (±4)
Abra alba (W. Wood, 1802)	97 (±227)	1 (±3)	49 (±69)	2 (±5)
Abra nitida (Müller, 1776)	5 (±13)	< 1	100 (±207)	7 (±14)
Abra prismatica (Montagu, 1808)		x		

	Slt	FSd	SSd	WB
Tellinidae				
Macoma balthica (Linnaeus, 1758)	2 (±5)		x	
Tellina spp.		x		
Tellina fabula Gmelin, 1791	9 (±39)	193 (±155)	12 (±54)	3 (±10)
[= *Fabulina fabula* (Gmelin, 1791)]	x	x	x	x
Tellina pygmea Lovén, 1846				
[= *Tellina pusilla* Philippi, 1836]		x		
Tellina tenuis da Costa, 1778		< 1		
Thyasiridae				
Thyasira flexuosa (Montagu, 1803)	< 1	x	109 (±107)	2 (±3)
Veneridae				
Chamelea gallina (Linnaeus, 1758)		9 (±15)	1 (±2)	11 (±16)
[= *Chamelea striatula* (da Costa, 1778)]				x
[= *Venus gallina* (da Costa, 1778)]		x	x	x
[= *Venus striatula* da Costa, 1778]		x	x	x
Clausinella fasciata (da Costa, 1778)		1 (±6)		
[= *Venus fasciata* da Costa, 1778]		x	x	
Dosinia lupinus (Linnaeus, 1758)				< 1
Venerupis pullastra (Montagu, 1803)			< 1	
Venus spp.		3 (±16)		< 1
Protobranchia				
Nuculoida				
Nuculidae				
Nucula spp.	< 1	< 1	7 (±38)	7 (±29)
Nucula nitidosa Winckworth, 1930	608 (±701)	< 1	132 (±109)	56 (±53)
[= *Nucula turgida* Leckenby & Marschall, 1875]	x		x	
Nucula nucleus (Linnaeus, 1758)		x		
Nucula tenuis Montagu, 1803			< 1	49 (±116)
Pteriomorphia				
Mytiloida				
Mytilidae				
Modiolus modiolus (Linnaeus, 1758)			< 1	
Mytilus edulis Linnaeus, 1758	< 1		< 1	

	Slt	**FSd**	**SSd**	**WB**
Gastropoda		x	x	x
Heterobranchia				
Heterostropha				
Pyramidellidae				
Chrysallida spp.			< 1	
Chrysallida interstincta (Adams, 1797)		< 1	< 1	< 1
[= *Parthenia obtusa* (Brown, 1827)]		x	x	x
Chrysallida pellucida (Dillwyn, 1817)				
[= *Partulida spiralis* (Montagu, 1803)]		x		
Odostomia spp.				< 1
Ondina divisa (Adams, 1797)				< 1
[= *Evalea divisa* (Adams, 1797)]				x
Opisthobranchia				
Cephalaspidea				
Acteonidae				
Acteon tornatilis (Linnaeus, 1758)		< 1	< 1	
Cylichnidae				
Cylichna cylindracea (Pennant, 1777)		2 (±2)	7 (±11)	57 (±44)
Philinidae				
Philine spp.		x	< 1	
Philine aperta (Linnaeus, 1767)			< 1	
Philine scabra (Müller, 1776)				2 (±3)
Retusidae				
Cylichnina umbilicata (Montagu, 1803)				7 (±14)
[= *Retusa umbilicata* (Montagu, 1803)]				x
Retusa truncatula (Bruguière, 1792)			< 1	
Nudibranchia		< 1		
Prosobranchia				
Mesogastropoda				
Calyptraeidae				
Crepidula fornicata (Linnaeus, 1758)		x		
Cerithiidae				
Bittium reticulatum (da Costa, 1778)		< 1	x	
Eulimidae				
Vitreolina philippi (de Rayneval & Ponzi 1854)		< 1	< 1	12 (±17)
[= *Balcis devians* (Rayneval & Ponzi 1854)]				x
Hydrobiidae				
Hydrobia spp.			< 1	
Hydrobia ulvae (Pennant, 1777)	< 1	< 1	< 1	
Iravadiidae				
Hyala vitrea (Montagu, 1803)		< 1	< 1	61 (±92)
[= *Cingula vitrea* (Montagu, 1803)]		x	x	x
[= *Onoba vitrea* (Montagu, 1803)]			x	
Naticidae				
Euspira puchella (Risso, 1826)	< 1	12 (±13)	12 (±17)	15 (±27)
[= *Lunatia intermedia* (Forbes, 1838)]	x	x	x	
[= *Lunatia nitida* (Forbes, 1838)]		x	x	x
[= *Natica alderi* Forbes, 1838]		x	x	x
[= *Natica nitida* of authors]	x	x	x	
[= *Natica poliana* (Forbes, 1838)]		x		
[= *Polinices polianus*(delle Chiaje, 1826)]		x	x	x
Rissoidae				
Onoba spp.		x		
Onoba semicostata (Montagu, 1803)			< 1	
[= *Cingula striata* (Montagu, 1803)]			x	
Turritellidae				
Turritella communis Risso, 1826				5 (±13)

	Slt	FSd	SSd	WB
Neogastropoda				
Buccinidae				
Buccinum undatum Linnaeus, 1758		< 1	x	
Colus spp.			x	
Conidae				
Oenopota turricula (Montagu, 1803)		< 1	< 1	
[= *Lora turricula* (Montagu, 1803)]		x	x	
Epitoniidae				
Epitonium spp.				
[= *Scala* spp.]		x	x	
Epitonium commune (Linnaeus, 1758)		< 1		
[= *Clathrus clathrus* (Linnaeus, 1758)]		x		
Aplacophora				
Caudofoveata				
Chaetodermatida				
Chaetodermatidae				
Chaetoderma nitidulum Lovén, 1844				5 (±6)
Aschelminthes				
Priapulida			x	
[= Priapuloidea]				
Priapulimorpha				
Priapulidae				
Priapulus caudatus Lamarck, 1816	x		< 1	< 1
Chordata				
Cephalochordata				
Amphioxiformes				
Branchiostomidae				
Branchiostoma lanceolatum (Pallas, 1774)		< 1		< 1
Cnidaria				
Anthozoa		< 1		< 1
Hexacorallia				
Actiniaria		< 1	< 1	< 1
Edwardsiidae				
Edwardsia spp.	< 1	69 (±146)	27 (±62)	4 (±3)
Metridiidae				
Metridium senile (Linnaeus, 1761)		< 1		
Sagartiidae				
Sagartia spp.		< 1		
Sagartia troglodytes (Price, 1847)		< 1	< 1	
Sagartiogeton undatus (O.F. Müller, 1788)		< 1		
Ceriantharia				
Spirularia				
Cerianthidae				
Cerianthus lloydi Gosse, 1859	x	< 1	3 (±11)	

	Slt	**FSd**	**SSd**	**WB**
Hydrozoa	x	x	x	x
Hydroida				
Athecata		x	x	
Bougainvilliidae				
Bougainvillia spp.				x
Corymorphidae				
Corymorpha nutans Sars, 1835		x		
Tubulariidae				
Tubularia spp.	x			
Tubularia indivisa Linnaeus, 1758	x	x	x	x
Thecata		x	x	
Campanulariidae				
Campanularia spp.		x		
Sertulariidae				
Sertularia cupressina Linnaeus, 1758	x			
Echiura				
Echiurida				
Echiuridae				
Echiurus echiurus (Pallas, 1774)	7 (±17)		< 1	
Nemertini	< 1	33 (±42)	16 (±13)	15 (±13)
Anopla				
Paleonemertini				
Cephalotrichidae		4 (±15)		5 (±24)
Cephalothrix spp.			1 (±6)	
Platyhelminthes				4 (±6)
Turbellaria		x	< 1	< 1
Sipunculida		< 1	< 1	5 (±5)
Golfingiidae				
Golfingia spp.				< 1
Golfingia elongata (Keferstein, 1862)				< 1
Golfingia vulgaris (de Blainville, 1827)				x
Thysanocardium procera (Möbius, 1875)				< 1
[= *Golfingia procera* of authors]				x
Tentaculata				
Bryozoa				
Gymnolaemata				
Cheilostomata				
Electridae				
Electra pilosa (Linnaeus, 1767)	x			
Phoronida			x	
Phoronidae				
Phoronis spp.	11 (±34)	518 (±765)	887 (±2453)	24 (±33)

A.2 Benthos data available in the database

This list contains:

- the cruise-code as listed in the database,
- the dates of the cruise,
- the type of gear employed and the number of replicates taken
  - vV: 0.1 m² van Veen grab if not indicated otherwise
  - 0.05 vV: 0.05 m² van Veen grab
  - 0.2 vV: 0.2 m² van Veen grab
  - 0.5 vV: 0.5 m² van Veen grab
  - RBC: 0.017 m² Reineck box corer
  - 0.1 BC: 0.1 m² box corer
- information on the data quality:
  - samples where only some taxonomic groups have been analysed:

    M: Mollusca
    P: Polychaeta
    E: Echinodermata
    C: Crustacea
    O: other taxa
  - for pooled samples the number of replicates is given in brackets behind the number of separate data sets available in the database.
- comments

Data from existing protocols are printed in normal typeface, data obtained by new analysis of stored samples are printed in boldface.

The data selected for the long-term analysis are shaded.

	Date		**Available data sets in DB99**								**Comments**
			H1		**P12**		**FSD**		**WB**		
Cruise	from	to	vV	RBC	vV	RBC	vV	RBC	vV	RBC	
HE130	10.04	14.04.2000	**5**		**5**		**5**		**5**		
HE118	06.04	30.04.1999	**5**		**5**		**5**		**5**		
HE 102	20.04	26.04.1998	**21**		**21**		**20**		**21**		
VH0197	24.03	25.03.1997	**5**		**5**		**5**		**5**		
VH0796	16.04	17.04.1996	**5**		**5**		**5**		**5**		
LI0695	25.04	27.04.1995	**5**		**5**		**5**		**5**		
VH0894	19.04	22.04.1994	**5**		**5**		**5**		**5**		
VH0693	23.04	24.04.1993	**5**		**5**		**5**		**5**		
VH0492	22.04	24.04.1992					5				+24 vV in surrounding of station; Heuers 1992; 1000µ
VH0192	31.03	03.04.1992	**5**		**5**		**5**		**5**		
VH4491	12.12	12.12.1991					5				+22 vV in surrounding of station; Heuers 1992; 1000µ
VH3391	15.08	16.08.1991			5P		5P				
VH1391	04.05	05.05.1991	**5**		**5**		1(7)		**1**		WB: only 1 vV!
SExx90	25.10	26.10.1990					5PM				
VH1290	19.04	21.04.1990	5				**5**	**6**	**5**		Crustacean data missing. Newly identified.
VH4389	07.11	08.11.1989					2P				
VH4089	23.10	25.10.1989					2P				
VH1089	21.04	21.04.1989	1		1						
VH0489	20.03	23.03.1989	**5**		**2**	**6**	**5**		**5**		
VH3788	19.10	20.10.1988			5P						
VH2888	01.08	04.08.1988	5P								
VH0688	05.04	08.04.1988	**5**		**5**		1(2)	(6)	**5**		
VH3287	31.08	03.09.1987	5CM		5PM						
VH1987	15.06	17.06.1987	5								
VH0687	17.03	22.03.1987			5PE				**3**		
VH0287	23.02	25.02.1987	5		5						
VH5086	11.11	14.11.1986	5		2PC						
VH1486	18.04	27.04.1986	5		**1+1***	**6**			**5**		*0.1 BC
VHxx85	13.11		5			6					
VH4085	05.08	07.08.1985	5								
VH3385	25.06	28.06.1985	2								
VH2785	12.06	13.06.1985	5		5						
VH1585	16.04	18.04.1985	5		2	6	2	6	**5**		
VH0985	18.03	21.03.1985	5								
VH5284	06.11	08.11.1984	5		5		5	2			
VH3884	03.09	06.09.1984	5								
VH3684	06.08	08.08.1984	5		2	6	2	6			
VH3184	09.07	10.07.1984	5								
VH1584	09.04	13.04.1984	2								
VH0984	12.03	15.03.1984	5		2	6	2	6	**5**		
VH5383	03.11	03.11.1983	5		2	6					
GAxx83	02.10	03.10.1983	2								
VH3783	15.08	18.08.1983	5								
VH3183	18.07	22.07.1983	5		2	6	2	6			
VH2883	21.06	24.06.1983	4(5)			6					
VH1483	11.04	15.04.1983	5						**5**		
VH0783	28.02	04.03.1983	5		2	6	2*	6			*0.2 vV
VH6582	25.10	27.10.1982			2	6					
GA3082	23.10	24.10.1982	2	2							
VH5582	06.09	08.09.1982	5				2	6			
VH4882	11.08	12.08.1982	2								
VH4582	02.08	04.08.1982	5								
VH4382	19.07	20.07.1982	5		2						
VH3582	14.06	16.06.1982	5		2	6	2	20			
VH2682	21.04	23.04.1982	5		2	6	2	6	**2/6**		
VH3082	14.03	15.03.1982	5					6			
VH0282	27.01	30.01.1982	5								
GAxx81	14.10	17.10.1981	5		2	6					
VH5981	25.08	26.08.1981	2		2	6		6			
VH5781	18.08	19.08.1981	5								
VH5581	27.07	29.07.1981	2		2	6	2	6			
VH5381	20.07	21.07.1981	5								
VH4181	19.06	20.06.1981			2	6					
VH3x81	25.05	27.05.1981	5								
GA1681	08.04	10.04.1981	5		2	6	2	6	**6**		WB: 3 stations x 2 vV each
VH1581	23.03	23.03.1981	5								
VH0581	24.02	25.02.1981	5								
VH0181	27.01	29.01.1981	5		5	6	5	6			
SExx80	22.12	23.12.1980	5	2							
VH3480	09.09	10.09.1980	5		2						
VH3280	28.08	28.08.1980	5	2	2						
VH2980	31.07	31.07.1980	5								
VH2280	25.06	26.06.1980	5	6	2	6	2	6			
VH1280	24.04	25.04.1980	5								
VH0980	25.03	26.03.1980	5	2	2	6	2	6			H1: Biomass per groups

	Date		Available data sets in DB99								Comments
			H1		P12		FSD		WB		
Cruise	from	to	vV	RBC	vV	RBC	vV	RBC	vV	RBC	
VH5179	14.11	15.11.1979	5					5			
FHxx79	09.10	11.10.1979	5	6	2	6	2	12			Fsd: MEC only
VH4179	29.08	29.08.1979	5								
VH3779	06.08	06.08.1979	5								
VH3279	09.07	10.07.1979	5				2	6			
VH2879	20.06	20.06.1979	5								
VH2679	14.06	14.06.1979	2	6		6					
VH1779	23.04	26.04.1979	5		1(2)	3(6)	1(2)	6(12)			
VH1379	22.03	23.03.1979	5					12			
VH1079	20.02	21.02.1979	5		2						
VH8278	19.12	20.12.1978		6*				6			*H1: each 2 RBC N,O,S,W from centre position
VH7578	02.11	03.11.1978	5	6	2	6	2	6			
VH6478	02.10	03.10.1978	3								
VH5678	30.08	31.08.1978	2	7							
VH5278	03.08	03.08.1978	2	6	2	6					
VH4878	19.07	20.07.1978	2*	6							*0.2vV
VH4078	14.06	14.06.1978		6							
VH3478	22.05	25.05.1978	2	6		6					
VH2578	25.04	01.05.1978	3+2*		2*	6		12			*0.2vV
VH1778	14.03	16.03.1978	5								
VH0878	13.02	14.02.1978	6		2	6		12			Fsd: 24 RBC (with April data combined: 0.4m²)
VH8177	14.12	15.12.1977	6				2	6			
VH7077	20.10	21.10.1977	6		2	6	2	12			
VH5977	21.09	21.09.1977	5	3							
VH4977	24.08	26.08.1977	5	6		12					
VH4277	12.07	13.07.1977	2								
VH3777	22.06	23.06.1977	5		2	12	2	12			
VH2077	28.04	29.04.1977	3*		2*						*0.2vV
VH1077	16.03	18.03.1977	5		2	6	2	7			
VH9476	15.12					6					
VH8976	25.11	26.11.1976	5				2	12			
VH8176	27.10	28.10.1976	6	3	5	6	5	12			
VH7576	26.09	28.09.1976					4	12			
VH7076	09.09	09.09.1976	8		5						
VH6376	16.08	17.08.1976	5			12	2	8			
VH5476	12.07	13.07.1976			6	9	****				Fsd: 4x 0.4vV+8x 0.2vV+16x 0.1vV+17x 0.05vV +25x RBC
VH5276	06.07	07.07.1976	5		2			6			
VH4876	22.06	26.06.1976	5		5		5*	9			*0.2vV
VH4376	03.06	03.06.1976	5								
VH4176	17.05	18.05.1976	2(5+2*)		3*	3**	3	9**			*0.2vV **0.1 BC
VH3476	22.04	23.04.1976	5		5		8	1			
VH2476	16.03	17.03.1976	8		3	12	3+2*	6			*0.2vV
VH1676	17.02	18.02.1976	5			6		12			
VH0376	14.01	14.01.1976				12	6	2*			*0.1 BC
VH5175	16.12	17.12.1975				12	5MC				
VH4775	24.11	25.11.1975	5		5		5				
VH4275	28.10	30.10.1975				12					
VH3775	03.10	03.10.1975				11		12MC			
VH3275	08.09	09.09.1975		12		11		12MC			
VH2375	11.08	14.08.1975						12			
VH1775	15.07	16.07.1975					2MC	10MC			
VH1075	26.06	26.06.1975						7MC			
VH0775	03.06	10.06.1975		6	2	12	5	24			
R77/75	28.05	31.05.1975			5						
R75/75	18.04	18.04.1975	5		1	5					
R74/75	24.03	25.03.1975			5*M			12			*0.2vV
R73/75	04.03	04.03.1975			3*M						*0.2vV
R72/75	31.01	31.01.1975	3+5°		2(5)M		2(5)				°0.05vV
R71/74	17.10	17.10.1974			1M	2M	1	13			
R70/74	19.09	20.09.1974	5		3M		3				
R69/74	01.07	01.07.1974			5M						
R68/74	30.05	30.05.1974	5								
R67/74	30.05	30.05.1974					1(3*)				*0.2vV
R66/74	21.03	22.03.1974	2(5)		2(5)MP		5				
R65/74	04.01	04.01.1974	6		3(5*)M		2(5*)				*0.2vV
R64/73	23.08	23.08.1973	8°								°0.05vV
R63/73	21.08	21.08.1973	5+5°		5*M		5*				*0.2vV; °0.05vV
R62/73	22.05	23.05.1973	[24]		2(1+5)M		10				[24] 4 stations each 1x 0.2vV; 2x 0.1vV; 3x 0.05vV
R61/73	12.03	12.03.1973	2(5)	+1(15°)	1(5*)M		2(5*)				°0.05vV; *0.2vV

			Available data sets in DB99								Comments
	Date		**H1**		**P12**		**FSD**		**WB**		
Cruise	from	to	vV	RBC	vV	RBC	vV	RBC	vV	RBC	
R60/72	15.12	15.12.1972	3*+5°		5*M		5*				*0.2vV; °0.05vV
R59/72	05.10	06.10.1972	5		5*M						*0.2vV
R58/72	12.09	12.09.1972	5*		5*M		5*				*0.2vV
R57/72	19.07	19.07.1972	3								
R56/72	14.06	14.06.1972	1(5)								
R55/72	08.05	10.05.1972	1(5)+25°		1(5)M						°0.05vV
R54/72	13.04	14.04.1972	1(5)		1(5)		1(5*)				*0.2vV
R53/72	02.03	03.03.1972									
R52/72	28.02	28.02.1972									
R51/72	31.01	02.02.1972	1(5*)		1(5*)M		1(5*)				*0.2vV
R50/72	07.01	07.01.1972			1**M						**0.5vV
R49/71	29.11	30.11.1971	5		5M						
R48/71	12.10	15.10.1971	5*		5*M		5*				*0.2vV
R47/71	20.09	20.09.1971					1**M				**0.5vV
R46/71	13.09	15.09.1971	5+5°		5M						°0.05vV
R45/71	17.08	17.08.1971	5								
R44/71	11.08	12.08.1971			1**M		1**M				**0.5vV
R43/71	27.07	29.07.1971	5		5M		5*				*0.2vV
R42/71	07.07	08.07.1971	15		5M		5				
R41/71	22.06	23.06.1971			5M						
R40/71	18.05	26.05.1971	1(3*)		1(3*)M		1(3*)PEC				*0.2vV
R39/71	19.04	22.04.1971	1(5)		1(5)		1(3*)				*0.2vV
R38/71	01.04	01.04.1971					1**				**0.5vV
R37/71	23.03	24.03.1971	1(5)		1(5)M						
R36b71	16.03	16.03.1971			1(2)M						
R36a71	03.03	03.03.1971	1(2)								
R36/71	19.02	19.02.1971					1**				**0.5vV
R35/71	11.02	12.02.1971	1(5)		1(5)M						
R34/71	27.01	29.01.1971	1(2*)		1(2*)M		1(3*)				*0.2vV
R33/70	15.12	18.12.1970	5				5				
R31/70	27.11	27.11.1970					2*				*0.2vV
R30/70	23.11	24.11.1970	5		5M		5				
R28/70	05.10	06.10.1970	5		5M		5				
R27/70	23.09	23.09.1970					1**ME				**0.5vV
R26/70	02.09	08.09.1970					5				
R25/70	26.08	27.08.1970	5		5M		5				
R24/70	13.08	14.08.1970	5		5M		5				
R23/70	23.07	23.07.1970	1*		1*M						*0.2vV
R22/70	29.06	30.06.1970	1(5)		1(5)M		1(5)				
R21/70	18.06	19.06.1970	1(5)		1(5)M		1(5)				
R20/70	28.05	28.05.1970	1(5)		1(5)M						
R19/70	09.05	14.05.1970	1**		1**M+2*M		1*+1**				*0.2vV; **0.5vV
R18/70	09.04	10.04.1970	4(5)		4(5)EM		4(5)				
R16/70	10.03	12.03.1970					4				
R15/70	12.02	13.02.1970	2(3*)		1(3*)EM						*0.2vV; H1: 2 grabs only "qualitative"
R14/70	11.02	11.02.1970					1**				**0.5vV
R13/69	17.12	18.12.1969			4M						
R12/69	04.12	04.12.1969			1**M						**0.5vV
R10/69	06.10	06.10.1969			1**M						**0.5vV
R09/69	08.09	12.09.1969	5		5MP						
R08/69	07.08	08.08.1969	5		5M		5				
R07/69	22.07	22.07.1969			1**M						**0.5vV
R05/69	23.06	23.06.1969	1(4)								
R04/69	11.06	12.06.1969			1ME**						**0.5vV
R03/69	20.05	22.05.1969	1(4)		4EM		4(8)				
R02/69	08.05	08.05.1969	4								
R01/69	28.04	30.04.1969	4(8)		4(8)		4(8)				
ST0667	05.06	05.06.1967	1(2)		1(2)		1(2)				from Stripp 1969a/b

A.3 Database structure and contents

The database is constituted by a series of hierarchical tables storing various levels of detailed information.

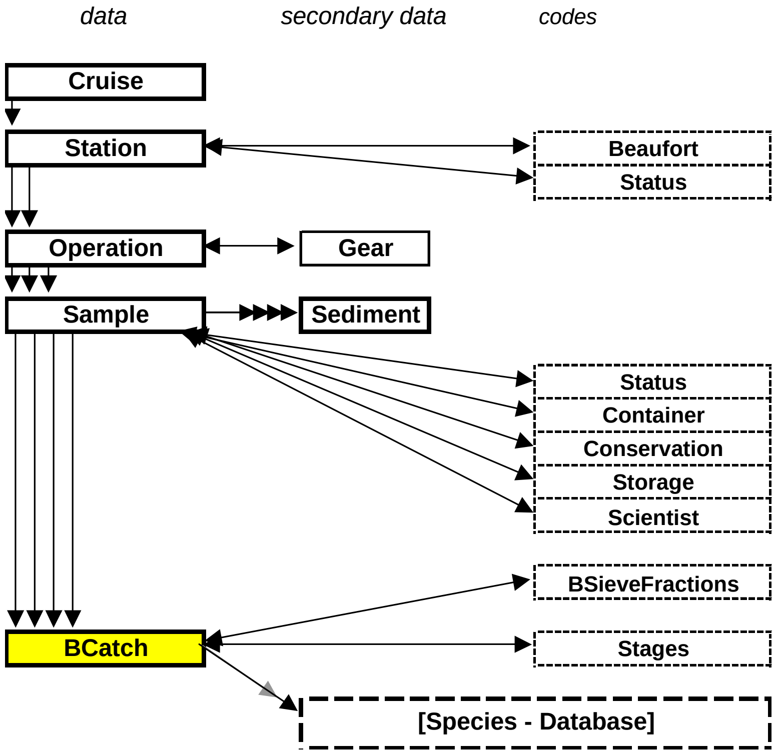

Fig. A.3: Database structure DB99; left column: primary data; middle column: auxiliary data; right column (broken lines): code tables used to ensure data consistency and to explain codes.

From general information about the respective cruise, over position, depth etc. of the stations down to the single sample, this relational database structure ensures that no information is lost. All different types of information can be linked e.g. to chose an appropriate subset of data or to retrieve background information related to a certain datum. The biological data containing abundance and biomass of each species as far as possible for single grabs is contained in the shaded table named "BCatch". All tables are linked via multiple key fields, thus allowing direct connections between all corresponding data tables.

A.4 Species Database

A.4.1 Contents and structure

A.4.2 Code generation principles

DB99_Species

Species-Database of the „AG Fish and Benthos Ecology (FiBÖ)

Alfred-Wegener-Institute for Polar and Marine Research

Alexander Schroeder

An updated taxonomic list of common North Sea Fauna (and more)

DB99_Species is a working list of taxonomic names, intended to be used as a link between different data sets and to store information on these species. It can be used to combine data into groups of higher systematic levels or trophic guilds. It is also designed to avoid confusions by synonyms and misspelling and to name each valid species by one single name.
Although great care has been taken to assure the validity of the taxonomic information contained in this list, it is NOT meant as a source of taxonomic expertise, which can be found in more detail in several databases listed in the references.

Contents

Presently (October 2002), the databases contains 6436 entries, out of which 2398 are valid species, 668 synonyms, 1567 genera plus all the higher systematic levels. Developed at first to suite the needs of the FiBÖ working group (AWI, VÖ), it contains all organisms encountered during our work. This means mostly North Sea macrozoobenthos, but also includes planctonic organisms as well as fish (also from the Antarctic) and some artifacts that appear in our samples. It includes species encountered in old data from the North Sea Long Term Series since 1969 by E. Rachor, IMPACT related work, EUROPIPE, etc. …

In order to cover most common North Sea organisms, it has been extended beyond the list of species that we encountered during our work by including published species lists from several other sources relation to North Sea (and Baltic Sea) research:

RubinCode of Baltic Invertebrates and Fish (Nordic Code Center 1992)
Niermann 1997
NSBS (Craemersch et al. 1997)
Species List of the Biologische Anstalt Helgoland (BAH, outdated web-page 1998)

Several other species list (connected more or less indirectly to the aims of this list) can be linked (via their codes in “…Connections.db”) to this table to provide additional information or alternative views:

UBA* Species List (German "Umweltbundesamt") [linked by "Species-No."]
Integrated Taxonomic Information System (ITIS; www.itis.usda.gov) [linked by "TSN"]
UK_Species-Directory (Howson & Picton 1997) [linked by "Taxon-ID"]

As these lists all have a different scope, many of the species listed in DB99_Species are not present in other lists (and the other way around) and a certain amount of missing links is unavoidable. However, as most of the connections have been established via the scientific name, some links may have also been missed and no responsibility is taken here for the completeness of these links.

Taxonomic status

Taxonomic status and systematic system have been revised and controlled intensively, nevertheless some error may still remain.

Besides the scientific names identified as the actually “*valid*” ones, the list also contains (old) “*synonyms*” encountered during the compilation of the list. This list of synonyms is quite extensive but by no means exhaustive and mostly several additional names can be found in more specialized taxonomic databases. Within this list, synonyms are intended to be able to extract data from several different sources, combining them under one scientific name. The opinion as to what name is actually “valid” differs depending on the source used and is subjected to more or less frequent changes. Although a great effort was made during the compilation of this list to identify the actually correct name, this list is NOT meant as a source of taxonomic expertise, but solely to avoid confusions by synonyms and misspelling and to name each valid species by one single name. To achieve this goal, some old or “*misspelled*” species names have been kept in the database in addition to the correct spelling in order to grant compatibility with other data if they are linked via the species name.
The classification of each entry is visible from the “TaxStatus”, also identifying “*artifacts*” appearing in the samples, entries with alternative (misspelled) Codes (“*CODE-error*”), old taxonomic units that are no longer used (“*not valid*”), questionable (“*?*”) entries and those not found in recent literature during the last revision of the list (“*unknown*”) [as listed in “TaxStatus_lkp”].

A comprehensive list of this kind can only improve with the help of all users. Any changes made in the accompanied form “Fauna 5.8” are marked with date and user to allow tracking of changes made by different users. Therefore if any changes are made not through this form, this has to be documented manually.

Structure

The complete species list consists of several tables, connected via the “*Code*”:

“DB99_Species”, the main table, contains the codes for each name (“Rubin”), the scientific name and author, the “Code” to connect to the assumed correct species name and the systematic hierarchy.

“DB99_CommonNames” contains common names in several languages.

”DB99_Feeding” contains feeding types.

”DB99_Connections” contains connection codes to other databases.

(Codes used in these tables are connected to explaining tables “…_lkp.db”)

The taxonomic level is indicated by the “Tax_Level” (as explained in “..TaxLevel_lkp”). Grouping at higher taxonomic levels can be achieved via the corresponding fields. As there are in several groups more systematic levels than fields in this table, these fields do not necessarily contain all possible levels (whose detail differ between major groups). The fields “Genus”, Family”, “Ordo”, “Class” and “Phylum” always contain exactly these groups, while intermediate levels like “SubOrder” and “SubClass” can also contain e.g. SuperFamilies or SuperOrders (and the like) respectively. The exact systematic hierarchy can be constructed via the “Parent” field. For each entry it contains the code of the next higher combining level.

Technical note:

The complete database consists of several tables. A couple of forms were added that simplify the handling of the tables. In order to allow all links to be established correctly between all tables and within the forms, all files should be placed in one directory. The alias “*TaxNet*” has to be created, pointing to this directory, as this is used in all references to other tables.

Code

The code has been created following the principles of the “Rubin Code”. It has been adjusted to fulfill some specific needs of this database (see: “Code Principles DB99_Species.doc”).

Sources

Systematic hierarchy follows the following sources:
Algae: Lüning (1985)
Annelida: Polychaeta: Hartmann-Schröder (1996)
Clitellata: Kästner (1984) {still valid see ERMS}
Arthropoda: Kästner (1993) {still valid see ERMS}
Brachiopoda: NEAT
Bryozoa: Hayward P. J. (1985); Hayward, P.J., & Ryland, J.S. (1985, 1998, 1999)
Chaetognatha: NEAT
Chordata: Pisces: Fishbase (Eschmeyer),
Tunicata: Hayward & Ryland (1998b)
Mammalia: NEAT
Cnidaria/*Ctenophora*: Kästner (1984) {still valid see ERMS}
Echinodermata: NEAT
Mollusca: ERMS
Nemathelminthes: Kästner (1984) {still valid see ERMS}
Nemertini: Kästner (1984) {still valid see ERMS}
Plathelminthes: Kästner (1984) {still valid see ERMS}
Porifera: Kästner (1980) {still valid see ERMS}
Sipunculida: ERMS

WWW-Links

…used in the preparation of this list, containing further details and additional information:

European Register of Marine Species (ERMS) (Costello et al. 2001):
http://erms.biol.soton.ac.uk

Check List of European Marine Mollusca (CLEMAM):
www.mnhn.fr/mnhn/bimm/clemam/page.htm

North East Atlantic Taxa (NEAT): www.tmbl.gu.se/libdb/taxon/taxa.html

Species 2000 Annual Checklist: www.sp2000.org/AnnualChecklist.html

Integrated Taxonomic Information System (ITIS): www.itis.usda.gov

FishBase: http://filaman.uni-kiel.de/search.cfm

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Kästner (1984): Lehrbuch der speziellen Zoologie Bd. I Teil 2, Fischer, Stuttgart

Kästner (1984): Lehrbuch der speziellen Zoologie Bd. I Teil 3, Fischer, Stuttgart.

Kästner (1993): Lehrbuch der speziellen Zoologie Bd. I Teil 4, Fischer, Stuttgart.

Lüning (1985): Meeresbotanik, Thieme, Stuttgart.

Niermann, U. (1997): Macrobenthos of the south-eastern North Sea during 1983-1988. Ber. Biol. Anst. Helgol. (13): 144 pp.

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Generation principles of the DB99_Species "Rubin-Code"

These codes are intended to simplify data storage and handling. Instead of meaningless numbers coding for species, a unique code has been created, according to the principles of the Rubin-Code with some minor additions.

The main purpose of the list is to ensure information retrieval from a database using valid species names, filtering of errors and synonyms and aggregation of higher taxa. The status of each entry is also listed. Although this list contains a large amount of (+/- checked) systematic information, this list is not meant to provide expertise on taxonomy. For a systematic dictionary or taxonomic checklist the references listed in the “Comments to DB99_Species” should be consulted.

ABBREVIATION PRINCIPLES

The codes have been formed from the scientific names according to the following principles:

Every code contains exactly eighth characters. Shorter names are filled with blanks.

Ranks higher than family:

The eight first character of the name.

`MYTILACE`	Mytilacea

Families

The seven first characters of the name and an X in the eighth position.

`MYTILIDX`	Mytilidae
`MYIDAE X`	Myidae

Genera

The seven first characters of the name and a Z in the eighth position.

`MYSELLAZ`	*Mysella* sp.	Angas, 1877
`MYA     Z`	*Mya* sp.	Linnaeus, 1758

Species

The four first characters of the genus name, one blank, and the three first characters of the species epithet.

`MYSE BID`	*Mysella bidentata*	(Montagu, 1803)
`MYA  ARE`	*Mya arenaria*	Linnaeus, 1758

Subspecies

The two first characters of the genus name, one blank, the two first characters of the species epithet, a point, and the two first characters of the species epithet.

`PR NO.HO`	*Processa nouveli holthuisi*	Al-Adhub & Williamson, 1975

Varieties

The two first characters of the genus name, one blank, the two first characters of the species epithet, a semi-colon, and the two first characters of the variety epithet.

`LE AD;FA`	*Leander adspersus* var. *fabrici*	(Rathke, 1837)

Species coll

The four first characters of the genus name, slash, and the three first characters of the species epithet.

`CAND/CAN`	*Candona candida* COLL

Misspelled names

The same principle as for normal entries, except if it would be the same code as for the properly spelled name. In the latter case a number replaces the eighth position (in all cases but for genera and families, where it replaces the seventh position).

`TRIG GU1` *Triglia gurnardus* = `TRIG GUR` *Trigla gurnardus* Linnaeus, 1758
`TRIGLI1Z` *Triglia* sp. = `TRIGLA Z` *Trigla* sp. Linnaeus, 1758

DEVIATING CODES

Misspelled species names are kept in the list to allow a link via this field, even if the compared list contains typing errors. These have been assigned the status “misspelled” and are linked to the actual code.

Alternative codes have been incorporated, where earlier lists contained deviating codes, to ensure backwards compatibility. These have been assigned the status “CODE-error” and are linked to the actual code.

When standard codes would become equal for two or more taxa, one of these codes is manually altered into a unique one.

All “Rubin”-codes are unambiguous within the list. There might, however, be similar codes in other lists. A combination of this list with other lists containing a “Rubin-Code” may thus lead to inconsistencies.

REFERENCES

Code List Baltic Invertebrates, 81195-SYST, SNV PM 1557, 1982.

A.5 Statistical tables

A.5.1 Results from pair-wise U-tests for differences between stations

A.5.2 ANOSIM results SSd

A.5.3 ANOSIM results WB

A.5.4 ANOSIM results Slt

A.5.5 ANOSIM results FSd

Tab.A.5.1: Results from pair-wise U-tests for differences between stations: adjusted p-values per sum parameter (Holm's procedure for 6 tests).

	P12/WB	**P12/Fsd**	**P12/H1**	**WB/H1**	**WB/Fsd**	**H1/Fsd**
N	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.201
WW	**0.001**	0.754	**0.008**	**<0.001**	**0.008**	**0.007**
WW_{red}	**0.001**	**0.001**	**<0.001**	0.423	0.808	0.808
S	0.074	**<0.001**	**<0.001**	**<0.001**	0.122	**<0.001**
J'	**<0.001**	0.938	0.080	**<0.001**	**<0.001**	0.080
H'	**<0.001**	**0.026**	**<0.001**	**0.026**	**<0.001**	**<0.001**

Tab. A.5.2: ANOSIM results for comparison of community similarity at **SSd** between years (Bray-Curtis similarity, 4th root transformation). *R*-values in lower and *p*-values [%] in upper triangular matrix. Dark grey shaded fields printed in bold indicate *non-significant* differences between the respective years. Lightly shaded fields in italics indicate comparisons based on few replicates (see first column). *including small Reineck Box Corers (RBC).

Samples	R \ p	69	71	72	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	91	92	93	94	95	96	97	98	99	2000
4	69		*20,0*	*20,0*	0,8	0,8	0,2	*11,1*	2,9	0,2	0,6	**9,9**	0,2	0,2	1	2,8	1,6	0,8	0,2	0,8	0,8	0,8	0,8	0,8	1,6	0,8	0,8	0,8	0,8
1	71	*1,00*			*16,7*	*16,7*	*11,1*	*22,2*	*20*	*11,1*	*11,1*	*33,3*	*22,2*	*11,1*	*22,2*	*22,2*	*16,7*	*16,7*	*11,1*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*
1	72	*1,00*			*16,7*	*16,7*	*11,1*	*33,3*	*20*	*11,1*	*22,2*	*33,3*	*22,2*	*11,1*	*22,2*	*11,1*	*16,7*	*16,7*	*11,1*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*
5	75	0,91	*1,00*	*1,00*		0,8	0,5	2,5	0,8	0,1	1,9	2,5	0,1	0,1	0,5	0,5	0,8	0,8	0,1	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	76	1,00	*1,00*	*1,00*	0,91		0,2	**7,6**	0,8	0,3	1,8	1,9	0,2	0,1	0,6	0,8	0,8	0,8	0,2	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
8*	77	0,92	*1,00*	*0,96*	0,86	0,88		0,1	0,2	0,1	0,1	0,2	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,2	0,1	0,1	0,5	0,1	0,2	0,2	0,1
8*	78	*0,21*	*0,44*	*0,27*	0,28	**0,20**	0,42		**10,5**	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,7	0,4	0,1	0,6	1,7	0,6	0,7	1,8	0,2	0,2	0,2	0,3	0,3
4*	79	0,89	*1,00*	*1,00*	0,91	0,89	0,87	**0,21**		0,6	0,2	**20,2**	0,2	0,2	4,8	0,8	0,8	0,8	0,2	0,8	0,8	0,8	0,8	0,8	1,6	0,8	0,8	0,8	0,8
8*	80	0,92	*0,89*	*0,80*	0,90	0,76	0,92	0,69	0,48		0,1	0,1	0,1	0,1	0,1	0,1	0,2	0,3	0,1	0,1	0,1	0,1	0,2	0,1	0,2	0,2	0,1	0,1	0,1
8*	81	0,55	*0,67*	*0,52*	0,37	0,40	0,72	0,55	0,58	0,77		0,4	0,1	0,1	0,1	0,1	0,4	0,5	0,2	0,1	0,1	0,1	0,2	0,3	0,1	0,1	0,2	0,1	0,2
8*	82	**0,23**	*0,28*	*0,27*	0,28	0,36	0,59	0,45	**0,12**	0,55	0,26		3	0,1	2,3	0,1	1,5	2,5	1,1	0,6	3	1,1	0,5	0,6	0,9	0,4	0,4	0,9	0,1
8*	83	0,65	*0,67*	*0,63*	0,69	0,62	0,72	0,68	0,50	0,66	0,44	0,16		0,1	0,1	0,3	0,3	0,5	1,2	0,2	0,4	0,1	0,1	0,2	0,1	0,2	0,1	0,1	0,1
8*	84	0,84	*1,00*	*0,95*	0,76	0,83	0,86	0,60	0,62	0,88	0,55	0,53	0,65		0,2	0,2	0,2	0,1	0,1	0,1	0,1	0,2	0,1	0,2	0,3	0,2	0,2	0,1	0,1
8*	85	0,47	*0,55*	*0,51*	0,51	0,56	0,69	0,56	0,31	0,58	0,41	0,19	0,31	0,29		2,1	**8,4**	3,4	0,2	1	3,2	0,2	0,5	0,6	0,2	0,5	0,2	1,4	0,3
8*	86	0,36	*0,18*	*0,46*	0,50	0,63	0,72	0,69	0,53	0,62	0,59	0,36	0,38	0,57	0,26		**5,1**	2	0,1	1,8	0,8	0,2	1,1	0,9	0,2	0,4	3,1	1,1	0,4
5	87	0,81	*1,00*	*0,96*	0,86	0,92	0,91	0,59	0,88	0,78	0,53	0,33	0,45	0,77	**0,20**	**0,24**		0,8	0,1	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	88	1,00	*1,00*	*1,00*	1,00	1,00	0,95	0,55	0,96	0,77	0,54	0,33	0,48	0,77	0,29	0,31	0,42		0,6	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
8*	89	0,63	*0,84*	*0,79*	0,70	0,73	0,84	0,71	0,70	0,84	0,55	0,21	0,22	0,52	0,40	0,40	0,66	0,61		0,3	0,1	0,1	0,2	0,2	0,3	0,2	0,3	0,6	0,1
5	91	1,00	*1,00*	*1,00*	0,96	1,00	0,95	0,54	0,99	0,87	0,67	0,47	0,64	0,68	0,50	0,35	0,79	0,96	0,69		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	92	0,92	*1,00*	*1,00*	0,93	0,97	0,91	0,36	0,93	0,80	0,62	0,30	0,58	0,83	0,28	0,46	0,78	0,95	0,71	0,82		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	93	0,84	*1,00*	*1,00*	0,99	0,90	0,97	0,43	0,93	0,95	0,85	0,39	0,76	0,98	0,64	0,59	0,98	0,99	0,86	0,83	0,62		0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	94	1,00	*1,00*	*1,00*	0,93	1,00	0,83	0,37	0,93	0,88	0,69	0,49	0,71	0,84	0,52	0,45	0,82	1,00	0,85	0,94	0,55	0,58		0,8	0,8	0,8	0,8	0,8	0,8
5	95	0,98	*1,00*	*1,00*	0,90	0,96	0,91	0,33	0,94	0,89	0,78	0,50	0,77	0,87	0,57	0,49	0,93	0,99	0,90	0,78	0,77	0,58	0,54		0,8	0,8	0,8	0,8	0,8
5	96	0,59	*0,52*	*0,72*	0,60	0,65	0,93	0,57	0,54	0,82	0,82	0,40	0,72	0,92	0,61	0,59	0,82	0,74	0,81	0,78	0,68	0,74	0,74	0,60		0,8	0,8	0,8	0,8
5	97	0,99	*1,00*	*1,00*	0,95	0,98	1,00	0,84	0,94	0,96	0,92	0,49	0,74	0,99	0,61	0,63	0,85	0,99	0,90	1,00	0,96	0,99	0,99	1,00	0,54		0,8	0,8	0,8
5	98	0,94	*0,88*	*0,92*	0,82	0,96	0,99	0,63	0,99	0,90	0,73	0,52	0,76	0,92	0,55	0,27	0,87	0,96	0,65	0,88	0,86	0,98	0,97	0,96	0,61	0,90		0,8	0,8
5	99	1,00	*1,00*	*1,00*	0,98	0,99	0,97	0,54	0,98	0,89	0,60	0,47	0,68	0,67	0,40	0,46	0,81	0,98	0,55	0,95	0,91	0,96	1,00	0,95	0,71	0,92	0,47		0,8
5	2000	1,00	*1,00*	*1,00*	0,99	1,00	0,98	0,65	0,99	0,91	0,64	0,61	0,81	0,72	0,56	0,59	0,89	1,00	0,84	0,99	0,97	0,98	1,00	0,96	0,77	1,00	0,84	0,91	

Tab. A.5.3: ANOSIM results for comparison of community similarity at **WB** between years (Bray-Curtis similarity, 4th root transformation). *R*-values in lower and *p*-values [%] in upper triangular matrix.
Dark grey shaded fields printed in bold indicate *non-significant* differences between the respective years. Lightly shaded fields in italics indicate comparisons based on few replicates (see first column). *including small Reineck Box Corers (RBC).

Samples	R \ p	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	2000
5	81		0,2	0,2	0,2	0,2	0,2	*1,2*	0,2	0,2	0,2	*14,3*	0,2	0,2	0,2	0,2	0,2	0,2	0,2	0,2	0,2
8*	82	0,66		0,2	0,1	0,1	0,2	0,6	0,1	0,1	0,1	*11,1*	0,2	0,1	0,4	0,1	0,1	0,2	0,2	0,2	0,1
5	83	0,68	0,66		0,8	0,8	0,8	*1,8*	0,8	0,8	0,8	*16,7*	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	84	0,61	0,77	0,30		2,4	0,8	*7,1*	0,8	0,8	0,8	*50,0*	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	85	0,77	0,75	0,69	0,36		0,8	*1,8*	0,8	0,8	0,8	*33,3*	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	86	0,94	0,95	0,76	0,54	0,42		*1,8*	1,6	0,8	0,8	*33,3*	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
3	87	*0,91*	0,90	*0,99*	*0,35*	*0,56*	*0,64*		*7,1*	*1,8*	*1,8*	*25,0*	*1,8*	*1,8*	*1,8*	*5,4*	*1,8*	*1,8*	*1,8*	*1,8*	*1,8*
5	88	0,84	0,88	0,91	0,51	0,60	0,50	*0,33*		0,8	0,8	*33,3*	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	89	0,95	0,92	0,98	0,71	0,77	0,99	*1,00*	0,60		0,8	*16,7*	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	90	0,90	0,86	0,97	0,70	0,72	0,77	*0,83*	0,42	0,75		*16,7*	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
1	91	*0,93*	*1,00*	*1,00*	*0,00*	*0,56*	*0,56*	*1,00*	*0,56*	*0,96*	*1,00*		*33,3*	*50,0*	*33,3*	*100,0*	*16,7*	*16,7*	*33,3*	*66,7*	*16,7*
5	92	0,77	0,97	0,87	0,66	0,75	0,87	*0,86*	0,85	0,83	0,78	*0,32*		0,8	1,6	0,8	0,8	0,8	0,8	0,8	0,8
5	93	0,76	0,97	0,84	0,73	0,83	0,69	*0,72*	0,76	0,74	0,68	*-0,08*	0,45		4,0	**23,8**	1,6	0,8	0,8	3,2	0,8
5	94	0,82	0,95	0,89	0,89	0,84	0,84	*0,76*	0,84	0,72	0,78	*0,52*	0,61	0,28		1,6	0,8	0,8	0,8	0,8	0,8
5	95	0,73	0,91	0,72	0,72	0,68	0,64	*0,41*	0,55	0,54	0,52	*-0,60*	0,41	**0,09**	0,42		0,8	0,8	0,8	**11,1**	0,8
5	96	0,94	0,99	0,94	0,86	0,95	0,89	*0,90*	0,91	0,93	0,94	*0,60*	0,90	0,49	0,74	0,38		0,8	0,8	**0,8**	0,8
5	97	0,98	0,97	0,91	0,84	0,87	0,94	*0,96*	0,97	0,94	0,96	*0,88*	0,93	0,93	0,88	0,79	0,87		0,8	0,8	0,8
5	98	0,98	1,00	0,95	0,70	0,94	0,86	*0,92*	0,86	0,98	0,86	*0,56*	0,79	0,76	0,84	0,46	0,89	0,88		1,6	0,8
5	99	0,84	0,96	0,79	0,53	0,70	0,60	*0,60*	0,75	0,80	0,68	*-0,04*	0,61	0,40	0,72	**0,18**	0,68	0,90	0,37		0,8
5	2000	1,00	1,00	1,00	0,76	0,86	1,00	*1,00*	0,99	1,00	1,00	*1,00*	0,93	0,76	0,86	0,68	0,98	0,97	0,97	0,73	

Tab. A.5.4: ANOSIM results for comparison of community similarity at **Slt** between years (Bray-Curtis similarity, 4th root transformation).
R-values in lower and *p*-values [%] in upper triangular matrix.
Dark grey shaded fields printed in bold indicate *non-significant* differences between the respective years.
Lightly shaded fields in italics indicate comparisons based on few replicates (see first column).

Samples	R \ p	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	2000
4	69		*2,9*	*20*	*40*	*6,7*	*13,3*	0,8	**6,5**	0,8	0,8	0,8	0,8	0,8	0,8	1,6	0,8	0,8	0,8	1,6	1,6	0,8	1,6	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
4	70	*0,97*		*40*	*20*	*6,7*	*6,7*	0,8	0,4	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	1,6	0,8	0,8	0,8	0,8	0,8	0,8	0,8
1	71	*0,75*	*0,33*			*33,3*	*33,3*	*16,7*	*22,2*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*50*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*33,3*	*16,7*
1	72	*0,42*	*1,00*			*33,3*	*33,3*	*16,7*	*44,4*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*33,3*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*	*16,7*
2	73	*0,50*	*0,61*	*1,00*	*1,00*		*33,3*	*4,8*	*20*	*4,8*	*23,8*	*4,8*	*4,8*	*4,8*	*4,8*	*42,9*	*4,8*	*4,8*	*4,8*	*14,3*	*4,8*	*14,3*	*9,5*	*4,8*	*4,8*	*4,8*	*4,8*	*4,8*	*4,8*	*4,8*	*4,8*	*4,8*	*4,8*
2	74	*0,54*	*1,00*	*1,00*	*1,00*	*1,00*		*4,8*	*22,2*	*9,5*	*4,8*	*4,8*	*4,8*	*4,8*	*19*	*33,3*	*4,8*	*14,3*	*4,8*	*4,8*	*4,8*	*4,8*	*47,6*	*4,8*	*4,8*	*4,8*	*4,8*	*4,8*	*14,3*	*4,8*	*4,8*	*4,8*	*4,8*
5	75	0,81	1,00	*1,00*	*1,00*	*0,96*	*1,00*		0,9	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
8	76	**0,29**	0,60	*0,56*	*0,13*	*0,23*	*0,21*	0,43		0,6	0,6	**5,0**	0,3	0,1	0,5	3,8	0,1	0,4	0,1	0,3	0,3	0,3	4,0	0,2	0,1	0,2	0,1	0,4	0,1	0,2	0,2	0,2	0,3
5	77	0,83	0,98	*1,00*	*1,00*	*0,67*	*0,35*	0,57	0,50		0,8	**0,8**	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	78	0,86	0,92	*0,96*	*0,96*	*0,26*	*0,96*	0,62	0,42	0,73		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	79	0,75	1,00	*1,00*	*1,00*	*1,00*	*1,00*	1,00	**0,24**	0,70	0,92		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	80	1,00	1,00	*1,00*	*1,00*	*1,00*	*1,00*	1,00	0,69	1,00	0,98	1,00		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	81	1,00	1,00	*1,00*	*1,00*	*1,00*	*1,00*	0,90	0,64	0,84	0,80	0,97	1,00		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	82	0,92	0,99	*0,96*	*1,00*	*0,89*	*0,33*	0,56	0,40	0,48	0,87	0,75	0,96	0,88		1,6	0,8	2,4	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	83	0,49	0,69	*0,20*	*0,20*	*0,07*	*0,16*	0,38	0,25	0,54	0,42	0,38	0,59	0,54	0,22		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	84	1,00	1,00	*1,00*	*1,00*	*1,00*	*1,00*	1,00	0,71	0,99	0,89	1,00	1,00	1,00	1,00	0,68		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	85	0,91	1,00	*1,00*	*1,00*	*0,96*	*0,49*	0,54	0,52	0,67	0,94	0,87	0,94	0,78	0,46	0,38	1,00		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	86	1,00	0,99	*1,00*	*1,00*	*1,00*	*1,00*	1,00	0,68	0,98	0,96	1,00	0,90	0,99	0,91	0,62	1,00	0,94		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	87	0,67	0,91	*0,84*	*1,00*	*0,36*	*0,91*	0,68	0,47	0,86	0,74	0,92	1,00	1,00	0,88	0,50	1,00	0,86	0,88		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	88	0,87	1,00	*1,00*	*1,00*	*0,71*	*0,95*	0,68	0,59	0,92	0,68	0,97	1,00	0,96	0,88	0,49	0,99	0,84	1,00	0,74		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	89	0,62	0,93	*1,00*	*1,00*	*0,40*	*0,95*	0,66	0,53	0,82	0,78	0,79	1,00	0,98	0,91	0,59	1,00	0,92	0,98	0,50	0,80		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	90	0,52	0,91	*0,88*	*0,52*	*0,42*	*0,04*	0,39	0,25	0,48	0,68	0,61	0,97	0,87	0,46	0,50	0,91	0,64	1,00	0,66	0,82	0,73		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	91	1,00	1,00	*1,00*	*1,00*	*0,98*	*1,00*	0,77	0,67	0,96	0,85	1,00	0,64	1,00	0,90	0,58	0,89	0,83	0,97	0,96	0,86	0,99	0,84		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	92	0,99	1,00	*1,00*	*1,00*	*0,98*	*1,00*	0,94	0,70	1,00	0,97	1,00	1,00	1,00	0,96	0,80	1,00	0,98	1,00	0,96	1,00	0,99	0,80	0,96		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	93	0,79	0,76	*0,96*	*0,88*	*0,53*	*0,93*	0,80	0,62	0,97	0,92	0,95	1,00	1,00	0,98	0,73	0,99	0,99	1,00	0,77	0,87	0,78	0,78	0,90	0,95		0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	94	1,00	1,00	*1,00*	*1,00*	*1,00*	*1,00*	1,00	0,73	1,00	1,00	1,00	1,00	1,00	1,00	0,87	0,99	1,00	1,00	1,00	1,00	1,00	1,00	0,94	0,98	0,90		0,8	0,8	0,8	0,8	0,8	0,8
5	95	1,00	1,00	*1,00*	*1,00*	*1,00*	*1,00*	0,96	0,68	1,00	0,95	1,00	1,00	1,00	1,00	0,78	0,92	1,00	1,00	0,97	1,00	1,00	0,89	0,93	0,76	0,95	0,57		0,8	0,8	0,8	0,8	0,8
5	96	0,81	0,81	*0,92*	*0,80*	*0,73*	*0,42*	0,73	0,64	0,60	0,92	0,93	0,96	0,97	0,80	0,78	0,94	0,84	0,80	0,75	0,97	0,89	0,68	0,94	0,76	0,98	0,93	0,54		0,8	0,8	0,8	0,8
5	97	0,99	0,99	*0,96*	*1,00*	*1,00*	*0,93*	0,99	0,71	1,00	1,00	1,00	0,99	1,00	0,94	0,89	0,99	0,96	0,97	0,98	1,00	1,00	0,85	1,00	0,98	1,00	1,00	0,98	0,60		0,8	0,8	0,8
5	98	0,78	0,83	*0,68*	*0,80*	*0,71*	*0,93*	0,86	0,53	0,93	0,91	0,92	0,98	1,00	0,88	0,64	0,99	0,97	0,96	0,64	0,97	0,75	0,65	1,00	0,98	0,90	1,00	0,92	0,76	0,55		0,8	0,8
5	99	0,90	0,84	*0,40*	*0,68*	*0,58*	*0,53*	0,62	0,70	0,81	0,91	0,97	0,86	0,98	0,75	0,76	0,88	0,87	0,87	0,68	0,92	0,88	0,63	0,81	0,69	0,96	0,93	0,72	0,40	0,46	0,59		0,8
5	2000	1,00	0,99	*1,00*	*1,00*	*1,00*	*1,00*	1,00	0,69	1,00	0,98	1,00	1,00	1,00	1,00	0,86	1,00	1,00	1,00	0,99	1,00	1,00	0,98	1,00	1,00	0,94	1,00	0,97	0,95	1,00	1,00	0,93	

Tab. A.5.5: ANOSIM results for comparison of community similarity at **FSd** between years (Bray-Curtis similarity, 4th root transformation).
R-values in lower and *p*-values in upper triangular matrix.
Dark grey shaded fields printed in bold indicate *non-significant* differences between the respective years.
Lightly shaded fields in italics indicate comparisons based on few replicates (see first column).

Samples	R \ p	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	88	89	90	91	92	93	94	95	96	97	98	99	2000
4	69		*2,9*	*20*	*20*	*6,7*	0,8	0,8	0,2	0,1	0,1	0,3	0,2	0,2	0,2	0,2	0,2	0,2	*20*	0,8	0,8	*20*	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
4	70	*0,48*		*60*	*80*	*6,7*	0,8	0,8	0,2	0,1	0,1	0,3	0,2	0,2	0,2	0,2	0,2	0,2	*20*	0,8	0,8	*20*	0,8	0,8	0,8	0,8	0,8	2,4	0,8	0,8	0,8
1	71	*0,58*	*0,08*			*33*	*17*	*17*	*11*	*10*	*4*	*13*	*22*	*11*	*11*	*22*	*11*	*11*		*17*	*17*		*17*	*17*	*17*	*17*	*17*	*50*	*17*	*17*	*17*
1	72	*0,58*	*0,17*			*33*	*50*	*17*	*11*	*10*	*4*	*13*	*22*	*11*	*11*	*44*	*22*	*11*		*17*	*17*		*17*	*17*	*17*	*17*	*17*	*50*	*17*	*17*	*17*
2	73	*0,93*	*0,93*	*1,00*	*1,00*		*4,8*	*4,8*	*2,2*	*1,8*	0,3	*2,8*	*8,9*	*2,2*	*2,2*	*2,2*	*2,2*	*2,2*	*33*	*4,8*	*4,8*	*33*	*4,8*	*4,8*	*4,8*	*4,8*	*4,8*	*4,8*	*4,8*	*4,8*	*4,8*
5	74	0,92	0,91	*0,80*	*0,16*	*0,82*		0,8	0,2	0,1	0,1	0,1	0,1	0,1	0,2	0,2	0,1	0,1	*17*	0,8	0,8	*17*	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	75	1,00	0,97	*1,00*	*1,00*	*1,00*	0,59		0,1	0,1	0,1	0,1	0,3	0,1	0,1	0,2	0,1	0,3	*17*	0,8	0,8	*17*	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
8	76	0,91	0,91	*0,91*	*0,84*	*0,90*	0,83	0,81		0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	*11*	0,1	0,4	*11*	0,3	0,2	0,2	0,1	0,2	0,2	0,1	0,1	0,1
9*	77	0,98	0,99	*0,91*	*0,99*	*0,98*	0,95	0,98	0,90		0,1	0,2	0,1	0,1	0,1	0,1	0,1	0,1	*10*	0,3	0,2	*20*	0,1	0,1	0,1	0,2	0,1	0,1	0,3	0,3	0,1
24*	78	0,98	0,97	*0,98*	*0,93*	0,94	0,91	0,82	0,80	0,83		0,1	0,1	0,1	0,1	0,1	0,1	0,1	*4*	0,1	0,1	*4*	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1
7*	79	1,00	0,96	*0,99*	*1,00*	*1,00*	0,83	0,96	0,96	0,83	0,68		0,1	0,1	0,1	0,1	0,1	0,2	*13*	0,1	0,1	*13*	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1
8*	80	0,85	0,87	*0,51*	*0,51*	*0,63*	0,80	0,75	0,93	0,77	0,97	0,68		0,1	0,1	0,2	0,1	0,1	*22*	0,1	0,5	*22*	0,1	0,2	0,1	0,1	0,1	0,1	0,2	0,4	0,1
8*	81	0,86	0,74	*0,63*	*0,46*	*0,73*	0,75	0,66	0,74	0,80	0,80	0,70	0,68		0,4	0,1	0,1	0,1	*11*	0,2	0,1	*11*	0,2	0,2	0,1	0,1	0,4	0,2	0,1	0,1	0,1
8*	82	0,92	0,95	*0,88*	*0,73*	*0,85*	0,74	0,78	0,81	0,84	0,79	0,81	0,81	0,25		0,1	0,1	0,1	*11*	0,3	0,3	*11*	0,2	0,1	0,1	0,2	0,1	0,1	0,1	0,1	0,1
8*	83	0,70	0,73	*0,29*	*0,13*	*0,73*	0,83	0,63	0,84	0,70	0,86	0,52	0,46	0,40	0,59		0,1	0,1	*11*	0,4	0,2	*22*	0,1	0,2	0,2	0,2	0,1	0,4	0,3	0,1	0,2
8*	84	0,82	0,89	*0,62*	*0,62*	*0,75*	0,87	0,92	0,87	0,61	0,83	0,50	0,69	0,61	0,58	0,49		0,1	*11*	0,3	0,1	*22*	0,2	0,4	0,2	0,3	0,2	0,1	0,1	0,3	0,1
8*	85	0,99	0,99	*0,95*	*0,83*	*0,96*	0,97	0,98	0,95	0,74	0,79	0,89	0,63	0,69	0,69	0,61	0,55		*11*	0,2	0,2	*11*	0,1	0,3	0,1	0,3	0,2	0,1	0,2	0,2	0,2
1*	88	*1,00*	*0,92*			*1,00*	*0,72*	*0,96*	*0,97*	*0,95*	*0,97*	*0,99*	*0,71*	*0,51*	*0,84*	*0,67*	*0,85*	*0,99*		*17*	*17*		*17*	*17*	*17*	*17*	*17*	*50*	*17*	*17*	*17*
5	89	1,00	0,99	*1,00*	*1,00*	*1,00*	0,85	0,96	0,87	0,79	0,89	0,99	0,65	0,60	0,75	0,54	0,54	0,60	*1,00*		0,8	*17*	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	90	1,00	1,00	*1,00*	*1,00*	*1,00*	0,86	0,97	0,89	0,91	0,91	0,97	0,73	0,91	0,84	0,81	0,80	0,81	*1,00*	0,78		*17*	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
1	91	*1,00*	*0,92*			*1,00*	*0,68*	*1,00*	*0,68*	*0,53*	*0,88*	*0,89*	*0,51*	*0,77*	*0,82*	*0,53*	*0,31*	*0,89*		*0,80*	*0,68*		*17*	*17*	*17*	*17*	*17*	*50*	*17*	*17*	*17*
5	92	1,00	1,00	*1,00*	*1,00*	*1,00*	0,94	1,00	0,91	0,98	0,92	0,94	0,68	0,94	0,95	0,74	0,75	0,86	*1,00*	0,97	0,96	*0,72*		0,8	0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	93	0,95	0,98	*0,88*	*0,84*	*0,75*	0,67	0,82	0,91	0,92	0,91	0,86	0,79	0,73	0,84	0,85	0,73	0,95	*0,84*	0,76	0,78	*0,48*	0,79		0,8	0,8	0,8	0,8	0,8	0,8	0,8
5	94	1,00	0,98	*0,96*	*0,96*	*1,00*	0,84	0,97	0,81	0,94	0,92	0,99	0,68	0,65	0,78	0,56	0,69	0,92	*1,00*	0,96	0,88	*0,92*	0,96	0,80		0,8	0,8	0,8	0,8	0,8	0,8
5	95	1,00	0,98	*1,00*	*1,00*	*1,00*	0,82	0,92	0,88	0,97	0,93	1,00	0,64	0,74	0,71	0,70	0,65	0,94	*1,00*	0,91	0,88	*0,64*	0,94	0,71	0,83		0,8	0,8	0,8	0,8	0,8
5	96	1,00	0,96	*1,00*	*1,00*	*1,00*	0,74	0,92	0,86	0,99	0,74	0,87	0,66	0,47	0,73	0,59	0,76	0,85	*1,00*	0,98	0,98	*1,00*	1,00	0,78	0,98	0,95		0,8	0,8	0,8	0,8
5	97	0,69	0,37	*0,24*	*-,04*	*0,60*	0,66	0,52	0,80	0,79	0,93	0,69	0,63	0,50	0,76	0,42	0,62	0,86	*-,04*	0,67	0,64	*0,16*	0,59	0,51	0,52	0,60	0,46		2,4	0,8	0,8
5	98	1,00	0,89	*1,00*	*0,96*	*1,00*	0,70	0,91	0,90	1,00	0,92	0,99	0,88	0,76	0,84	0,76	0,96	1,00	*1,00*	0,99	0,99	*1,00*	0,96	0,88	0,95	0,99	0,85	0,27		0,8	0,8
5	99	1,00	0,96	*1,00*	*1,00*	*1,00*	0,65	0,95	0,91	1,00	0,89	0,95	0,84	0,93	0,89	0,68	0,83	0,97	*1,00*	0,97	1,00	*1,00*	1,00	0,78	0,99	0,96	0,90	0,50	0,85		0,8
5	2000	1,00	1,00	*1,00*	*1,00*	*1,00*	0,85	1,00	1,00	0,98	0,98	1,00	0,69	0,97	0,91	0,84	0,76	0,95	*1,00*	1,00	0,94	*1,00*	0,98	0,86	1,00	0,97	1,00	0,74	1,00	1,00	

A.6 Supplementary figures

A.6.1 Mean density of organisms in relation to sample size

A.6.2 Mean total biomass in relation to sample size

A.6.3 Mean total biomass excluding large species in relation to sample size

A.6.4 Frequency distribution of mean similarity

A.6.5 Community similarity and time lag

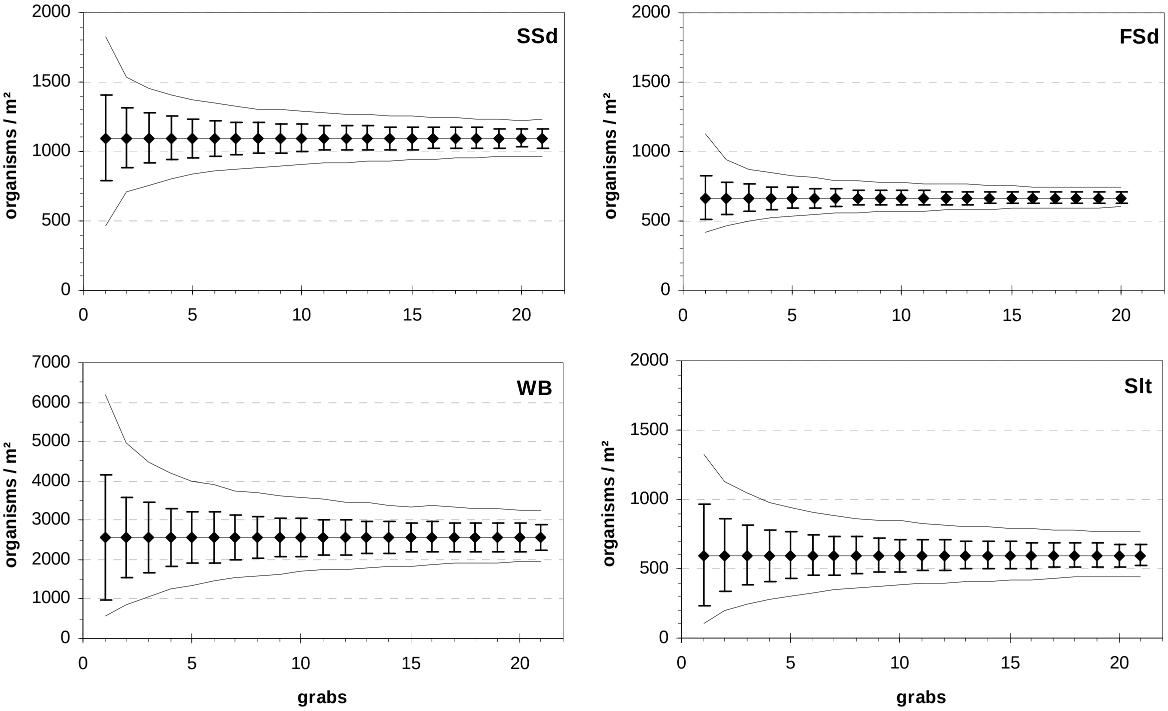


Fig. A.6.1.: Mean density of organisms in relation to sample size. Error bars indicate the SD for single grabs and the SE for pooled samples (see methods). Simple lines delineate the empirical 95% confidence interval. (note the different y-scale for WB)

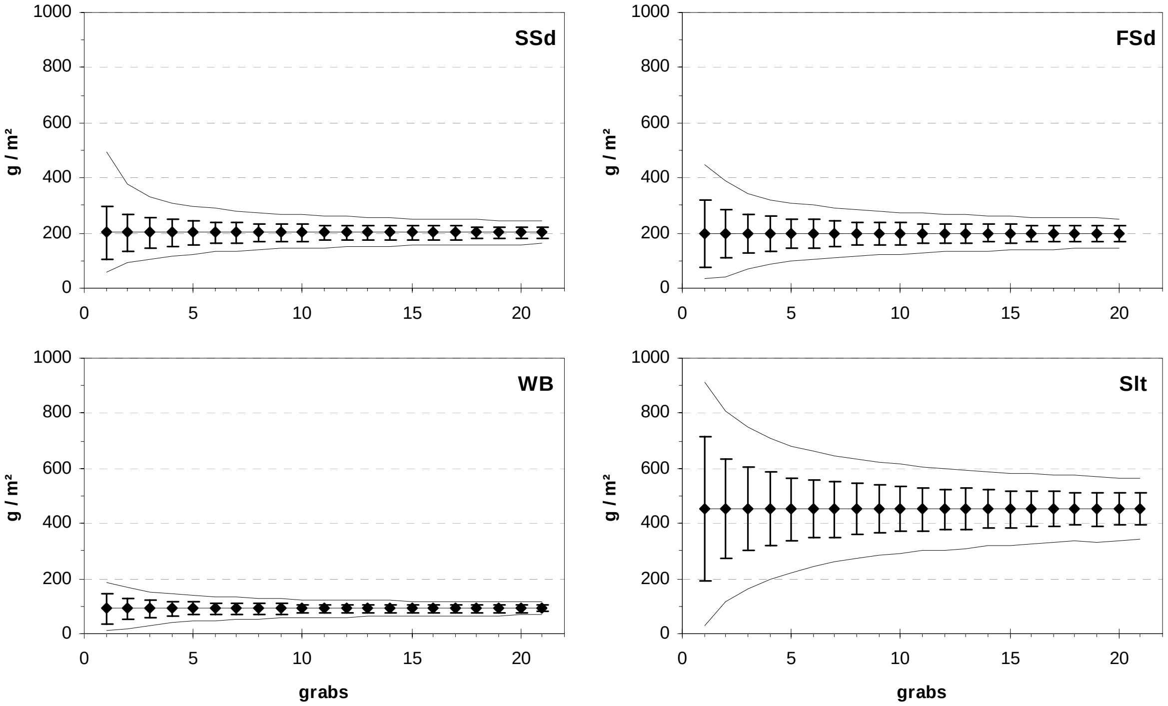


Fig. A.6.2.: Mean total biomass as wet weight per m² in relation to sample size. Error bars indicate the SD for single grabs and the SE for pooled samples. Outer lines delineate the empirical 95% confidence interval.

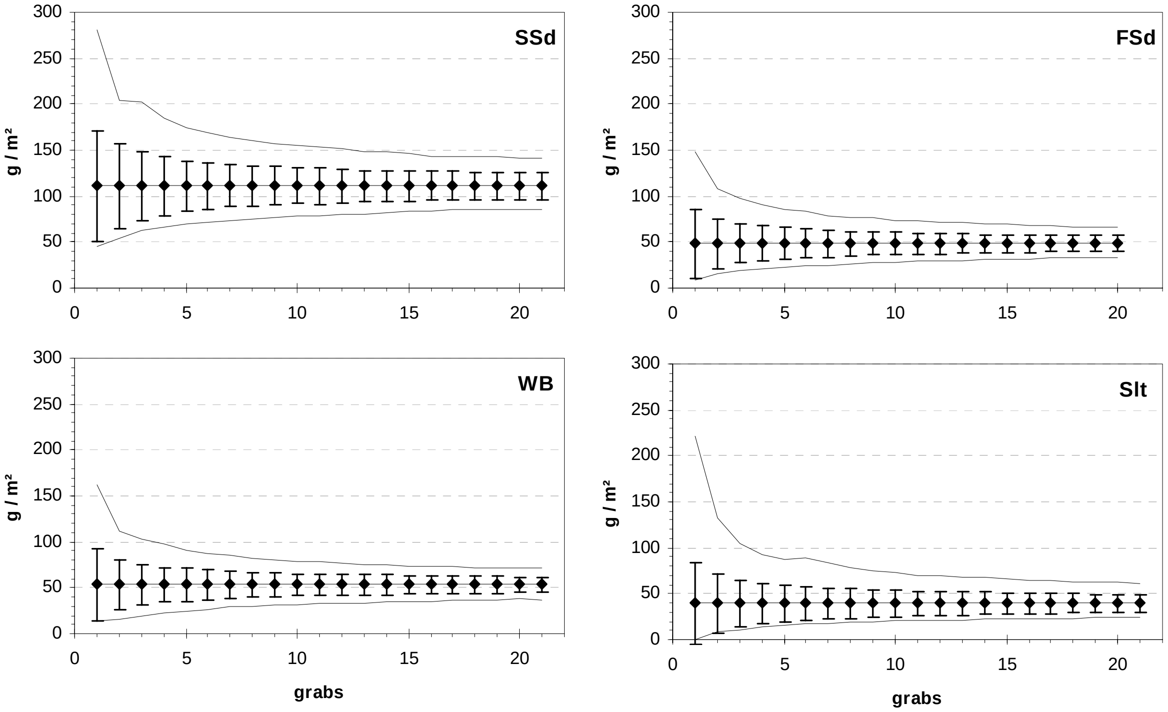


Fig. A.6.3.: Mean total biomass excluding large species (see text) as wet weight in relation to sample size. Error bars indicate the SD for single grabs and the SE for pooled samples. Outer lines delineate the empirical 95% confidence interval.

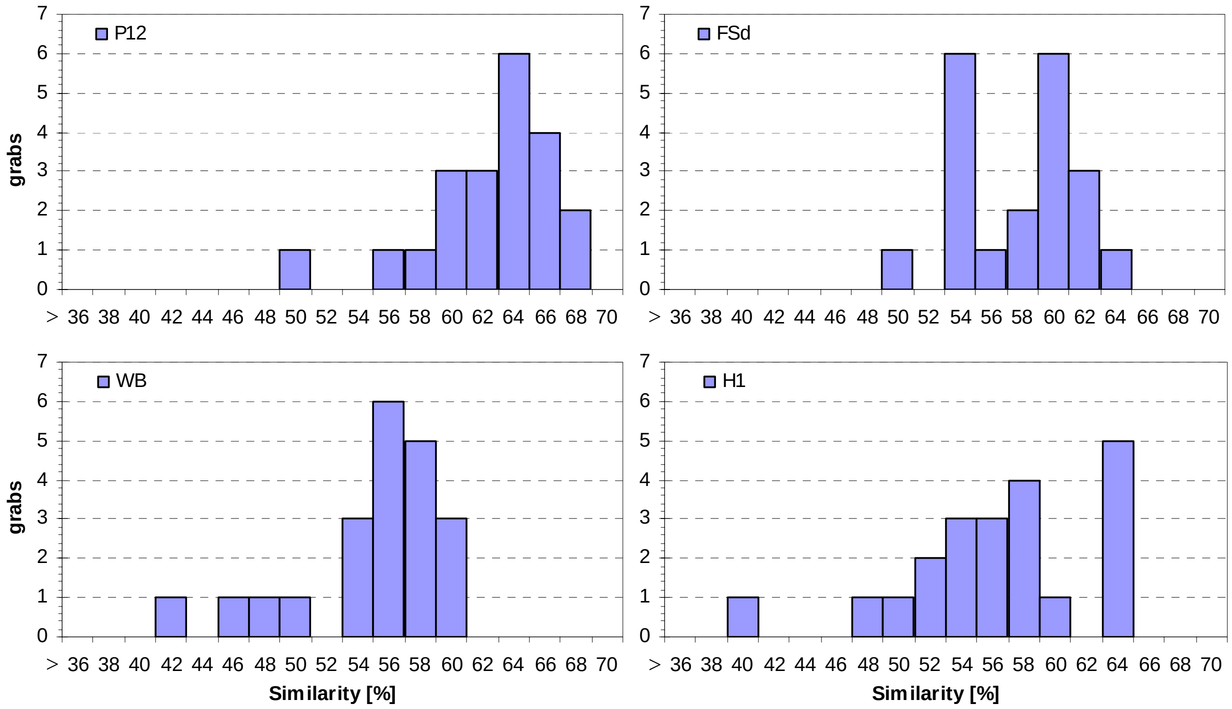


Fig. A.6.4.: Frequency distribution of mean similarity between each single grab and all other grabs per station; Bray-Curtis similarity, 4th root transformed abundances.

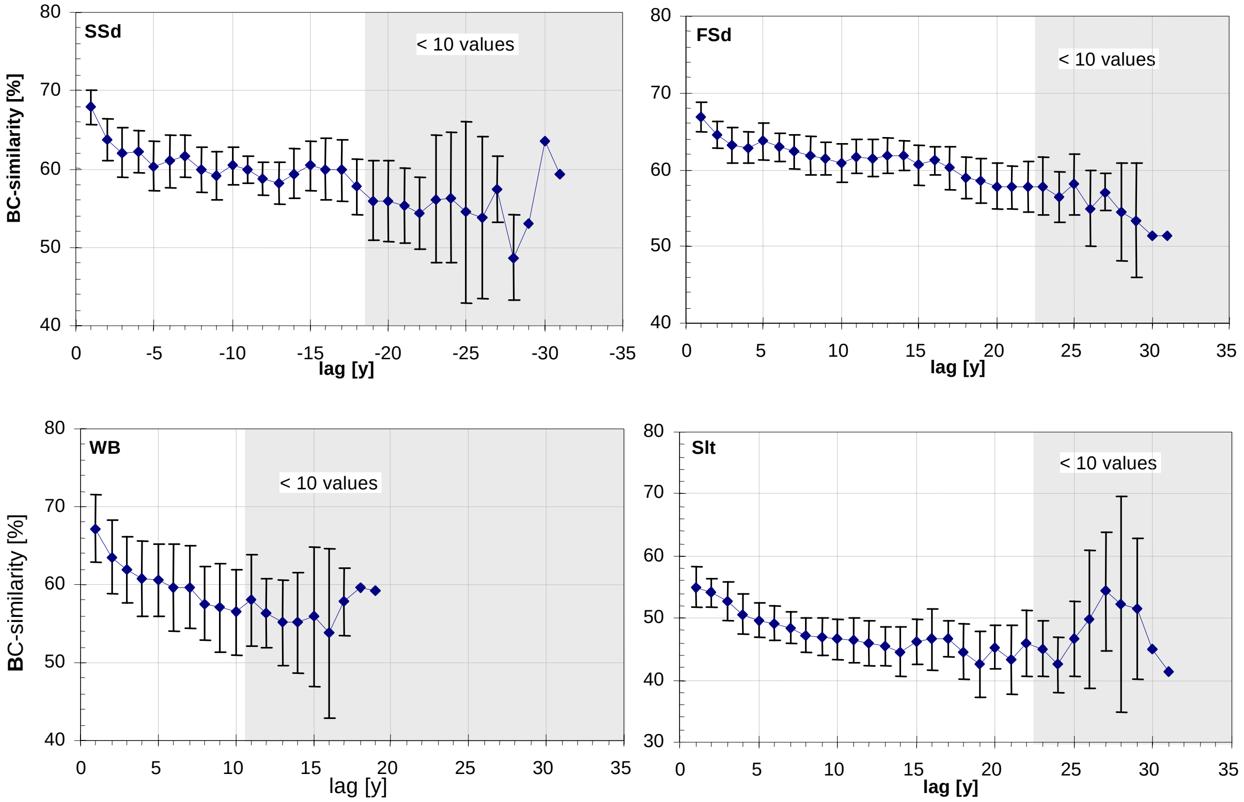


Fig. A.6.5: Similarity between samples separated by an increasing number of years (lag) (± 95% confidence limits).

A.7 Single species temporal development plots

A.7.1 SSd

A.7.2 WB

A.7.3 Slt

A.7.4 FSd

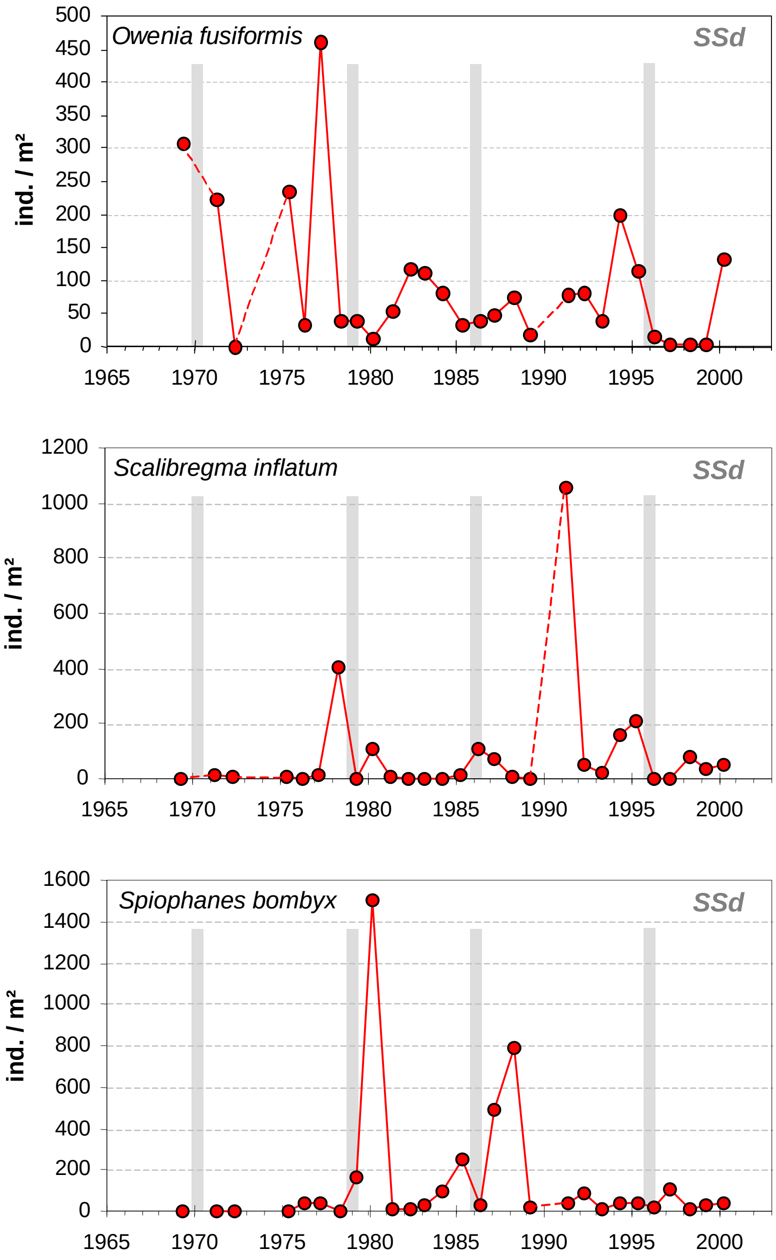


Fig. A.7.1.1: Development of the density of selected species at SSd; broken lines: missing years; vertical bars: cold winters.

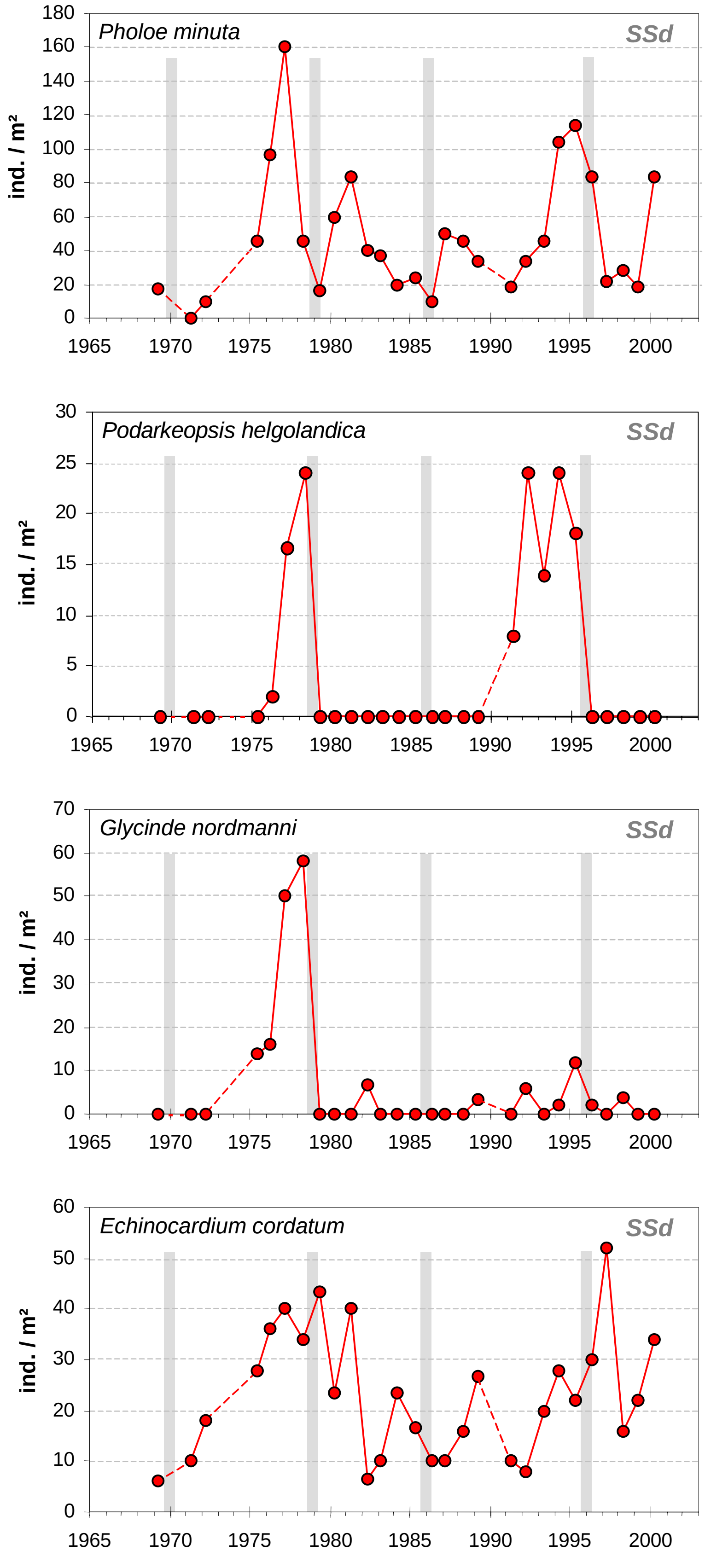


Fig. A.7.1.2: Development of the density of selected species at SSd; broken lines: missing years; vertical bars: cold winters.

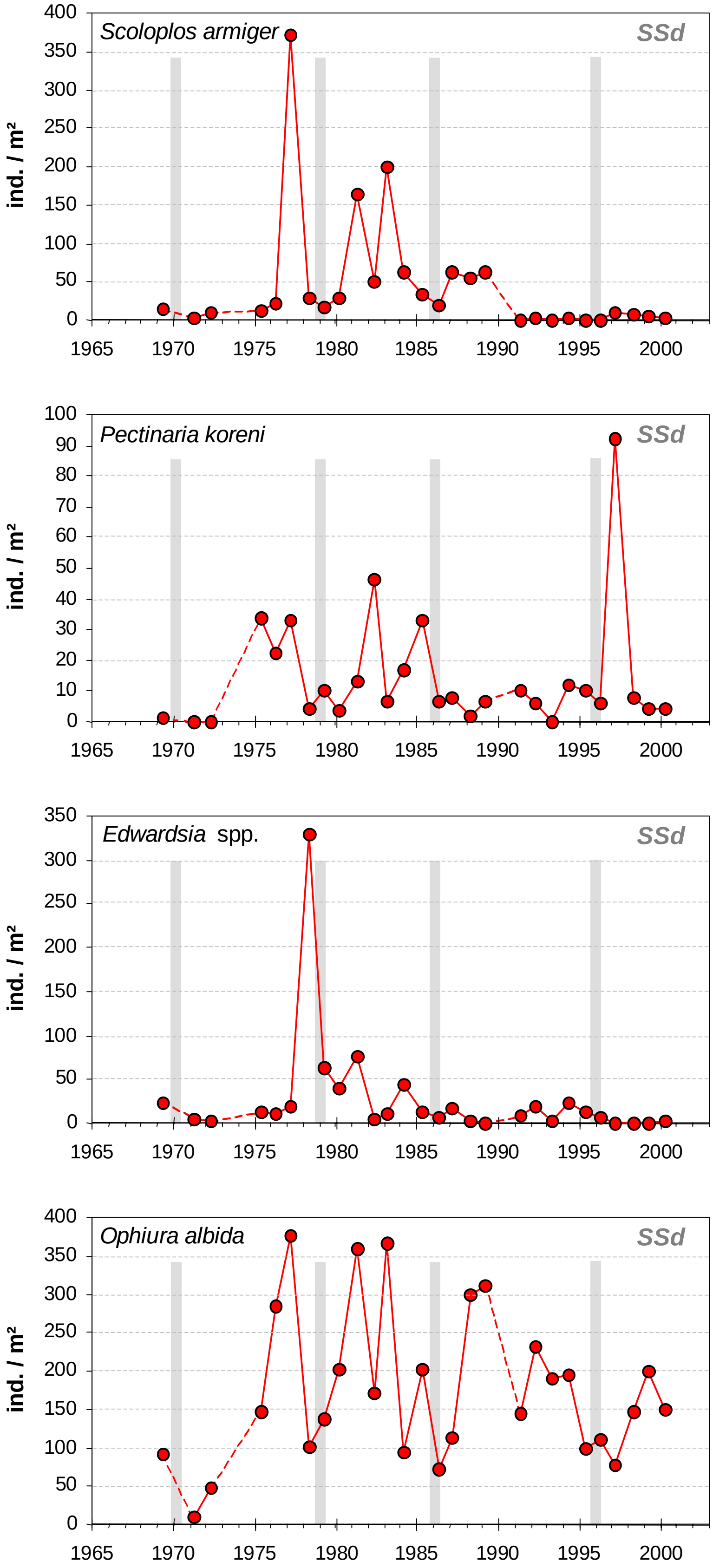


Fig. A.7.1.3: Development of the density of selected species at SSd; broken lines: missing years; vertical bars: cold winters.

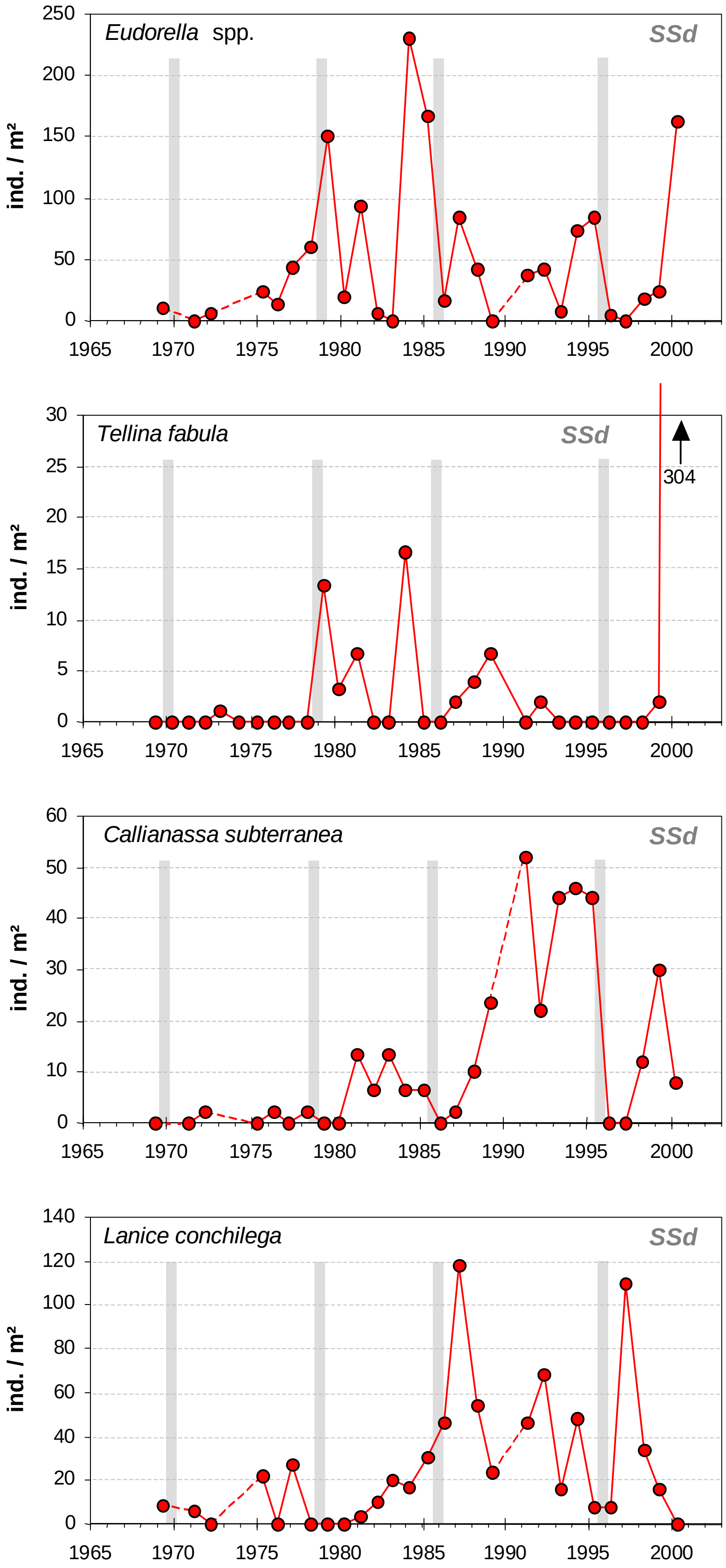


Fig. A.7.1.4: Development of the density of selected species at SSd; broken lines: missing years; vertical bars: cold winters.

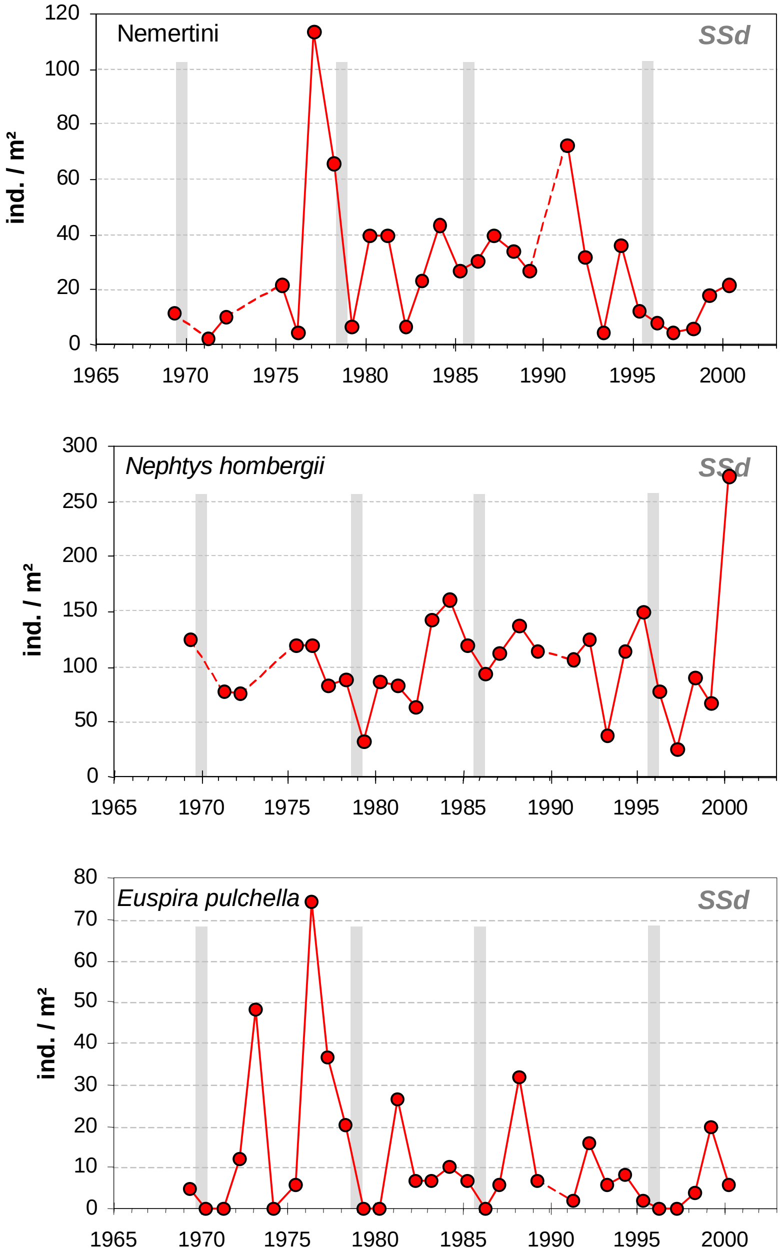


Fig. A.7.1.5: Development of the density of selected species at SSd; broken lines: missing years; vertical bars: cold winters.

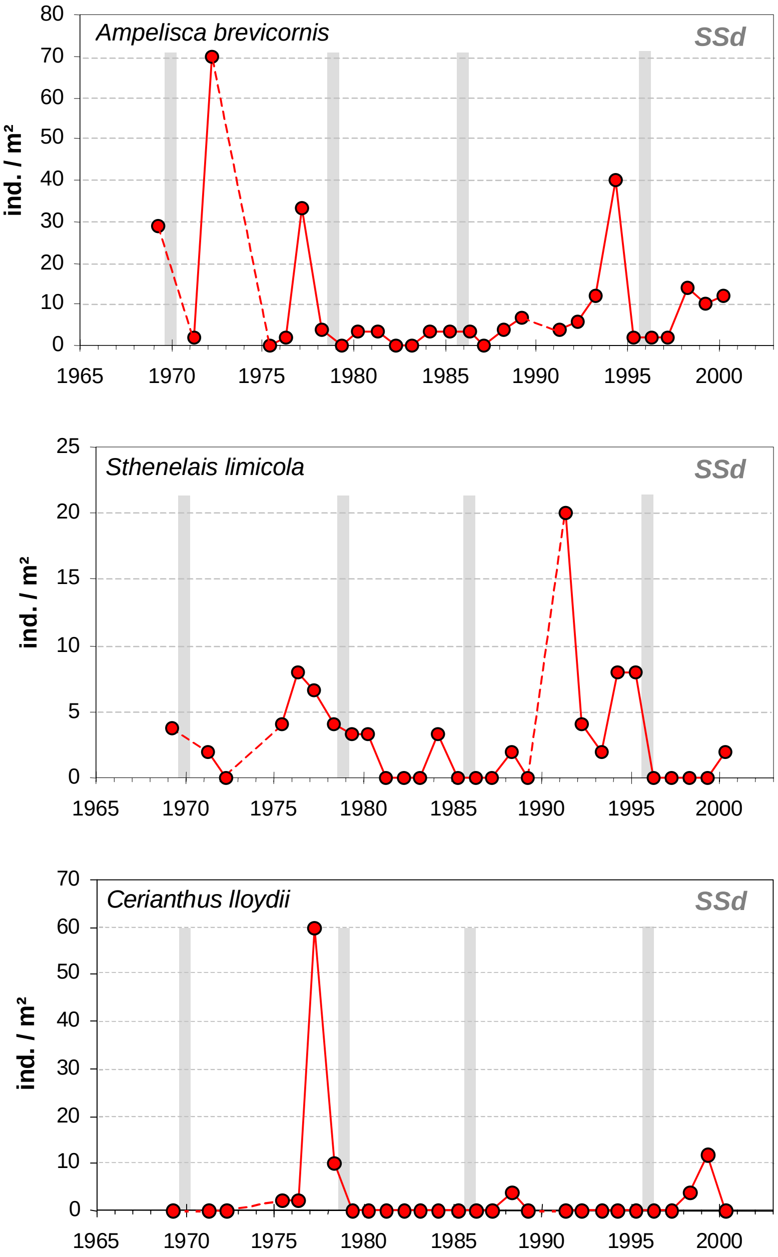
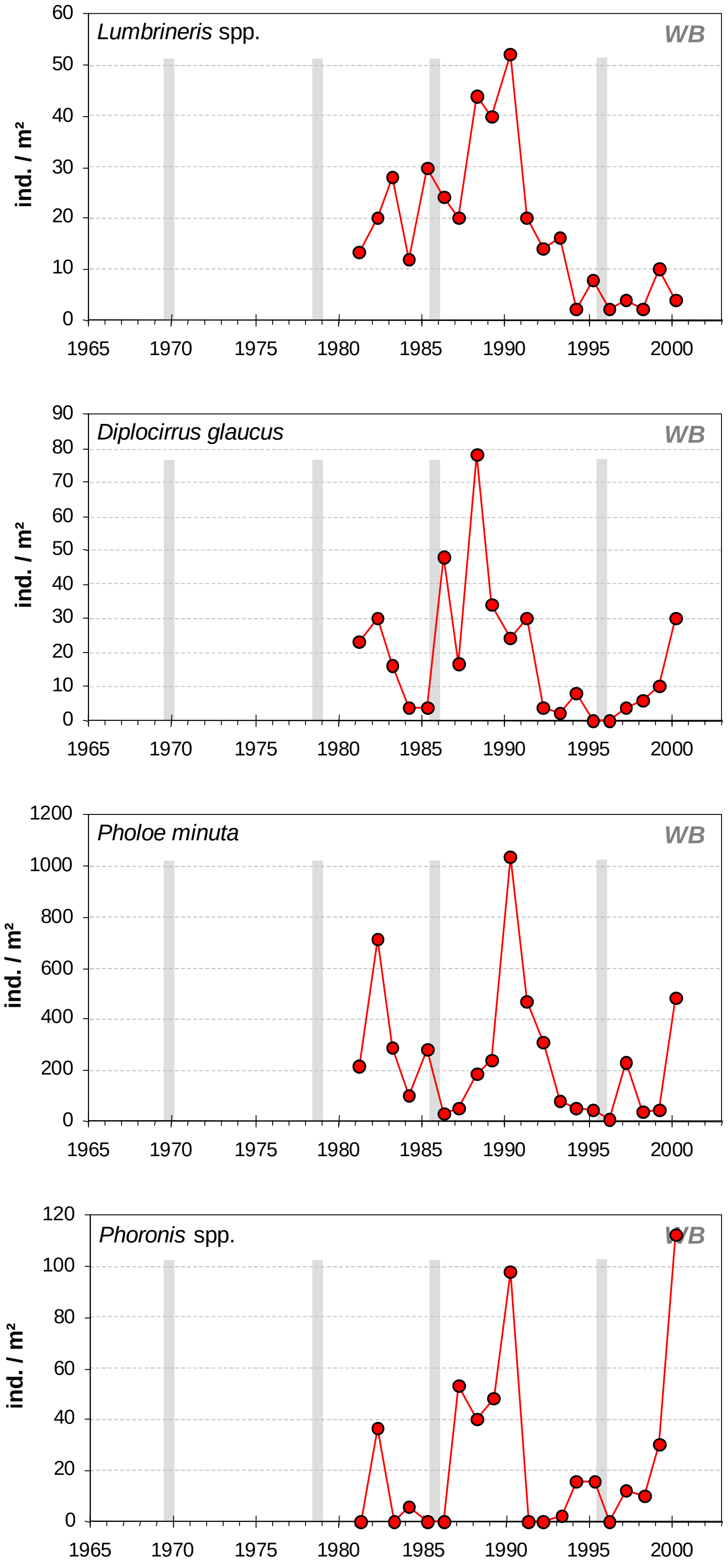


Fig. A.7.1.6: Development of the density of selected species at SSd; broken lines: missing years; vertical bars: cold winters.


Lumbrineris spp.

Diplocirrus glaucus

Pholoe minuta

Phoronis spp.

Fig. A.7.2.1: Development of the density of selected species at WB; vertical bars: cold winters.

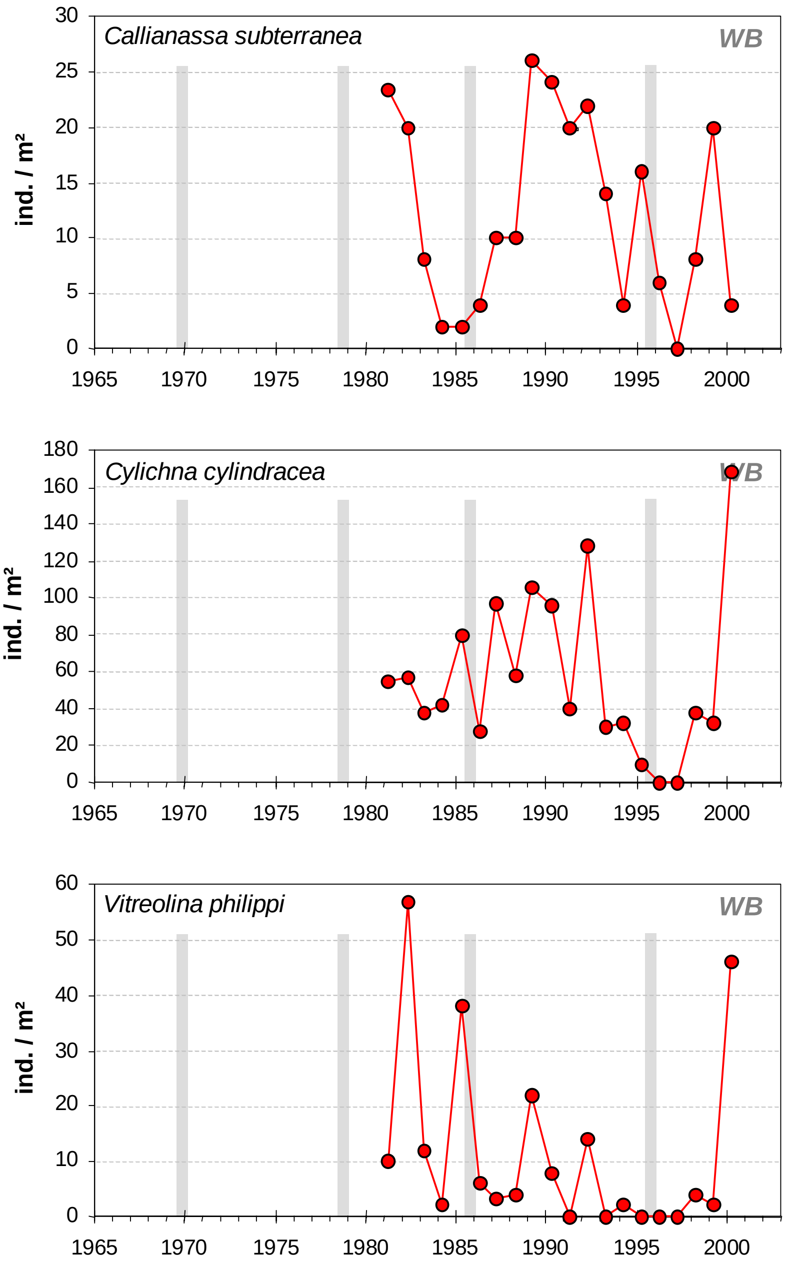


Fig. A.7.2.2: Development of the density of selected species at WB; vertical bars: cold winters.

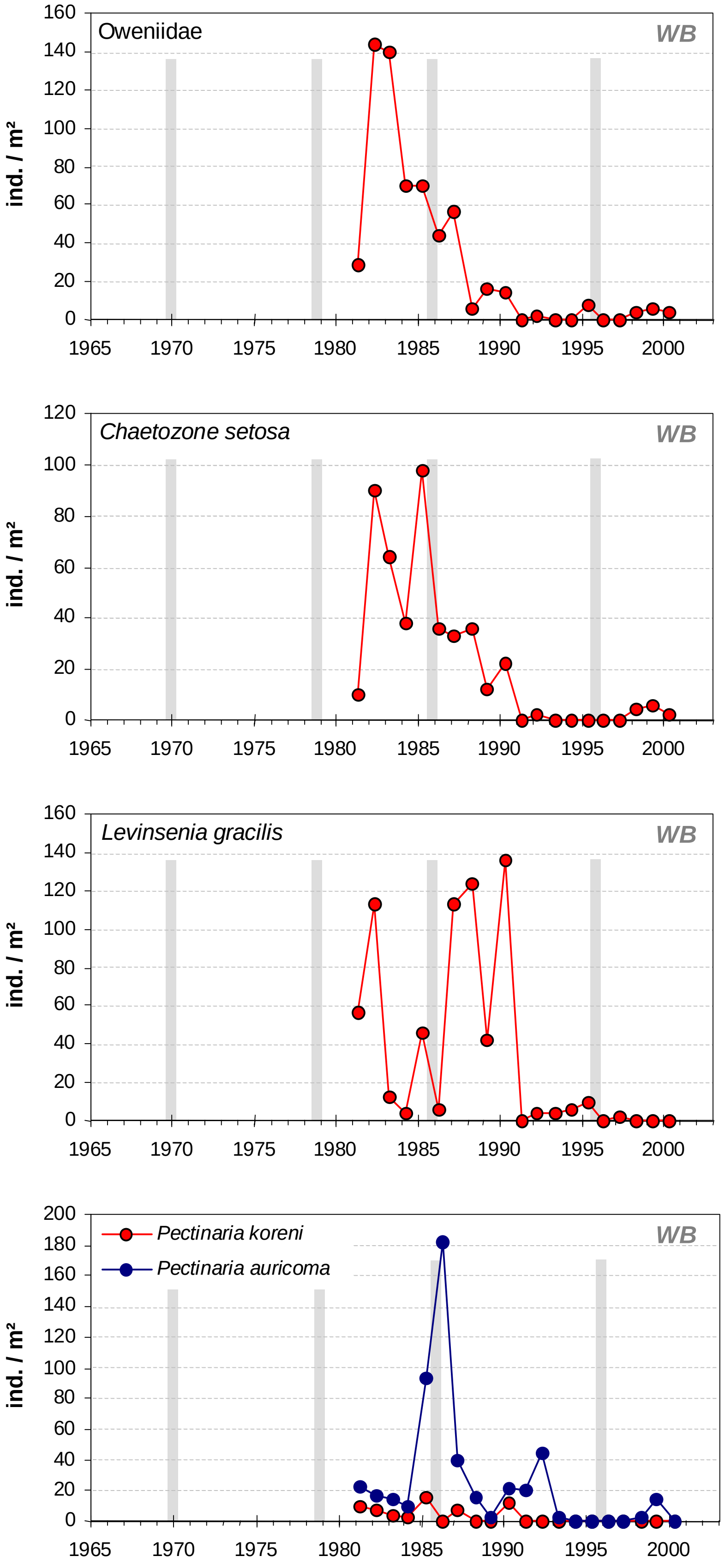


Fig. A.7.2.3: Development of the density of selected species at WB; vertical bars: cold winters.

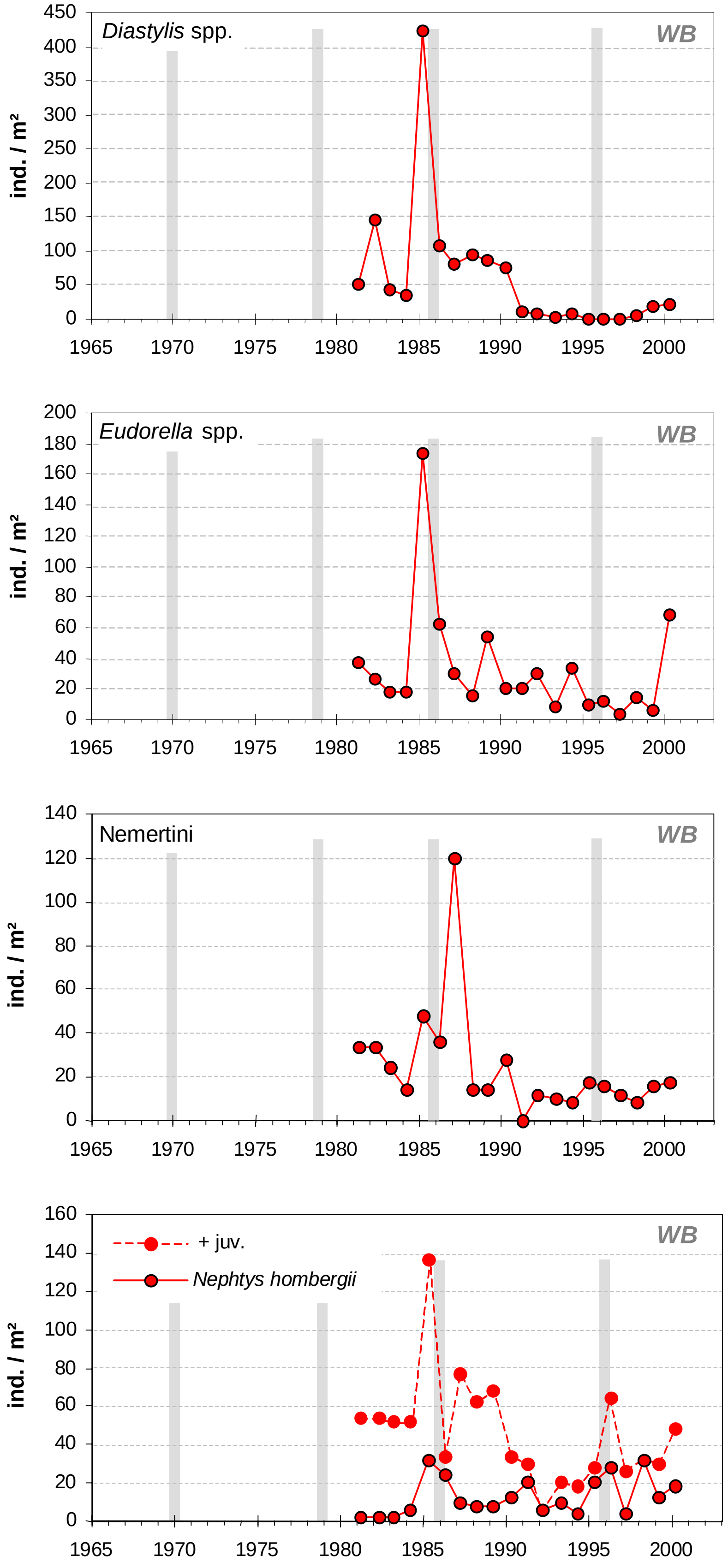


Fig. A.7.2.4: Development of the density of selected species at WB; vertical bars: cold winters.

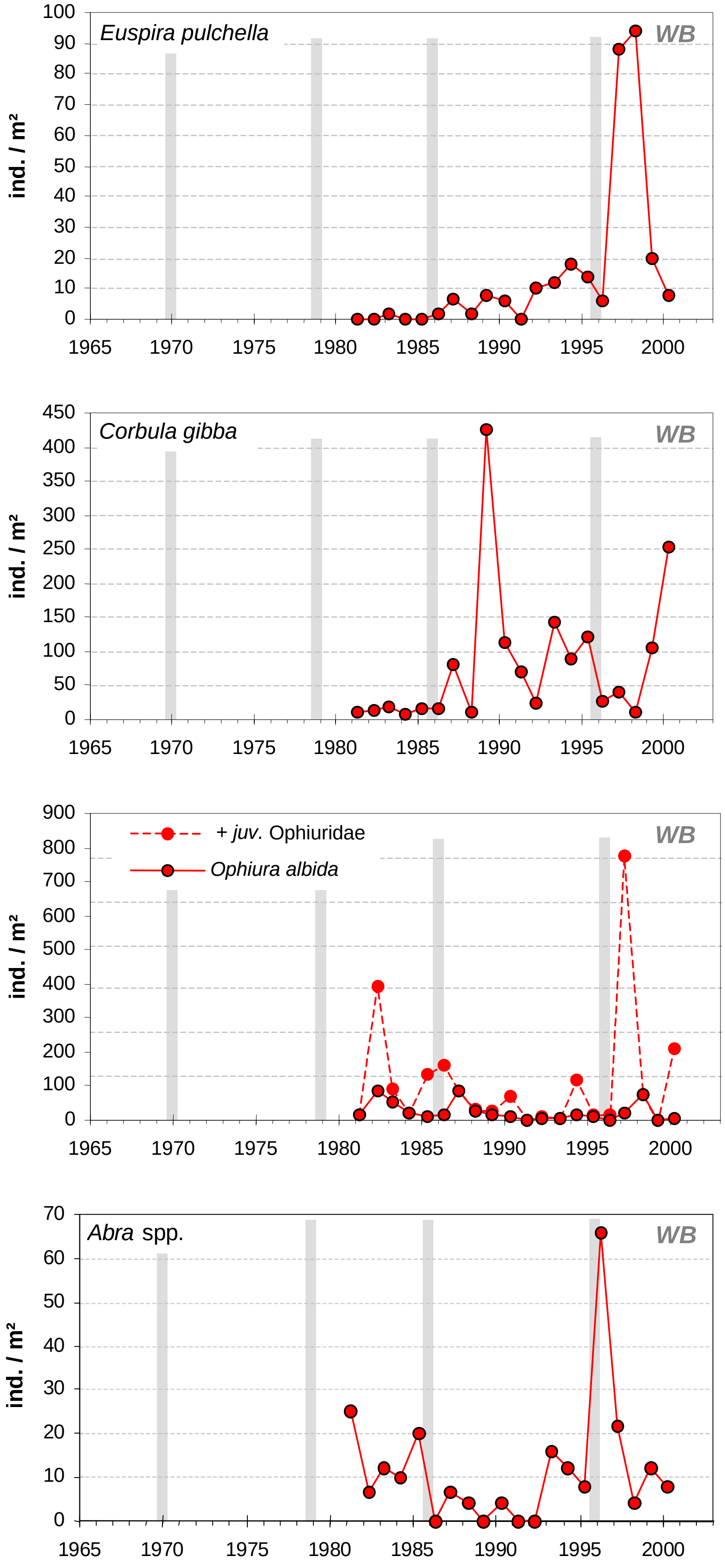


Fig. A.7.2.5: Development of the density of selected species at WB; vertical bars: cold winters.

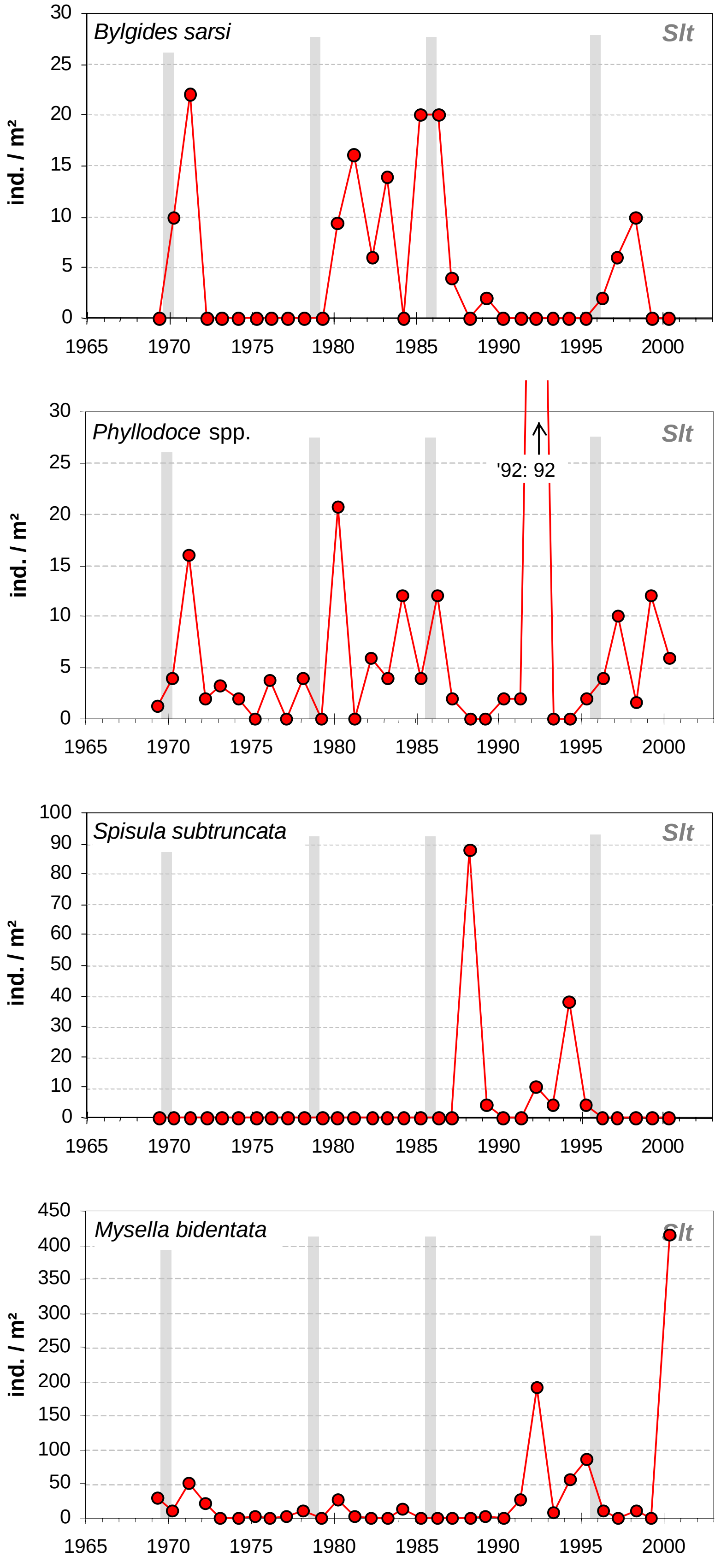


Fig. A.7.3.1: Development of the density of selected species at Slt; vertical bars: cold winters.

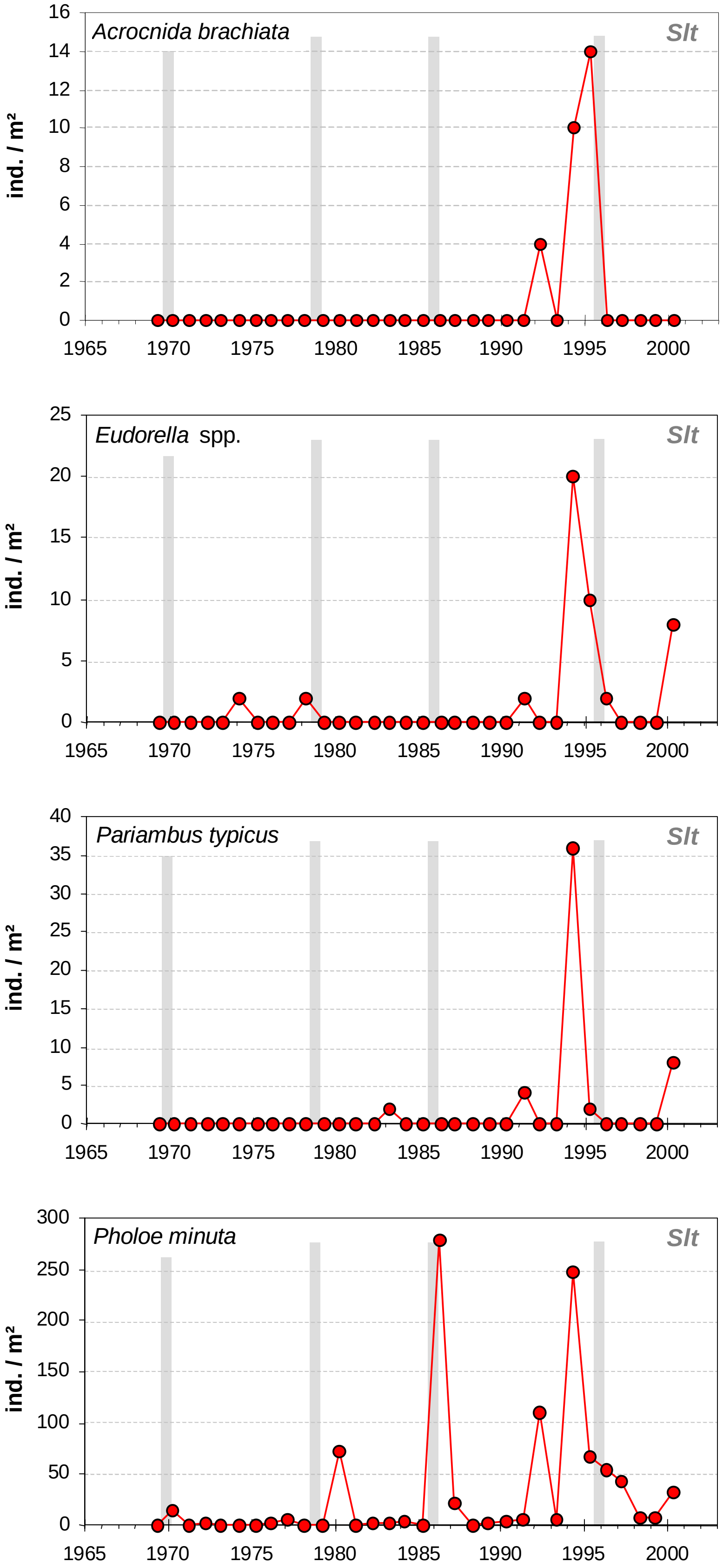


Fig. A.7.3.2: Development of the density of selected species at Slt; vertical bars: cold winters.

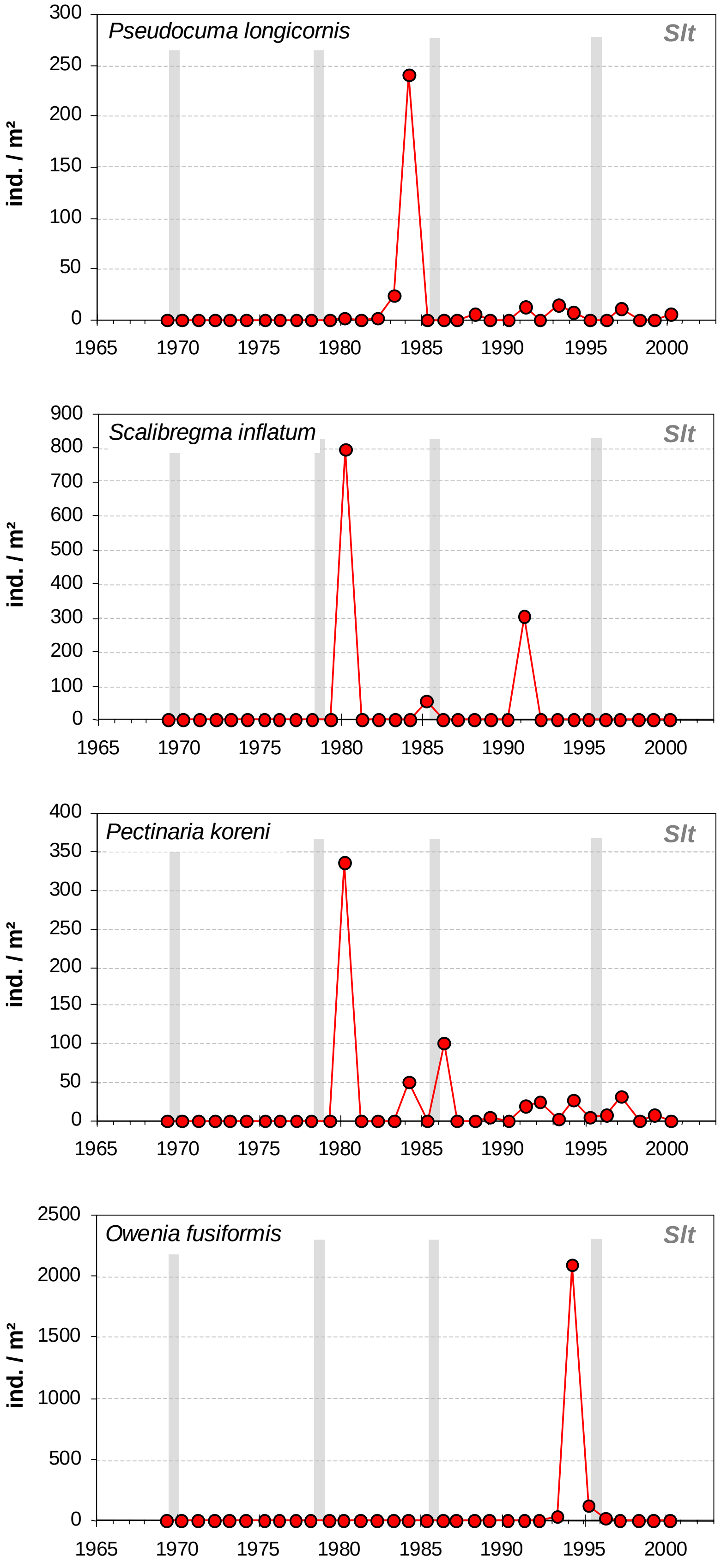


Fig. A.7.3.3: Development of the density of selected species at Slt; vertical bars: cold winters.

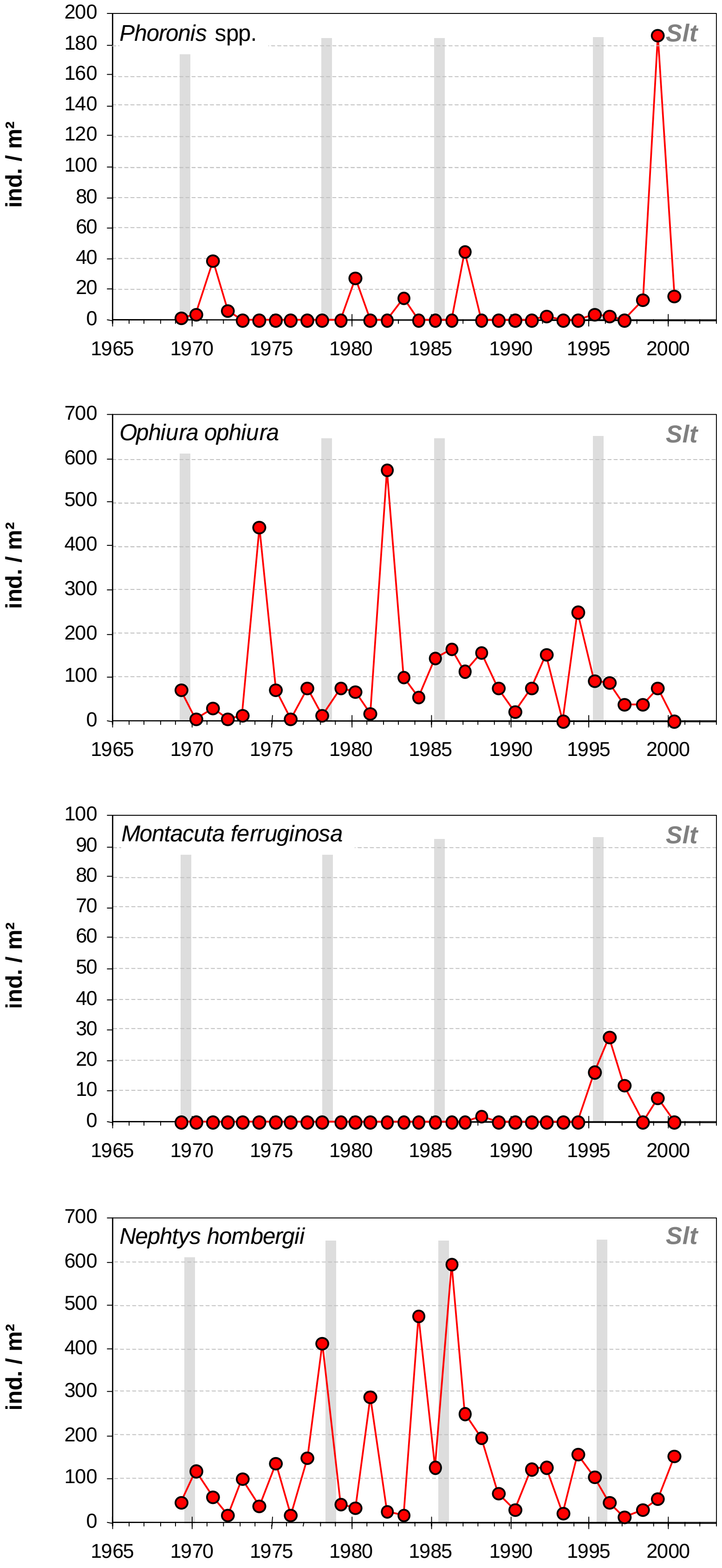


Fig. A.7.3.4: Development of the density of selected species at Slt; vertical bars: cold winters.

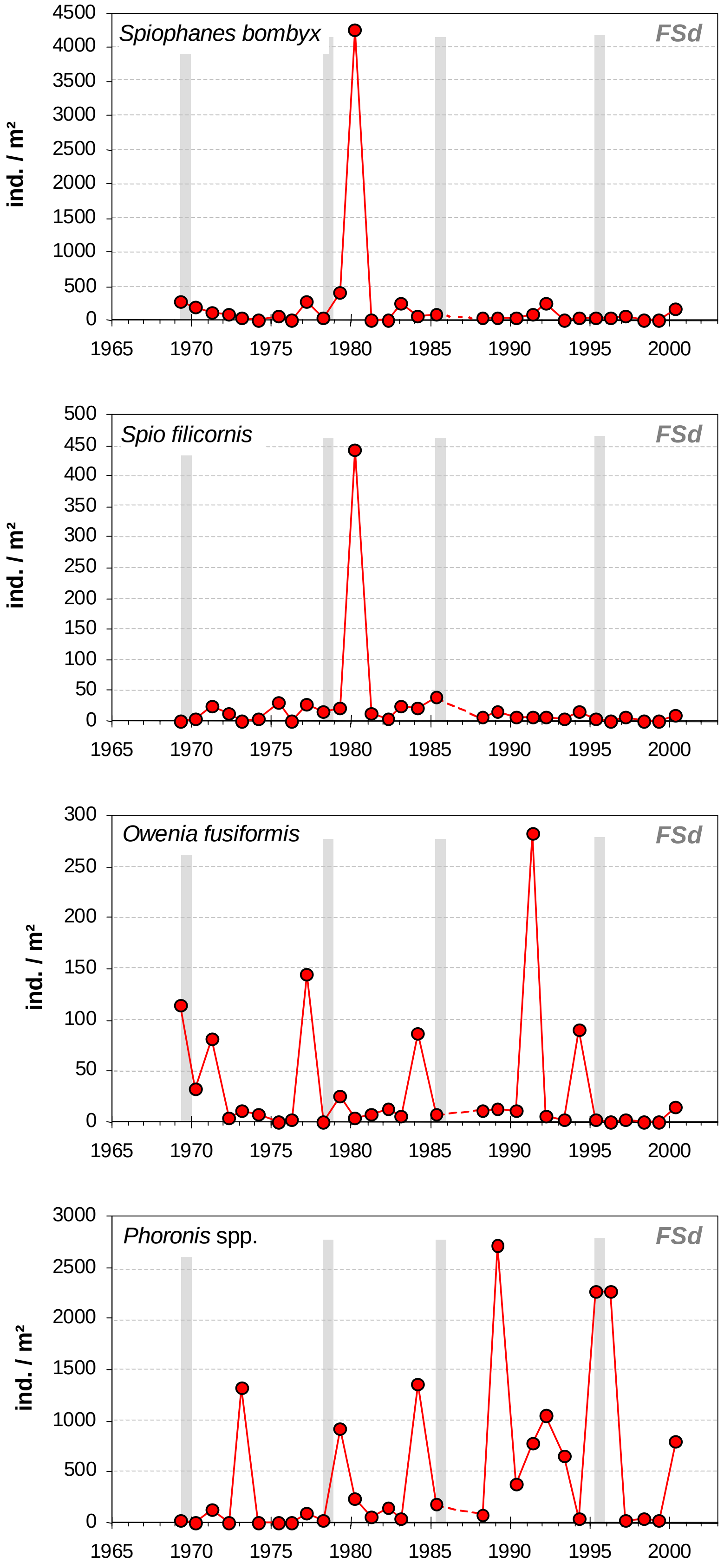


Fig. A.7.4.1: Development of the density of selected species at FSd
broken lines: missing years; vertical bars: cold winters.

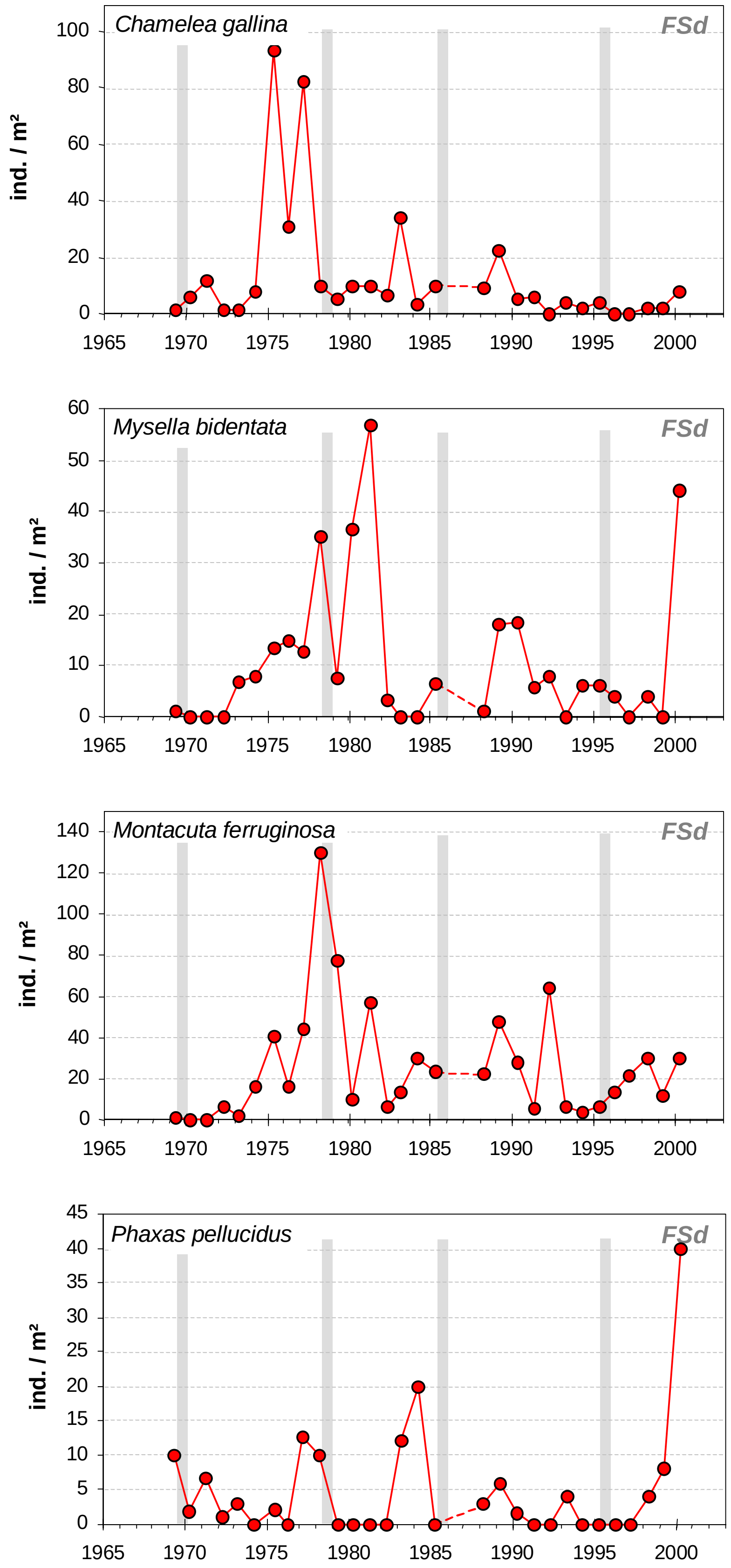


Fig. A.7.4.2: Development of the density of selected species at FSd
broken lines: missing years; vertical bars: cold winters.

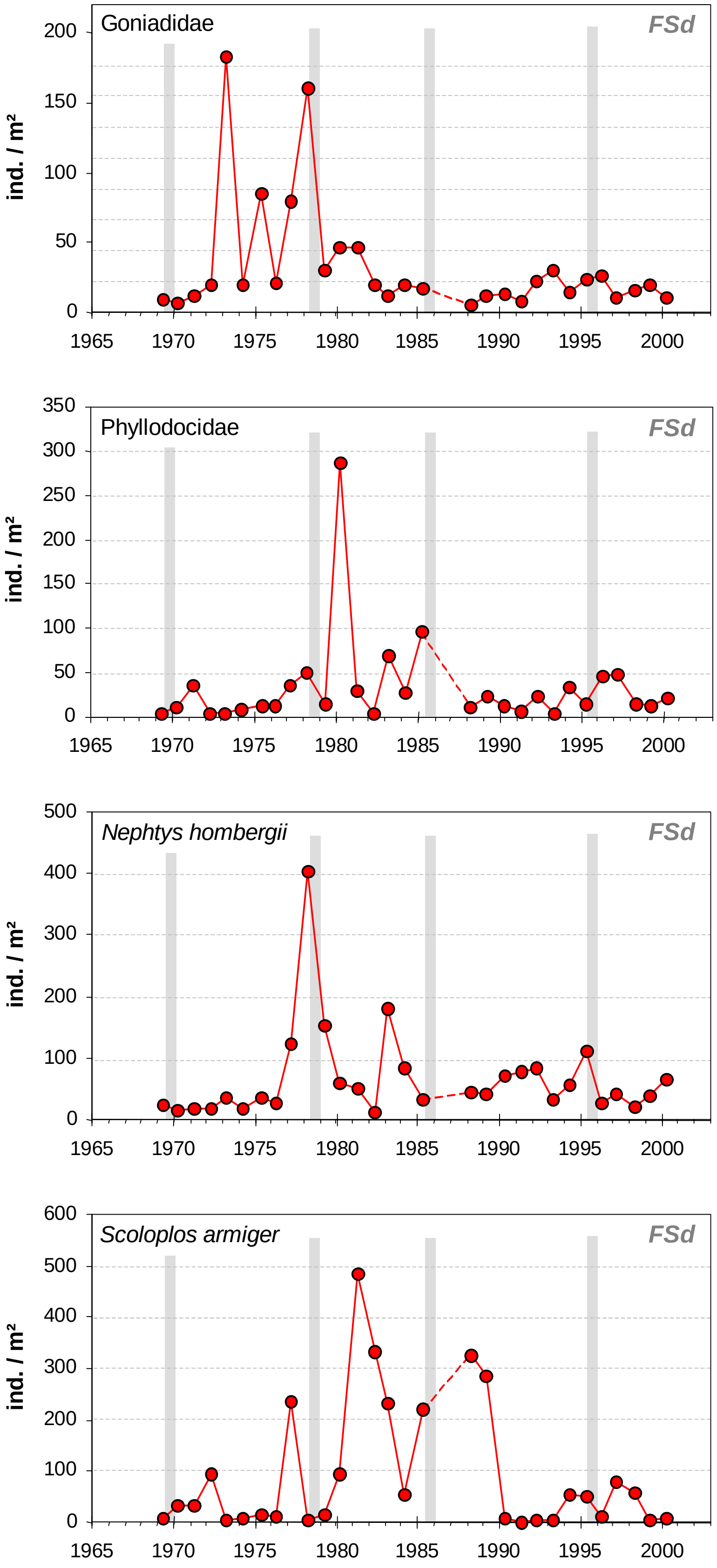


Fig. A.7.4.3: Development of the density of selected species at FSd broken lines: missing years; vertical bars: cold winters.

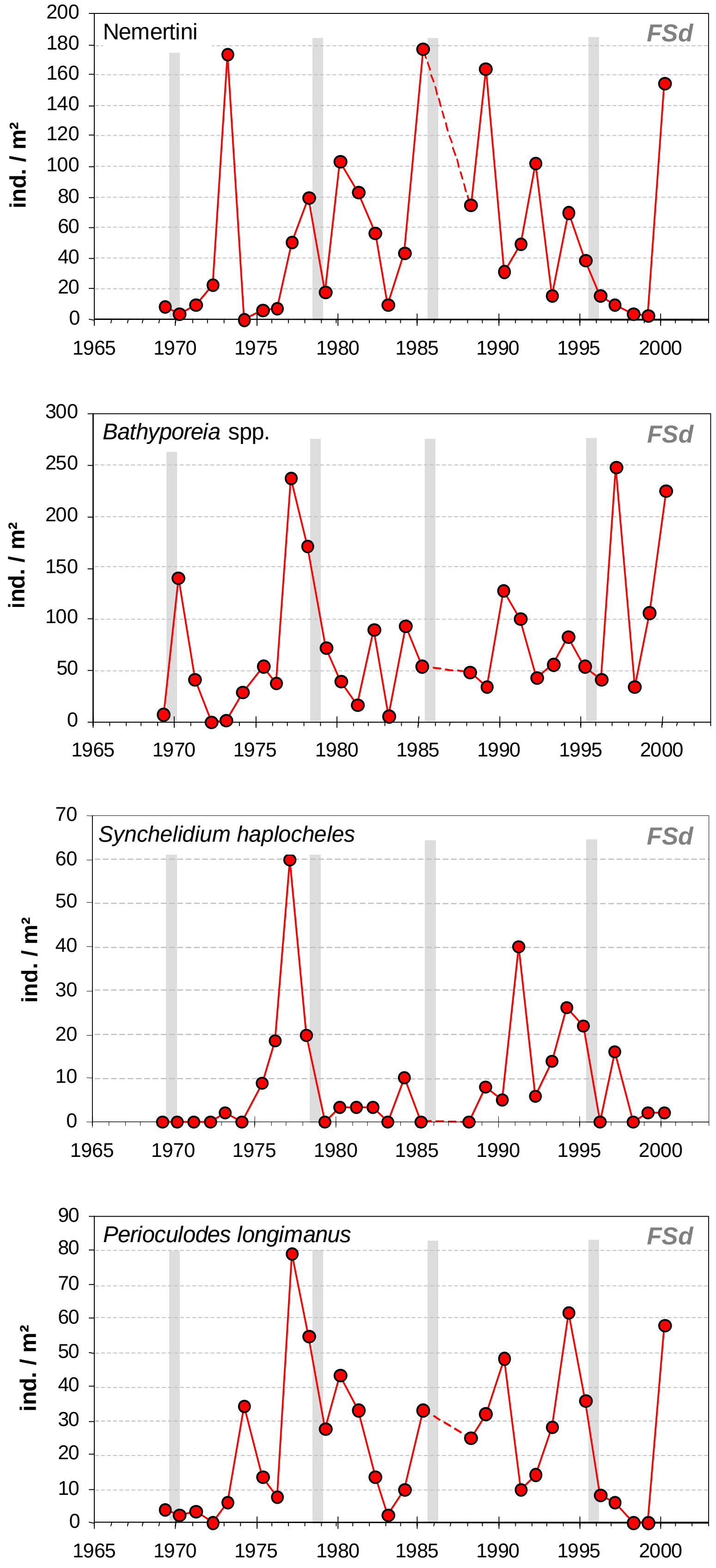


Fig. A.7.4.4: Development of the density of selected species at FSd
broken lines: missing years; vertical bars: cold winters.

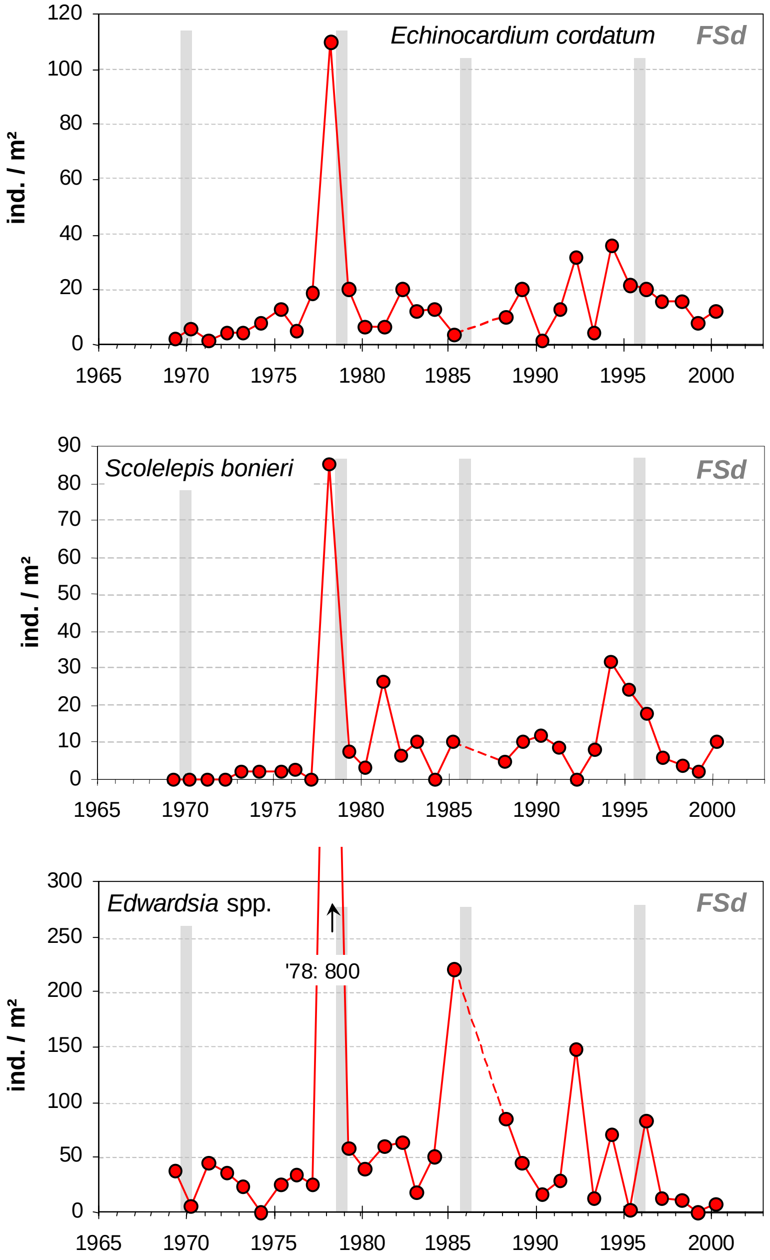


Fig. A.7.4.5: Development of the density of selected species at FSd broken lines: missing years; vertical bars: cold winters.

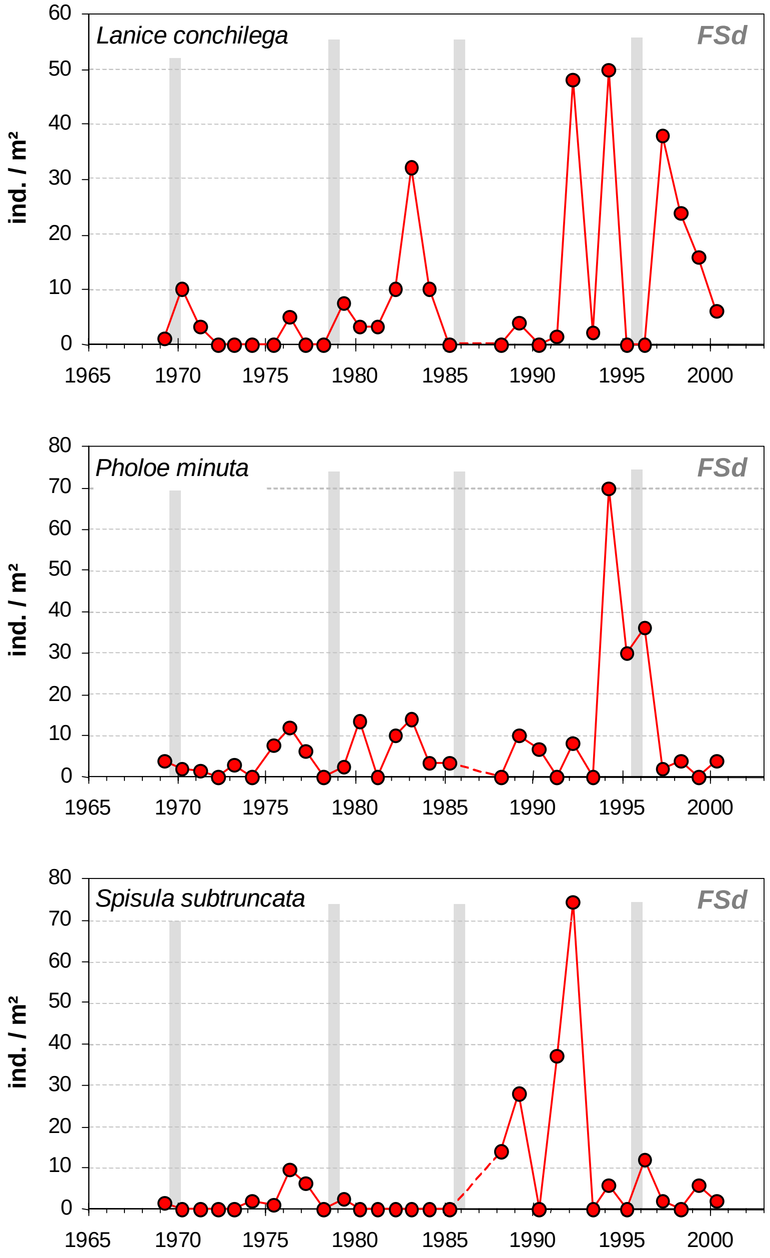


Fig. A.7.4.6: Development of the density of selected species at FSd
broken lines: missing years; vertical bars: cold winters.

A.8 Glossary

FSd:	"Fine Sand" station
SSd:	"Silty Sand" station
Slt:	"Silt" station
WB:	"White Bank" station

station:	permanent sampling station of long-term study
position:	sampling location within station
sample:	composed of several replicates (sampling units)
sampling unit:	grab

vV:	van Veen grab (0.1 m^2 if not stated otherwise)
RBC:	Reineck box corer (0.017 m^2)

S:	number of species
N:	total number of organisms
n_i:	number of organisms in species *i*

SD:	standard deviation
SE:	standard error (of the mean)
CV:	coefficient of variation
C.I.:	confidence interval
s^2:	variance
ø:	mean
s^2/ø:	variance to mean ratio

I_d:	Morisita's index of dispersion
I_p:	standardisation of Morisita's index of dispersion
H’:	Shannon-Wiener index of diversity
J’:	Pielou's index of evenness
BC:	Bray-Curtis index of similarity
MDS:	nonmetric multidimensional scaling

NAO:	North Atlantic oscillation
NAOI:	North Atlantic oscillation index
W-NAOI:	winter- (December – March) NAOI
A-NAOI:	annual NAOI
Bft.:	Beaufort wind-speed
PO_4:	phosphate
DIN:	dissolved inorganic nitrogen
SiO_4:	silicate
PSU:	SI-unit for salinity: "Practical Salinity Units" ≈ ‰

Acknowledgements

Last but not least, I would like to thank all those without whom this work would not have been possible:

Prof. Dr. Wolf Arntz for supervising this work and constructive comments and discussion of an earlier version of the manuscript;

Dr. Rainer Knust for his support with whatever problems arose during the preparation of this work over the years and for his comments on the manuscript;

Dr. Eicke Rachor for supplying the largest part of the benthic community data and samples and for helpful comments on the manuscript;

The crew of FS "Victor Hensen" and FS "Heincke" and all those people that helped during the sampling at sea, sorting of the samples or entering the data into the database;

Various people that made accessory data available for the interpretation of the faunal data: Dr. Karen Wiltshire and Peter Mangelsdorf (AWI/BAH) supplied the "Helgoland Reede" data on water temperature, salinity and nutrients; the Deutscher Wetterdienst (DWD) provided weather data from over 30 years; Dr. Eggert (BfG) supplied water discharge data of the river Elbe; Dr. James Hurrel (Climate Analysis Section, NCAR, Boulder, USA) provided the "North Atlantic Oscillation Index" (NAOI) data;

Inken for a choice of sea bottom photographs, Jan for honest comments on an earlier draft and all the other colleagues at the institute, especially the members of the FiBÖ working group, for help, discussions, conversations etc.;

… and (l.b.n.l. again) Pitty for good times, never-ending support, fruitful discussions and helpful hands and words whenever I needed some.

This work was supported by the bilateral cooperation program between The Netherlands and the city of Bremen NEBROC (NEtherlands BRemen OCeanography) as part of sub-project 2.3: "Decadal and centennial variations and long term changes of the North Sea and Wadden Sea ecosystems".